



# Breeding system evolution influenced the geographic expansion and diversification of the core Corvoidea (Aves: Passeriformes)

Petter Z. Marki,<sup>1,2,3,\*</sup> Pierre-Henri Fabre,<sup>1,4</sup> Knud A. Jønsson,<sup>1,5,6</sup> Carsten Rahbek,<sup>1,5</sup> Jon Fjeldså,<sup>1</sup> and Jonathan D. Kennedy<sup>1,\*</sup>

<sup>1</sup>Center for Macroecology, Evolution and Climate, Natural History Museum of Denmark, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen, Denmark

<sup>2</sup>Department of Environmental and Health Studies, Telemark University College, Hallvard Eikas Plass, N-3800 Bø, Norway

<sup>3</sup>E-mail: petterzmarki@snm.ku.dk

<sup>4</sup>Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, Massachusetts 02138

<sup>5</sup>Department of Life Sciences, Imperial College London, Silwood Park Campus, Ascot, West Berkshire, SL5 7PY, United Kingdom

<sup>6</sup>Department of Life Sciences, Natural History Museum, Cromwell Road, London SW7 5BD, United Kingdom

Received July 9, 2014

Accepted May 20, 2015

Birds vary greatly in their life-history strategies, including their breeding systems, which range from brood parasitism to a system with multiple nonbreeding helpers at the nest. By far the most common arrangement, however, is where both parents participate in raising the young. The traits associated with parental care have been suggested to affect dispersal propensity and lineage diversification, but to date tests of this potential relationship at broad temporal and spatial scales have been limited. Here, using data from a globally distributed group of corvoid birds in concordance with state-dependent speciation and extinction models, we suggest that pair breeding is associated with elevated speciation rates. Estimates of transition between breeding systems imply that cooperative lineages frequently evolve biparental care, whereas pair breeders rarely become cooperative. We further highlight that these groups have differences in their spatial distributions, with pair breeders overrepresented on islands, and cooperative breeders mainly found on continents. Finally, we find that speciation rates appear to be significantly higher on islands compared to continents. These results imply that the transition from cooperative breeding to pair breeding was likely a significant contributing factor facilitating dispersal across tropical archipelagos, and subsequent world-wide phylogenetic expansion among the core Corvoidea.

**KEY WORDS:** Cooperative breeding, dispersal, islands, passerine birds, speciation.

Across the animal world, parental investment strategies range from a complete lack of care, in the case of brood parasites, to cooperative breeding, where more than two individuals assist in the raising of young. Although the evolution of this diversity has been difficult to explain (Lack 1968; Tinkle et al. 1970; Weir and Rowlands 1973; Clutton-Brock and Harvey 1978; Greenwood

1980; Newton 1989; Koenig and Dickinson 2004), it is suggested that different levels of parental investment affect other organismal traits, including sexual dimorphism (Zahavi 1975), natal philopatry (Weatherhead and Forbes 1994), and long-distance dispersal (Cockburn, 2003; Hatchwell 2009). The traits associated with different systems of parental care have also been suggested to influence lineage diversification (Cockburn, 2003), but to date tests of this potential relationship at broad temporal and spatial scales

\*These authors contributed equally to this study.

have been limited. Birds, particularly the global radiation of the order Passeriformes (about 6000 species), are especially suited for such studies as they exhibit a wide range of types of parental care, with the different breeding systems well documented for a large proportion of species (Brown 1987; Cockburn 2003, 2006). The relative frequency of different modes of parental care varies greatly, however, with biparental care being by far the most common system (Cockburn 2006), suggesting the potential for a correlation between the life-history traits associated with breeding systems and diversification.

Previous comparative studies have suggested that the prevalence of species exhibiting alternative breeding strategies may be related to environmental variables, such as precipitation and temperature (Arnold and Owens 1999; Rubenstein and Lovette 2007; Covas et al. 2008; Jetz and Rubenstein 2011). However, while ecological factors may influence the present-day distribution of groups, they cannot provide the sole explanation for regional differences in diversity, which must also reflect biogeographic and evolutionary history (Ricklefs 1987; Edwards and Naeem 1993; Ligon and Burt 2004; Cockburn 2006; Cockburn and Russell 2011; Jetz and Rubenstein 2011), specifically the differences among clades in terms of their overall age, rates of net diversification and/or dispersal (Mittelbach et al. 2007; Rabosky 2009). Using passerine sister-clade comparisons, Cockburn (2003) suggested that cooperatively breeding clades had lower rates of speciation compared to those of pair breeders, attributing this to higher rates of long-distance dispersal among the pair breeders (but see Ricklefs 2005). Furthermore, a comparison of four passerine families demonstrated declining rates of net diversification among uniparental breeders, but a constant rate among pair breeders, differences which were also attributed to dispersal mediated via the breeding system (Fritz et al. 2012). Available evidence thus suggests that certain modes of parental care, including cooperative breeding, may have inhibitory effects on speciation, because high levels of natal philopatry make these lineages comparatively poor dispersers and colonizers (Cockburn 2003). Consequently, if dispersal is limited in some breeding systems this should reduce rates of range expansion and allopatric speciation that involve founder events (Cockburn 2003; Heinsohn and Double 2004; Phillimore et al. 2006; Phillimore and Price 2008), particularly in highly fragmented landscapes, such as island archipelagos (Mayr and Diamond 2001; but see Weeks and Claramunt 2014). If this mechanism is general, it may lead to differences in the amount of accumulated species diversity, and in the geographic distributions of groups with alternate breeding systems. Here, we test these predictions among the passerine infraorder core Corvoidea (Barker et al. 2004), a group that displays great variation in both mating strategies and species distributions.

A clade of passerine birds informally referred to in the recent literature as the “core Corvoidea” (since Barker et al. 2004) repre-

sents a speciose radiation (about 760 species), which are suggested to have originated in the proto-Papuan archipelago (Jönsson et al. 2011; Aggerbeck et al. 2014). Many old lineages still persist only in the modern Australo-Papuan region (Jönsson et al. 2011), while others have dispersed and subsequently diversified on all of the world’s major zoographic realms barring Antarctica (Barker et al. 2004; Jönsson et al. 2011; Aggerbeck et al. 2014). The past decade has seen a renewed interest in the phylogenetics and systematics of this radiation, which has led to an increased understanding of the relationships among families and genera, the placement of odd taxa, and biogeographical patterns of dispersal (Jönsson et al. 2011; Aggerbeck et al. 2014). The combined efforts of these studies, in concordance with further data collection have enabled the construction of a well-resolved phylogeny spanning the entire radiation, thus allowing the application of broad scale comparative methods. Given the heterogeneous distribution of breeding systems (with both cooperative and pair breeding found in several distantly related clades), and their origin within a dynamic island archipelago, the core Corvoidea therefore represent a suitable model group in which to study the effects of different breeding systems on rates of diversification and colonization.

In this study, we investigate this relationship using multi-state speciation and extinction models (FitzJohn 2012) that allow simultaneous estimation of speciation, extinction, and transition rates among states (Maddison et al. 2007; FitzJohn 2012). By reconstructing ancestral states in concordance with these models, we infer that the accumulation of diversity among cooperative breeders has slowed through time, whereas that of pair breeders continues to arise at a constant rate. In addition, we assess the correlation between breeding systems and island dwelling/migratory behavior, before highlighting spatial differences in their island and continental distributions (particularly in the Australo-Papuan region). Finally, we use a geographic state speciation and extinction model (GeoSSE; Goldberg et al. 2011) to demonstrate the alternate diversification dynamics between islands and continents. Collectively, these results provide empirical support for the hypothesis that cooperative and pair breeders have undergone differential rates of net diversification, which we suggest reflects the increased dispersal propensity of pair breeders.

## Methods

### PHYLOGENETIC DATA

We generated a time-calibrated species-level phylogeny for 604 species of the core Corvoidea, with taxonomy broadly following the International Ornithological Congress (IOC) classifications version 2.7 (Gill and Donsker 2010). This phylogeny was constructed using a total of four mitochondrial and seven nuclear loci (for a total of 12,221 sites), and was calibrated using a number of fossil and biogeographic age estimates sampled across a

broad taxonomic and temporal range. Previous phylogenetic studies of this group generally cover all deeper lineages. Thus, the 159 species (about 20% of the overall radiation) for which molecular phylogenetic data were still unpublished at the time of the phylogeny generation are assumed based on current taxonomic knowledge, to be nested within terminal groups of closely related species. Half of the missing species are in the families Laniidae and Vireonidae, which are broadly accepted as being monophyletic units. To perform a complete species-level analysis, these taxa were added randomly as polytomies, with their phylogenetic placement inferred using taxonomic information from the Handbook of the Birds of the World (del Hoyo et al. 2005–2010). To overcome the potential bias of analyzing diversification rates on trees with polytomies (FitzJohn 2010), we applied the methods of Kuhn et al. (2011), which uses a birth–death model to resolve these and assign branch lengths. This method places constraints on the resolved topology and node ages, leaving the branch lengths of the unresolved polytomies to be permuted. Polytoomy resolution was performed using the R package Ape, and BEAST (Paradis et al. 2004; Drummond et al. 2012; R Development Core Team 2012), utilizing a Markov Chain Monte Carlo (MCMC) approach. The MCMC chain was run for 11,100,000 iterations, sampling every 111,000th iteration. Parameter estimates were inspected in Tracer (Rambaut et al. 2013) to assess mixing, convergence, and burn-in. This process resulted in a pseudo-posterior distribution of 100 trees on which subsequent comparative analyses were performed. To assess the potential impact of the manual placement of missing taxa and the polytoomy resolution process, all analyses were repeated on a fully resolved distribution of 100 trees that contained approximately 80% of the species. Full details on the methods used to build the phylogenetic trees can be found in Appendix A.

#### CHARACTER DATA

Data on breeding systems were primarily based on the dataset compiled by Cockburn (2003, 2006), with taxonomic updates following the IOC version 2.7 (Gill and Donsker 2010). Species that evidently live in pairs during the breeding season, and where both parents participate in feeding the young were classified as pair breeding. Cooperative breeders are those species in which a reasonable proportion (>10%) of broods are fed by more than two individuals, whereas uniparental species were those where only a single parent provides care for the offspring. Although the extent to which a species breeds in pairs or cooperatively is likely to vary along a continuum from occasional to obligate, detailed data on the variability and mode of cooperation were lacking for the majority of species (Heinsohn and Double 2004; Cockburn 2006). Finer division of the character states would therefore increase the amount of missing data, and bias this toward well-studied groups, which would further decrease the number of data points for parameter estimation, and hence increase the complexity and

interpretation of the evolutionary models (Price et al. 2012). This dataset therefore represents the best broad-scale approximation of breeding systems in birds to date (Hatchwell 2009) and has been used in several previous comparative analyses (e.g., Jetz and Rubenstein 2011; Covas 2012; Feeney et al. 2013). Despite this, a large proportion of species remain to have their breeding systems thoroughly documented (about 48.8% of the overall core Corvoidea). By using information on natural history habits, and by determining close relatives from molecular phylogenies (i.e., predominantly membership of the same genus), Cockburn (2006) inferred the breeding system for a large number of species in which this was unknown (see Cockburn 2006). This approach assumes that these strategies have been conserved among close relatives (Ligon and Burt 2004; Cockburn and Russell 2011). We updated these classifications based on more recent phylogenetic information, where available. To investigate the uncertainty in this breeding system classification, we performed two sets of analyses (described below), the first using both the known and inferred states, and the second where all inferred states were classified as unknown. The final dataset included 586 biparental (53.8% inferred), 124 cooperative (27.4% inferred), and 35 uniparental (14.2% inferred) breeders. In addition, as a consequence of the lack of data, and a large phylogenetic distance from their closest relatives, 18 species were classified as unknown in their breeding system in all analyses.

All species of core Corvoidea were additionally classified as being restricted to islands, restricted to continental landmasses, or as being widespread, that is, occurring in both settings. We characterized species as being an island resident if its breeding distribution was restricted to one or several islands, whether continental or oceanic, but separated from continental landmasses by deep water channels (see Appendix B for full documentation of the island/continental classification). As such, we did not consider a minimum island size, but we chose to define islands in this way so that their colonization would likely have had to include over-water dispersal, as opposed to intermittent land bridges. The final dataset included 90 widespread, 508 continental, and 165 island species.

Finally, we distinguished species that are migratory from those that are sedentary using an extensive review of available literature (see Appendix B). Species that undertake considerable seasonal movements (generally >1000 km) were classified as migratory, whereas year-round residents and species that only undertake altitudinal or local/nomadic movements were classified as sedentary. Our final dataset included 683 sedentary and 80 migratory species.

#### BREEDING SYSTEMS AND DIVERSIFICATION

Analyses of diversification were performed using the multiple-state speciation and extinction (MuSSE) models in diversitree

(FitzJohn 2012; R Development Core Team 2012). The original formulation of these models tested the effect of binary characters on rates of diversification (Maddison et al. 2007), but were extended to include multiple states (FitzJohn 2012). The model computes a minimum of three parameters for each character: (1) the speciation rate ( $\lambda$ ), (2) the extinction rate ( $\mu$ ), and (3) its rate of transition to the other character states ( $q$ ). Using maximum likelihood, models differing in the number of estimated parameters can be compared. We performed our analyses with breeding state classified into the three states defined above (uniparental, pair, or cooperative). However, both due to the rarity of uniparental breeders, and because they form a monophyletic clade, parameters involving this state were not able to be estimated accurately (Davis et al. 2013) and are thus excluded from the results we present. We also assessed the effect of the inclusion of the uniparental species by pruning these species from the phylogeny, and repeating our analyses using the binary-state speciation and extinction (BiSSE) model (Maddison et al. 2007) both with the polytomy-resolved trees and those generated using molecular data only. The results remain qualitatively similar (Figs. S1 and S2) to those from MuSSE, which we present in the main text.

To assess whether speciation, extinction, and transition rates were independent of breeding system, we fit eight different evolutionary models to each tree. We compared the fit of a full model in which speciation, extinction, and transition rates were free to vary to those in which the complexity (in terms of the number of parameters) was progressively reduced, until all rates were set to be equal (see Table 1, for the individual model parameters). Among all models, transitions between uniparental and cooperative breeding were not allowed, as direct transitions between these modes of parental care (without transitioning through the pair breeding state) seem biologically unlikely. Model fit was compared using  $\Delta AIC$ . Models with  $\Delta AIC \leq 2$  are considered to have high support, those between  $4 \leq \Delta AIC \leq 7$  have moderate support, and those with  $\Delta AIC > 10$  have little or no support (Burnham and Anderson 2002). The relative likelihood of each model is thus represented by its Akaike weight.

We analyzed these models using both maximum-likelihood (all models) and a Bayesian MCMC approach. In the maximum-likelihood analysis, to overcome apparent issues with the optimization of the likelihood function, mean point estimates from short chain (1000 iterations) MCMC runs were used as starting points (R. G. FitzJohn, pers. comm. 2013). In addition to this approach, the full 10-parameter model was analyzed in a Bayesian framework to account for uncertainty in parameter estimation, assessing their posterior distribution using MCMC. The MCMC algorithm was run for a total of 10,000 generations using an exponential prior. All runs were examined in Tracer (Rambaut et al. 2013) to assess chain mixing and convergence, with the first 500 steps discarded as a burn-in. MCMC analyses were performed

**Table 1. Model fitting and parameter estimates of the three-state diversification models in MuSSE.**

Model specifications			Speciation rates			Extinction rates			Transition rates				
Speciation rates	Extinction rates	Transition rates	No. of parameters	$\Delta AIC$	AIC weight	Pair	Cooperative	Pair	Cooperative	Pair	Cooperative	P $\rightarrow$ C	C $\rightarrow$ P
Free	Free	Free	10	4.0 $\pm$ 13	0.118	0.128 $\pm$ 0.001	0.094 $\pm$ 0.001	0.000 $\pm$ 0.000	0.000 $\pm$ 0.000	0.004 $\pm$ 0.000	0.000 $\pm$ 0.000	0.004 $\pm$ 0.000	0.036 $\pm$ 0.001
All constrained	Free	Free	8	10.0 $\pm$ 13	0.006	0.124 $\pm$ 0.001	0.124 $\pm$ 0.001	0.000 $\pm$ 0.000	0.034 $\pm$ 0.003	0.004 $\pm$ 0.000	0.000 $\pm$ 0.000	0.004 $\pm$ 0.000	0.031 $\pm$ 0.001
Free	All constrained	Free	<b>8</b>	0	0.872	<b>0.128 <math>\pm</math> 0.001</b>	<b>0.094 <math>\pm</math> 0.001</b>	<b>0.000 <math>\pm</math> 0.000</b>	<b>0.000 <math>\pm</math> 0.000</b>	<b>0.004 <math>\pm</math> 0.000</b>	<b>0.000 <math>\pm</math> 0.000</b>	<b>0.004 <math>\pm</math> 0.000</b>	<b>0.036 <math>\pm</math> 0.001</b>
Free	Free	All constrained	7	60.7 $\pm$ 12	5.75e <sup>-14</sup>	0.127 $\pm$ 0.001	0.083 $\pm$ 0.002	0.000 $\pm$ 0.000	0.000 $\pm$ 0.000	0.006 $\pm$ 0.000	0.000 $\pm$ 0.000	0.006 $\pm$ 0.000	0.006 $\pm$ 0.000
All constrained	All constrained	Free	6	10.8 $\pm$ 13	0.004	0.118 $\pm$ 0.001	0.118 $\pm$ 0.001	0.000 $\pm$ 0.000	0.000 $\pm$ 0.000	0.003 $\pm$ 0.000	0.000 $\pm$ 0.000	0.003 $\pm$ 0.000	0.038 $\pm$ 0.000
All constrained	Free	All constrained	5	80.4 $\pm$ 13	3.03e <sup>-18</sup>	0.121 $\pm$ 0.001	0.121 $\pm$ 0.001	0.000 $\pm$ 0.000	0.012 $\pm$ 0.005	0.006 $\pm$ 0.000	0.000 $\pm$ 0.000	0.006 $\pm$ 0.000	0.006 $\pm$ 0.000
Free	All constrained	All constrained	5	68.9 $\pm$ 12	9.53e <sup>-16</sup>	0.125 $\pm$ 0.001	0.083 $\pm$ 0.002	0.000 $\pm$ 0.000	0.000 $\pm$ 0.000	0.005 $\pm$ 0.000	0.000 $\pm$ 0.000	0.005 $\pm$ 0.000	0.005 $\pm$ 0.000
All constrained	All constrained	All constrained	3	79.7 $\pm$ 12	4.30e <sup>-18</sup>	0.118 $\pm$ 0.001	0.118 $\pm$ 0.001	0.000 $\pm$ 0.000	0.000 $\pm$ 0.000	0.005 $\pm$ 0.000	0.000 $\pm$ 0.000	0.005 $\pm$ 0.000	0.005 $\pm$ 0.000

Pair represents biparental species. Cooperative represents species in which cooperative breeding is present in at least 10% of broods. Parameter estimates for uniparental taxa are not shown due to uncertainty in estimates as a consequence of a high tip ratio bias, and a single evolutionary origin. Model specifications indicate whether rates have been constrained to be equal, or whether they are free to vary depending on character state. Speciation, extinction, and transition rates are given as median and interquartile ranges estimated across the 100 polytomy resolved phylogenies. Model fit is compared using the Akaike information criterion (AIC).  $\Delta AIC$  indicates relative AIC value to that of the best-fitting model. AIC weight represents the relative likelihood of each model. The best fitting model is indicated in bold.



separately for 10 random trees, including the two most disparate trees, as calculated using the Robinson-Foulds symmetric difference metric (Robinson and Foulds 1981). We performed these analyses both on the polytomy-resolved trees (763 species) and on those generated only with molecular data (604 species), using the data including inferred states, in addition to that where the inferred states were classified as unknown (see Figs. S3, S4, and S5 for these results). In analyses performed on the molecular data only trees, missing species were accounted for by using the proportions of sampled species within each character state (97% uniparental species, 79% pair breeding species and 79% cooperative species), as suggested by FitzJohn et al. (2009).

### **ANCESTRAL STATE ESTIMATION AND DIVERSIFICATION THROUGH TIME**

Ancestral states have been shown to be unreliably estimated if the trait in question influences rates of speciation and extinction, as this will bias the proportion of extant species with the respective trait (Maddison 2006; Maddison et al. 2007; Goldberg and Igić 2008). However, utilization of the MuSSE models allows their assessment while controlling for these influences (Maddison et al. 2007). We therefore assessed the ancestral states of breeding system among the core Corvoidea using this method, and also the accumulation of lineage diversity through time, applying the approach of Weir (2006) to generate lineage through time (LTT) plots for each breeding system separately. This analysis assigns character states to each internal node based on the likelihoods from the ancestral state estimations (a node was assigned the state with the highest probability in the reconstructions; Weir 2006; Bloom et al. 2013). The LTT plots were then assessed to determine whether lineages of the respective states accumulate diversity at a constant rate, increase or decrease toward the present (Weir 2006; Rabosky and Lovette 2008; Bloom et al. 2013).

### **DIVERSIFICATION ON ISLANDS AND CONTINENTS**

To test for differences in diversification as a consequence of continental or insular occurrence, we employed the GeoSSE (Goldberg et al. 2011). Formulation of the GeoSSE model is similar to that of MuSSE, but includes the estimation of an additional parameter, which calculates speciation events between the two regions analyzed ( $S_{AB}$ ). This between-region mode of speciation represents a widespread species (present in both regions) that diverges along the boundary separating the regions (Goldberg et al. 2011), resulting in one of the daughter lineages remaining widespread (present on both islands and continents) and the other being present either on islands or continents only, or with the daughter lineages found in one or the other state, respectively (one continental and one island). As with those of breeding system, we computed these models using both maximum-likelihood and Bayesian methods (the methods for the MCMC analysis were the same as those listed in the above section). We compared the fit of a full model in

which speciation, extinction, and transition rates were free to vary to those in which the complexity and number of parameters were reduced until eventually all rates were set to be equal. In total, we compared six alternative models on the polytomy-resolved tree (see Table 3 for the estimated model parameters and constraints). As above, the Bayesian analyses were also computed on the trees generated with molecular data only, with the missing species accounted for using the proportion of sampled species within each character state (80% continental species, 72% island species, and 93% widespread species; FitzJohn et al. 2009).

### **CORRELATED EVOLUTION OF BREEDING SYSTEM WITH ISLAND DISTRIBUTION AND MIGRATORY BEHAVIOR**

Breeding system has been suggested to influence dispersal distances among birds (Zack 1990; Hatchwell 2009) and hence their potential to colonize remote locations, such as islands (Cockburn 2003), and evolve migratory habits (Brown 1987; Russell 1989; Cockburn 2003). To test for this relationship through time, we used migratory behavior as a proxy for dispersal, and modeled potential correlated evolution between this trait, in addition to island/continental presence as a dependent and independent function of breeding system, using BayesTraits version 2.0 (Pagel and Meade 2006). This program uses reverse jump MCMC to sample the two alternative evolutionary models in proportion to their posterior probabilities over a sample of phylogenetic trees. We used an exponential hyper prior for both the independent and dependent models, and the chains were run for 20,000,000 iterations, with the first 5,000,000 states discarded as a burn-in. Each run was repeated three times to ensure that harmonic means did not significantly differ between runs. To assess support for the dependent model, the harmonic means of the independent and dependent models were compared with Bayes factors. A Bayes factor  $> 5$  indicates strong support for a model of correlated evolution (Pagel and Meade 2006). To assess the robustness of our results, we also explored the effect of different treatment of uniparental breeders, coding them either as pair or cooperative breeders, or totally pruning them from the trees.

### **SPATIAL DATA AND ANALYSIS**

We obtained distributional data for the same species of cooperative and pair breeders as listed in Appendix B from a global distributional database (Rahbek and Graves 2001; Rahbek et al. 2012), where the geographic ranges of all species are recorded at a resolution of  $1^\circ \times 1^\circ$ , and are considered to represent a conservative estimate of the extent of the breeding area at this scale. These maps were rasterized at the same spatial resolution for each class of breeding system using ArcGIS 10.1, to create maps of species richness. To estimate areas containing more species of a certain class than expected given the overall species richness patterns, we assessed the residuals of linear models in which we regressed

the richness of each individual breeding state against that of the total species richness per cell. In this analysis, we excluded the uniparental breeders, which strongly influence these patterns, due to their overrepresentation in New Guinean highlands, most likely reflecting a lack of dispersal from their area of origin (Jönsson et al. 2011; Fritz et al. 2012).

## Results

### BREEDING SYSTEM DEPENDENT DIVERSIFICATION

The MuSSE analyses of breeding system dependent diversification showed significant differences in speciation and transition rates across all analyzed trees. In the maximum-likelihood analyses, the best-fitting model was one in which speciation and transition rates were free to vary between breeding systems, but extinction rates were constrained to be equal (Akaike weight = 0.872, Table 1). The second best model was one in which all rates were free to vary ( $\Delta\text{AIC} = 4$ , Akaike weight = 0.118, Table 1), and the poorest fitting model was one in which speciation and transition rate estimates were fixed to be equal across breeding systems ( $\Delta\text{AIC} = 80.4$ , Akaike weight =  $3.03 \times 10^{-18}$ , Table 1). The estimated model parameters from the MCMC analyses (and also the best fitting maximum-likelihood model, see Table 1) suggest that there are differential rates of lineage diversification among breeding systems within the core Corvoidea, with higher rates of speciation in biparental lineages relative to cooperative ones (Fig. 1). Transition rate estimates also suggest a greater number of transitions from cooperative to biparental breeding systems relative to the reverse scenario. Extinction rate estimates in the full 10 parameter model did not appear to differ significantly between breeding systems, with both rates approaching zero. Posterior distributions of parameter values from the MCMC analyses of the best-fitting model support these conclusions, as overlap in the 95% credibility intervals for cooperative versus pair breeders was absent or minimal in the 10 trees analyzed (Fig. 1). Results from analyses performed on the trees inferred from molecular data only were qualitatively the same (Table S1 and Fig. S5).

### ANCESTRAL STATE RECONSTRUCTION AND LINEAGE ACCUMULATION AMONG BREEDING SYSTEMS

Ancestral reconstructions computed using the MuSSE models suggest that cooperative breeding has the highest probability of being the breeding system of the most recent common ancestor of the core Corvoidea (in all analyzed trees, the probability of this node being cooperative was 1), with subsequent transitions to pair breeding occurring in several independent lineages (Fig. 2). Results from analyses performed on trees inferred from molecular data only were qualitatively the same (Fig. S6). LTT plots (Fig. 3) indicate high initial rates of diversification in cooperative lineages, but with a subsequent slowdown toward the present. Conversely,

the LTT plots for pair breeders indicate a more constant rate of lineage accumulation through time.

### CORRELATED EVOLUTION OF BREEDING SYSTEM WITH ISLAND DISTRIBUTION AND MIGRATORY BEHAVIOR

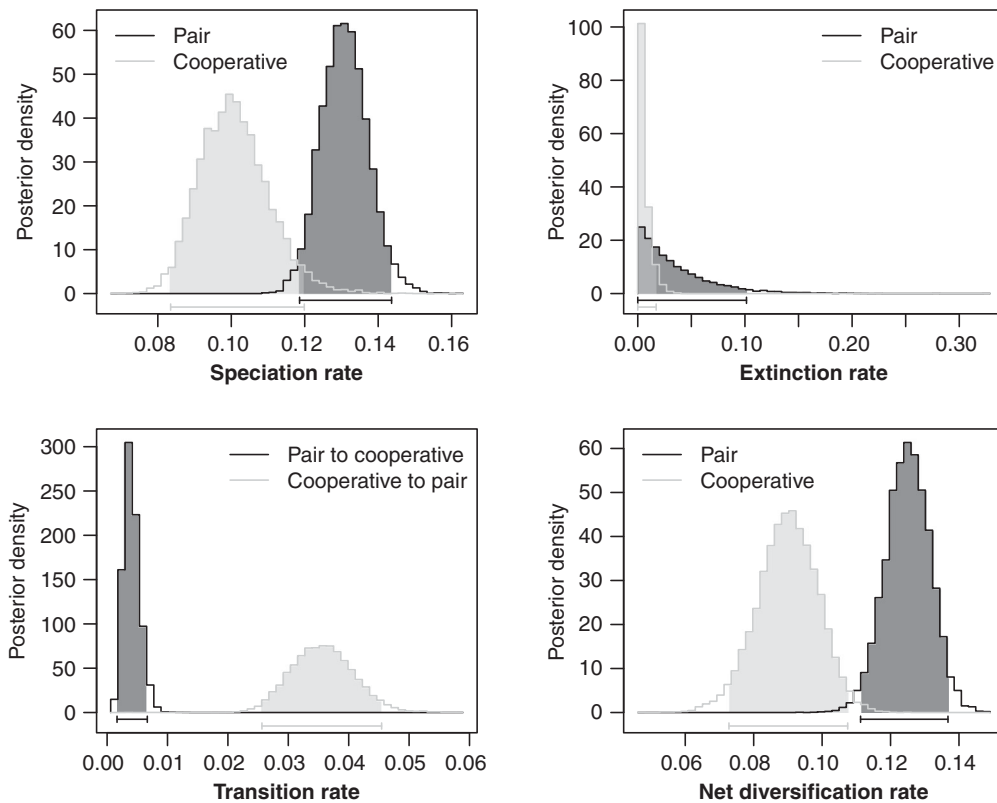
Using BayesTraits (Pagel and Meade 2006), we obtained strong support for a model of correlated evolution between pair breeding and migratory behavior (log Bayes factor > 10; Table 2). However, the correlation between breeding system and island distribution was significant only when applied to the trees based on molecular data, but not among those for the pseudodistribution of polytomy-resolved trees. Among all analyses, results were consistent regardless of whether uniparental breeders were grouped with cooperative or pair breeders, or completely pruned from the trees (Table S2).

### REGION-DEPENDENT DIVERSIFICATION

Maximum-likelihood estimation of the GeoSSE models indicated significant differences in speciation, extinction, and transition rates between regions (Table 3). The best model was the full, seven parameter model in which all rates were free to vary (Akaike weight = 0.924, Table 3), whereas the second best model was one in which the between-region speciation rates was set to zero ( $\Delta\text{AIC} = 5$ , Akaike weight = 0.076, Table 3). Speciation and extinction rate estimates from the full model were higher on islands compared to continents, whereas transition rate estimates, representing the per lineage rate of colonization, indicated that dispersal from islands to continents was more frequent than the reverse scenario (Table 3). The posterior probability distributions from the Bayesian MCMC analyses support these results (Fig. 4), with those from analyses performed on trees inferred with the molecular data only also similar (Table S3 and Fig. S7).

### THE GEOGRAPHICAL DISTRIBUTION OF BREEDING SYSTEMS

At a resolution of  $1^\circ \times 1^\circ$ , there are clear differences among the distribution of pair and cooperative breeders at the global scale (Fig. S8), with cooperative breeders reaching their highest species richness values in both eastern Australia and eastern Africa, as previously recognized by a number of studies (e.g., Grimes 1976; Rowley 1976; Cockburn 1996; Cockburn 2006; Jetz and Rubenstein 2011). Conversely, pair breeders are most diverse in the Indo-Pacific and the Sino-Himalayan montane region (Fig. S8). Upon examining the residual patterns of breeding system diversity ~ overall species richness (among cooperative and pair breeders combined), it becomes clear that the Australasian and Indo-Pacific areas reflect the main differences among the two groups, with cooperative breeders overrepresented in Australia and



**Figure 1.** Posterior probability distributions of parameter rate estimates generated from a MuSSE analysis examining the effect of breeding system (pair, cooperative, and uniparental) on lineage diversification and transitions, using an MCMC approach. Due to uncertainty in the parameter estimates for uniparental breeders, these data are not shown. Bars at the bottom of the plots highlight the 95% credibility intervals of these estimates. Results are presented for a single tree, but remain consistent across all 10 trees analyzed. Phylogenies were inferred using the polytomy resolver method, and thus are complete at the species level (see Methods for further information).

**Table 2.** Likelihood and Bayes factors of evolutionary models in which breeding systems are suggested to be dependently or independently related to island distribution or migratory behavior, as implemented in BayesTraits.

Correlation analysis	Tree distribution	<i>n</i> taxa	Independent model			Dependent model			Log BF
			Mean lnL	Max lnL	SD lnL	Mean lnL	Max lnL	SD lnL	
Island distribution	Polytomy resolved	763	-497.15	-496.48	0.58	-497.08	-496.62	0.42	-0.28
Migratory behavior	Polytomy resolved	763	-402.49	-402.02	0.41	-398.34	-398.27	0.06	7.50
Island distribution	Fully resolved	604	-393.53	-393.47	0.09	-386.63	-386.44	0.21	14.06
Migratory behavior	Fully resolved	604	-364.36	-363.68	1.13	-360.72	-360.09	0.66	7.18

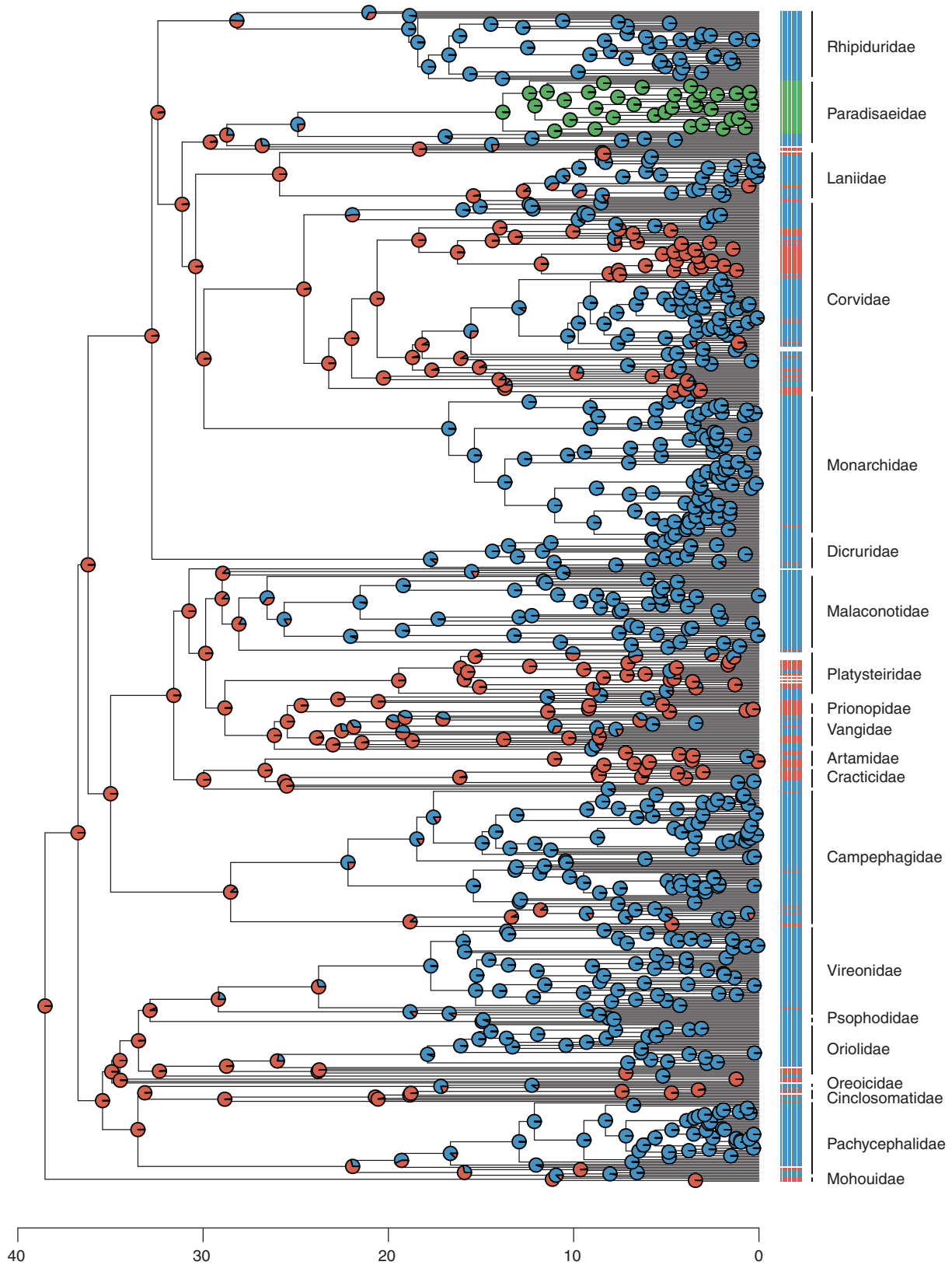
Log Bayes factors (BF) > 5 indicate strong support for a model assuming correlated evolution between traits. Log BF values are calculated using the maximum harmonic means from the best dependent and independent runs.

underrepresented in the Indo-Pacific, whereas the reverse trend is true of the pair breeders (Fig. 5 and S9).

### Discussion

The relationship between lineage diversification and modes of parental care remains contentious. Although some evidence suggests parental investment can be important in determining the

evolution of life-history traits among birds (Thomas et al. 2006), it is less clear whether variation in these traits influences population divergence. Here, studying a species rich and widely distributed group of passerine birds, we show that rates of lineage diversification appear to be correlated with breeding systems (Fig. 1). These differences are particularly evident among cooperative and pair breeding groups, and may reflect differences in their frequency of colonizing islands and continental areas (Fig. 5).



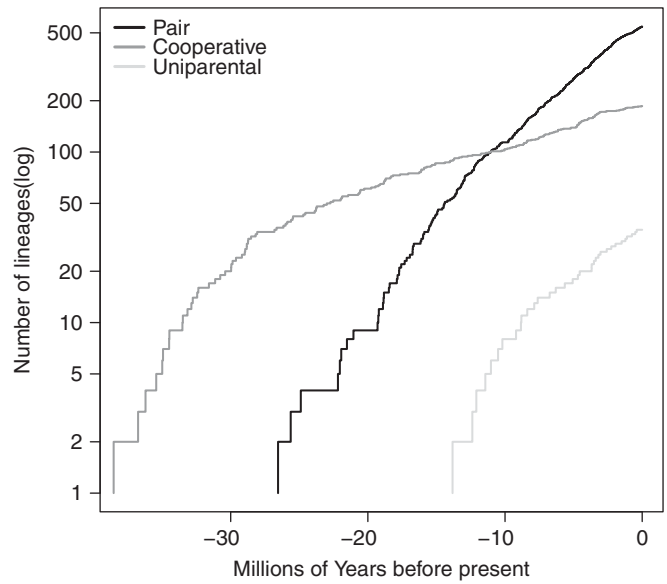
**Figure 2.** Ancestral reconstructions of breeding system using MuSSE. The nodal probabilities are presented for a single tree, but remain consistent across all 10 trees analyzed. Pie charts and tip states are colored to represent uniparental (green), biparental (blue), and cooperative (red) breeding systems. White represents species for which breeding system cannot be confidently inferred. Phylogenies were inferred using the polytomy resolver method, and thus are complete at the species level (see Methods for further information).



**Table 3. Model fitting and parameter estimates of the region-dependent diversification models in GeoSSE.**

Model specifications				Speciation rates			Extinction rates			Dispersal rates		
Speciation rates	Extinction rates	Dispersal rates	No. of parameters	$\Delta AIC$	AIC weight	Continental	Island	Widespread	Continental	Island	C → I	I → C
<b>Free</b>	<b>Free</b>	<b>Free</b>	<b>7</b>	<b>0.0</b>	<b>0.924</b>	<b>0.078 ± 0.002</b>	<b>0.209 ± 0.012</b>	<b>0.073 ± 0.029</b>	<b>0.014 ± 0.004</b>	<b>0.125 ± 0.017</b>	<b>0.004 ± 0.000</b>	<b>0.135 ± 0.007</b>
Between region = 0	Free	Free	6	5 ± 18	0.076	0.080 ± 0.003	0.246 ± 0.007	0.000 ± 0.000	0.023 ± 0.005	0.174 ± 0.009	0.004 ± 0.001	0.132 ± 0.006
Free	All constrained	Free	6	22.4 ± 15	1.26e <sup>-5</sup>	0.085 ± 0.003	0.145 ± 0.002	0.208 ± 0.014	0.021 ± 0.005	0.021 ± 0.005	0.002 ± 0.000	0.169 ± 0.005
Free	Free	All constrained	6	93.5 ± 16	4.60e <sup>-21</sup>	0.085 ± 0.002	0.302 ± 0.013	0.008 ± 0.024	0.000 ± 0.000	0.281 ± 0.015	0.051 ± 0.002	0.051 ± 0.002
All constrained	Free	Free	5	62.7 ± 15	2.24e <sup>-14</sup>	0.113 ± 0.002	0.113 ± 0.002	0.113 ± 0.002	0.035 ± 0.004	0.028 ± 0.003	0.004 ± 0.001	0.158 ± 0.007
All constrained	All constrained	All constrained	3	174.6 ± 13	1.13e <sup>-38</sup>	0.106 ± 0.001	0.106 ± 0.001	0.106 ± 0.001	0.002 ± 0.001	0.002 ± 0.001	0.023 ± 0.000	0.023 ± 0.000

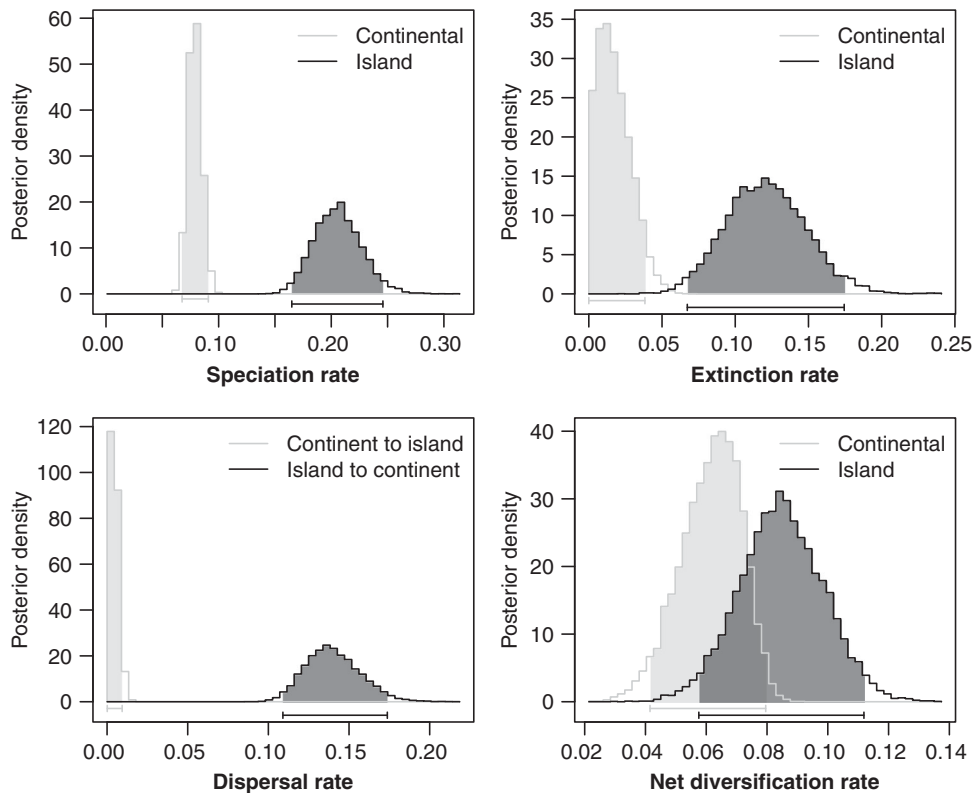
Continental represents species only found on continental landmasses and/or closely adjacent islands. Island represents species that are endemic to one or several oceanic or continental islands generally separated by deep water channels. Widespread represent species found in both continental and island regions. Model specifications indicate whether rates have been constrained to be equal, or whether they are free to vary depending on character state. Speciation, extinction, and dispersal rates are given as median and interquartile ranges estimated across the 100 polytomy-resolved phylogenies. Model fit is compared using the Akaike information criterion (AIC).  $\Delta AIC$  indicates relative AIC value to that of the best-fitting model. AIC weight represents the relative likelihood of each model. The best fitting model is indicated in bold.



**Figure 3. Lineage through time plot showing separate evolutionary trajectories for uniparental (light gray), pair (black), and cooperative (dark gray) lineages. States were inferred by summarizing the marginal likelihoods from the MuSSE analyses averaged across the 10 polytomy resolved trees, assigning each node the state with the highest likelihood.**

We suggest that different selection pressures among the alternate breeding systems may have led to the evolution of alternative life-history strategies that are important in determining the differential diversification among groups, possibly by mediating dispersal propensity.

The analyses presented here not only highlight potential differences among pair and cooperative breeders in terms of their rates of speciation and colonization of remote areas, but also suggest that these rates are correlated with one another (Table 2). Thus, one possible explanation of these results is that high dispersal abilities and the colonization of new geographic areas promote speciation (Owens et al. 1999; Phillimore et al. 2006; Moore and Donoghue 2007; Moyle et al. 2009; Bocxlaer et al. 2010). Hence, the lack of diversification and historical dispersal among cooperative breeders reflects high natal philopatry, which reduces opportunities for geographic isolation and allopatric speciation among populations (Cockburn 2003). Cockburn (2003) reported that when migrants and species endemic to oceanic islands were excluded from his analyses, the relationship between breeding system and species richness was no longer significant. This suggests an important role of geographic isolation, mediated by dispersal, as a mechanism explaining the differences in diversity among breeding systems (Cockburn 2003). Lack of dispersal may explain why many cooperative species are restricted in their distributions to Australia (Fig. 5), and potentially only diversify when relatively rare historical changes in landscape



**Figure 4.** Posterior probability distributions of parameter rate estimates generated from a GeoSSE analysis examining the effect of island and continental dwelling on lineage diversification and transitions, using an MCMC approach. Bars at the bottom of the plots highlight the 95% credibility intervals of these estimates. Results are presented for a single tree, but remain consistent across all 10 trees analyzed. Phylogenies were inferred using the polytomy resolver method, and thus are complete at the species level (see Methods for further information).

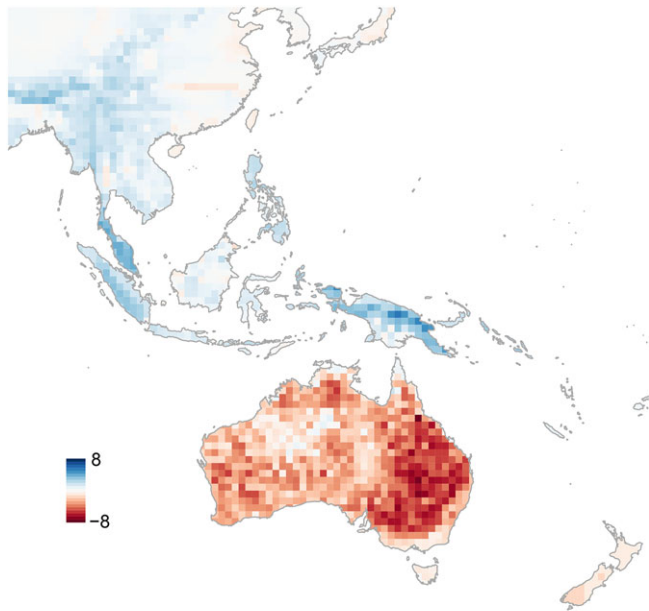
connectivity gave rise to a vicariance event within that continent. Contrastingly, many rapidly speciating pair-breeding lineages are overrepresented in the Indo-Pacific archipelago (Fig. 5).

In this respect, it is not only the cooperative breeding system that is suggested to lead to limited dispersal, but also that of uniparental care. This system has only evolved a single time within the core Corvoidea, in the family Paradisaeidae (the birds-of-paradise). Although we were unable to accurately estimate historical rates of speciation and extinction among this group in the present study, previous empirical work has illustrated both that they are heavily restricted in their distributions (the majority of species only being present in New Guinea), and have undergone a slowdown in their rate of net diversification toward the present (Fritz et al. 2012). These analyses suggest lineages within this group have limited ability to undergo range expansion. This may reflect their high fidelity toward male display areas, which combined with the high independence of males and females could limit the potential for concerted dispersal among the two sexes. Finally, the evolution of extreme ornamentation may restrict the long-distance dispersal capabilities of some lineages.

Although we suggest the differences in diversification recovered among the breeding systems generally reflect dispersal propensity and founding events, at present systematic comparisons of the appropriate traits to directly measure these factors are generally lacking, and should be an avenue of future research (Hatchwell 2009, but see Rusk et al. 2013). Furthermore, high levels of dispersal may lead to continued gene flow between populations, limiting genetic differentiation. Thus, while geographic isolation is necessary for speciation, it may be that intermediate levels of dispersal maximize the rate at which geographic isolation and population differentiation occur, before facilitating continued gene flow among populations (Claramunt et al. 2012; Weeks and Claramunt, 2014). However, the shape of this relationship may well also depend on regional levels of landscape fragmentation, and as such could be different between continental and insular settings, although this idea remains to be tested.

#### THE EVOLUTIONARY HISTORY OF BREEDING SYSTEMS

Our transition rate estimates from pair to cooperative breeding are much lower than the reverse scenario (Fig. 1; Table 1), consistent



**Figure 5.** Map of Australian and Indo-Pacific regions showing studentized residuals of linear models examining the relationship between species richness of  $1^\circ \times 1^\circ$  grid cells, among pair breeders  $\sim$  pair and cooperative breeders combined. Red and blue colors highlight areas where cooperative and pair breeders are overrepresented, respectively.

with the findings of Cornwallis et al. (2010). This, in addition to the high prevalence of cooperative breeding in the older corvid lineages, and the apparent low levels of promiscuity among the ancestral lineages of the group (Cornwallis et al. 2010) further support our suggestion that cooperative breeding was found in the most recent common ancestor of the core Corvoidea. These patterns are corroborated by the presence of cooperative breeding in several other closely related groups, including the phylogenetically most basal group of oscine songbirds that are largely endemic to Australia (Edwards and Naeem 1993; Nicholls et al. 2000; Ligon and Burt 2004; Cockburn 2006).

Pair breeding appears to have evolved independently many times (Fig. 2). If the evolution of pair breeding was also associated with an increase in dispersal propensity, this may have facilitated the initial movement of several lineages out of the Australo-Papuan region to Africa and Asia (with subsequent colonization of the New World), in addition to the extensive colonization of the Pacific islands (Cockburn 2003). In further support of this idea, among the sister group of the core Corvoidea, the Passerida, lineages that colonized Australia from Asia are all members of clades that are currently almost exclusively pair breeding (Russell 1989; Cockburn 2003). Available evidence thus suggests that the bidirectional movement of passerines through Wallacea has been mainly limited to highly dispersive pair breeders.

In light of previous studies that have assessed the geographic origins of the core Corvoidea (Jönsson et al. 2011; Aggerbeck et al. 2014), our results imply that the ancestor of this radiation inhabited islands that emerged in the epicontinental seas at the periphery of the Australasian plate, and apparently retained the cooperative breeding system prevalent in the deeper lineages of the songbird radiation (Cockburn 1996). Although cooperative breeding among island species is generally rare, there are a few instances of species endemic to islands evolving cooperative habits (Gill 1971; Brown 1987; Komdeur 1992; Brooke and Hartley 1995; Cockburn 1996; Saul et al. 1998). However, the high asymmetry in state transitions between cooperative and pair breeding may reflect that cooperative breeding is an evolutionary complex behavior that rarely reappears once lost, and is unlikely to be found among populations that colonize islands (Covas 2012).

### CORRELATED EVOLUTION OF PAIR BREEDING WITH ISLAND COLONIZATION AND MIGRATORY BEHAVIOR

The finding that breeding systems show temporal correlations with both migratory behavior and island dwelling lends further support to the suggestion that cooperative breeders are less likely to colonize remote areas compared to pair breeders. However, we report some ambiguity in terms of the correlation with island distribution, with support found only among the trees generated using the molecular data alone (Table S2). Several factors may explain this discrepancy. First, five of seven species of cooperative/uniparental breeders that are distributed on islands (e.g., *Pomarea dimidiata*) were not present in the trees generated using only the molecular data, hence their presence may influence the lack of support for a dependent model of evolution between these two traits in the complete trees. Furthermore, the evolution of helping behavior in island taxa is generally believed to appear postcolonization (Komdeur 1992; Covas 2012), which may confound these models. Finally, the correlation may also be weakened as a consequence of short branch lengths and taxonomic inconsistencies resulting from the polytomy resolution process.

One factor to have potentially influenced the geographic expansion of corvid birds out of Australasia, or at least enabled higher dispersal propensity, may have been the evolution of seasonal nomadism/migratory strategies. We cannot exclude that Australian corvid birds may have had to migrate during the early evolution of the group in the Oligocene, when Australia was located much further south, and experienced a period of cold as a consequence of the first Antarctic chill (Sanmartin and Ronquist 2004). Significant irruptive movements associated with such environmental instability still occur among many extant species. Elsewhere in the world, most corvid species are residents or show only partial migration in response to weather, and only a few species (which are among the northernmost breeders, and phylogenetically terminal in their respective groups) are obligate

migrants. In general, obligate migrant birds are faithful to specific sites, for breeding as well as staging and wintering, and therefore this behavior may be less conducive to geographical range expansion than more weather-dependent facultative migration, nomadism, and postnatal dispersal (Winkler 2005). Nevertheless, migratory birds will occasionally settle in their wintering areas (e.g., Whittington et al. 1999; Billerman et al. 2011), a process that has recently been suggested to promote colonization of the tropics and subsequent radiations in these regions (Rolland et al. 2014; Winger et al. 2014).

Although most cooperative breeders are considered to be highly sedentary and thus poor dispersers characterized by comparatively short rounded wings (e.g., Moffatt 1982; Wolfenden and FitzPatrick 1984; Zack 1990), a few are evidently good fliers (e.g., woodswallows). Although there is also a prevalence of highly sedentary species among the pair breeders, the number of good dispersers as evidenced by migratory behavior, island occurrence, and wing morphology is considerably higher than among cooperatively breeding species. Thus, a major contributor to the groups' expansion seems likely to be related to breeding system, or social organization in a broader sense, as indicated by, for example, *Perisoreus infaustus*, which is pair breeding but highly social and resident, even in areas with extreme winter cold (Ekman et al. 1994).

#### HISTORICAL ACCUMULATION OF BREEDING SYSTEM DIVERSITY

One caveat of the MuSSE and GeoSSE models is that estimates of speciation, extinction, and transition are assumed to have been constant through time. However, accumulating evidence suggests that rates of speciation and extinction have the potential to vary through both time and space (Pybus and Harvey 2000; Phillimore and Price 2008; Jetz et al. 2012; Rabosky et al. 2012; Pennell et al. 2013). Therefore, the estimates of speciation for both the continental and cooperative breeders could mask temporal variation, and a higher historical rate that has slowed toward the present. The LTT plots do suggest a slowdown in the accumulation of diversity among cooperative breeders, whereas the diversity of pair breeders arises at a more constant rate (Fig. 3). Although these results depend on the accuracy of the phylogenetic hypothesis, ancestral state reconstructions, and the state-dependent speciation-extinction (SSE) framework more generally, they do appear consistent with the idea that cooperative breeders are limited in their capacity to undergo continual range expansions, which may ultimately lead to a slowdown in the rate of allopatric speciation (Mayr 1947; Price 2008). Results from the MuSSE analyses indicated high rates of speciation for pair breeders, with little or no extinction, suggesting differential rates of speciation are the actual drivers of this pattern, not extinction. However, the difficulty in accurately estimating extinction

rates from molecular phylogenies should be acknowledged (Rabosky 2010; Davis et al. 2013), whereas another possible explanation for the observed differences is that these are driven by the island dwelling species, for which both speciation and extinction estimates are suggested to be high (Fig. 4; see Price 2008). We suggest the higher dispersal propensity of pair breeders may enable them to repeatedly enter novel and underexploited ecological space on islands and other biogeographic regions, allowing them to continue to accumulate diversity at a near constant rate.

#### SOURCE-SINK DYNAMICS BETWEEN CONTINENTS AND ISLANDS

The theory of island biogeography, as formulated by MacArthur and Wilson (1967), explains the build-up of island diversity as an equilibrium between immigration from continents, and extinction, with the islands ultimately contributing little to continental diversity, and thus “downstream colonization” being the major influence (reviewed in Bellemain and Ricklefs 2008). The core Corvoidea represent an apparent exception to this paradigm, as this was apparently an island radiation by ancestry, from which species have subsequently colonized all of the world's continental areas (Jönsson et al. 2011; Aggerbeck et al. 2014). However, the very high rates of dispersal from islands to continents that we estimated, compared to the very low rates of the reverse scenario could also potentially be an artifact of the low frequency, and potentially high rates of speciation and/or extinction among island taxa (165 species). Both island and continental lineages are characterized by a small number of species-rich clades, with the latter also containing a disproportionately large number of species-poor, ancient taxa, which likely explain the lower rates of speciation recorded on continents. The young age of many island species suggest high turnover in these areas, supporting previous empirical work (Price 2008). This could be a consequence of limited available resources in these locations, plus their continual colonization by new competitors, hence representing the interplay between high turnover, and diversity-dependence in a broader sense. However, the high estimated rates of dispersal from islands to continents seem less biologically plausible, which may suggest an inability of GeoSSE to adequately account for the differential rates of speciation, given the frequency of the island/continental states.

#### OUTSTANDING ISSUES

Although our study does highlight general trends that may further our understanding of the causes of asymmetrical species richness across the core Corvoidea, there are some idiosyncrasies that do not fit these patterns. For example, some biparental lineages disperse and diversify, whereas others do not. Thus, pair breeding seems prevalent in a few species-poor genera within the Australo-papuan region (*Psophodes*, *Strepera*, *Oreoica*, *Coluricincla*, and presumably also *Ptilorrhoa*), and can even be



found within lineages that colonized the Old World tropics (e.g., *Aegithina*, *Tephrodornis*, and *Hemipus*). Therefore, heterogeneity in the rates of lineage diversification and range expansions among both cooperative and pair breeding taxa require additional explanatory factors. These could reflect further differences in life-history traits, such as long-distance dispersal ability, rates of behavioral innovation (Wyles et al. 1983; Sol et al. 2005a, b; Sol and Price 2008), and/or generalism, which we were unable to account for at such a broad analytical scale. Rates of clade-level annual mortality have also been suggested to vary with breeding system (Arnold and Owens 1999), which could conceivably also influence the potential for establishment in new areas. So although our results suggest significant differences in diversification rates between species with cooperative and pair breeding systems, and with island or continental distributions, we cannot exclude the possibility that other codistributed characters could be responsible for the observed differences (Maddison et al. 2007). Despite the potential for intrinsic life-history differences among groups, there are also likely to be differences in regional diversification rates (Cardillo et al. 2005; Jetz et al. 2012) and/or clade age/the timing of regional colonization (Stephens and Wiens 2003), which could impact these results. Additionally, the classification of a diverse array of breeding systems as simply being either cooperative or pair breeding may inhibit more detailed interpretation of the effect of breeding systems on the dynamics of dispersal and diversification. As more avian life-history data becomes available, finer division of breeding system classifications may allow us to gain a better understanding of how variation in sociality and modes of parental care affect these patterns.

Finally, although the statistical power of BiSSE depends on the size of the phylogeny, and the ratio of the tip states analyzed (Davis et al. 2013), a recent study highlights that this model may also be prone to high rates of type I error when assessing state-dependent speciation among neutrally evolving traits (Rabosky and Goldberg 2015). These latter findings suggest the results from our analyses implementing the SSE models should therefore be interpreted with some caution. However, given the relationships, we illustrate between breeding systems, migratory behavior, and island colonization/distribution via alternative analytical approaches, there remain good reasons to suggest their relationship with diversification rates to be nonneutral. Although the type I error rates of BiSSE are a cause for general concern (Rabosky and Goldberg 2015), they do not necessarily preclude that state-dependent diversification, as we propose among core corvid breeding systems, may in fact be real.

## Conclusions

The results presented here illustrate the potential importance of breeding systems in influencing rates of lineage diversification

among the core Corvoidea. The evolution of pair breeding strategies in several independent lineages could represent a significant behavioral shift that enabled certain dispersive lineages to undergo extensive phylogenetic expansion. We suggest dispersal to and diversification within the island setting of the Indo-Pacific is important in explaining the differences in diversification rates between the breeding systems and thus contemporary distributional patterns among the core Corvoidea. These results should help us gain better insight into the macroecological and macroevolutionary patterns that underlie the build-up of island and continental assemblages, although future work should aim to highlight instances where these rates have varied between taxa in both time and space.

## ACKNOWLEDGMENTS

We thank R. FitzJohn, S. A. Price, E. Goldberg, R. Maia, and G. Thomas for assistance with software implementation and helpful suggestions with regards to the methodological approaches. We thank the following curators and institutions for kindly providing tissue samples: S. van der Mije at the Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands and M. Brooke of the University Museum of Zoology, Cambridge. The comments of A. Phillimore, T. Price, and one anonymous reviewer greatly helped us to improve the quality of this manuscript. KAJ acknowledges support from the People Programme (Marie Curie Actions) of the European Union's Seventh Framework Programme (FP7/2007–2013) under REA grant agreement no. PIEF-GA-2011-300924. Finally, we also thank the Danish National Research Foundation for its support to the Center for Macroecology, Evolution and Climate.

## DATA ARCHIVING

The doi for our data is 10.5061/dryad.g4f84.

## LITERATURE CITED

- Aggerbeck, M., J. Fjeldså, L. Christidis, P. H. Fabre, and K. A. Jønsson. 2014. Resolving deep lineage divergences in the core corvid passerine birds supports a proto-Papuan island origin. *Mol. Phylogenet. Evol.* 70:272–285.
- Arnold, K. E., and I. P. F. Owens. 1999. Cooperative breeding in birds: the role of ecology. *Behav. Ecol.* 10:465–471.
- Barker, F. K., A. Cibois, P. Schikler, J. Feinstein, and J. Cracraft. 2004. Phylogeny and diversification of the largest avian radiation. *Proc. Natl. Acad. Sci. USA* 105:12145–12149.
- Bellemain, E., and R. E. Ricklefs. 2008. Are islands the end of the colonization road? *Trends Ecol. Evol.* 23:461–468.
- Billerman, S. M., G. H. Huber, D. W. Winkler, R. J. Safran, and I. J. Lovette. 2011. Population genetics of a recent transcontinental colonization of South America by breeding barn swallows (*Hirundo rustica*). *Auk* 128:506–513.
- Bloom, D. D., J. T. Weir, K. R. Piller, and N. R. Lovejoy. 2013. Do freshwater fishes diversify faster than marine fishes? A test using state-dependent diversification analyses and molecular phylogenetics of new world silversides (Atherinopsidae). *Evolution* 67:2040–2057.
- Bocxlaer, I. V., S. P. Loader, K. Roelants, S. D. Biju, M. Menegon, and F. Bossuyt. 2010. Gradual adaptation toward a range-expansion phenotype initiated the global radiation of toads. *Science* 327:679–682.
- Brown, J. L. 1987. Helping and communal breeding in birds. Princeton Univ. Press, Princeton, NJ.



- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi-model inference: a practical information-theoretic approach. Springer, New York.
- Cardillo, M., C. D. L. Orme, and I. P. F. Owens. 2005. Testing for latitudinal bias in diversification rates: an example using New World birds. *Ecology* 86:2278–2287.
- Claramunt, S., E. P. Derryberry, J. V. Remsen, and R. T. Brumfield. 2012. High dispersal ability inhibits speciation in a continental radiation of passerine birds. *Proc. R. Soc. B* 279:1567–1574.
- Clutton-Brock, T.H., and P. H. Harvey. 1978. Mammals, resources and reproductive strategies. *Nature* 273(569):191–195.
- Cockburn, A. 1996. Why do so many Australian birds cooperate: social evolution in the Corvidae? Pp. 451–472 in R. B. Floyd, A. W. Sheppard, and P. J. De Barro, eds. *Frontiers of population ecology*. CSIRO, East Melbourne.
- . 2003. Cooperative breeding in oscine passerines: does sociality inhibit speciation? *Proc. R. Soc. Lond. B* 270:2207–2214.
- . 2006. Prevalence of different modes of parental care in birds. *Proc. R. Soc. B* 273:1375–1383.
- Cockburn, A., and A. F. Russell. 2011. Cooperative breeding: a question of climate? *Curr. Biol.* 21:195–197.
- Cornwallis, C. K., S. A. West, K. E. Davis, and S. A. Griffin. 2010. Promiscuity and the evolutionary transition to complex societies. *Nature* 466:969–972.
- Covas, R. 2012. Evolution of reproductive life histories in island birds worldwide. *Proc. R. Soc. B* 279:1531–1537.
- Covas, R., M.A. Du Plessis, and C. Doutrelant. 2008. Helpers in colonial cooperatively breeding sociable weavers *Philetairus socius* contribute to buffer the effects of adverse breeding conditions. *Behav. Ecol. Sociobiol.* 63:103–112.
- Davis, M. P., P. E. Midford, and W. Maddison. 2013. Exploring power and parameter estimation of the BiSSE method for analyzing species diversification. *BMC Evol. Biol.* 13:38.
- del Hoyo, J., A. Elliot, and D. A. Christie. 2005–2010. *Handbook of the Birds of the World*. Vol. 10–15. Lynx Edicions, Barcelona, Spain.
- Dickinson, J. L., and B. J. Hatchwell. 2004. Fitness consequences of helping. Pp. 48–66 in W. Koenig, and J. Dickinson, eds. *Ecology and evolution of cooperative breeding in birds*. Cambridge Univ. Press, Cambridge, U.K.
- Drummond, A. J., M. A. Suchard, D. Xie, and A. Rambaut. 2012. Bayesian phylogenetics with BEAUti and BEAST 1.7. *Mol. Biol. Evol.* 29:1969–1973.
- Edwards, S. V., and S. Naem. 1993. The phylogenetic component of cooperative breeding in perching birds. *Am. Nat.* 141:754–789.
- Ekman, J., B. Sklepkovych, and H. Tegelström. 1994. Offspring retention in the Siberian jay (*Perisoreus infaustus*): the prolonged brood care hypothesis. *Behav. Ecol.* 5:245–253.
- Feeney, W. E., I. Medina, M. Somveille, R. Heinsohn, M. L. Hall, R. A. Mulder, J. A. Stein, R. M. Kilner, and N. E. Langmore. 2013. Brood parasitism and the evolution of cooperative breeding in birds. *Science* 342:1506–1508.
- FitzJohn, R. G. 2010. Quantitative traits and diversification. *Syst. Biol.* 59:619–633.
- . 2012. Diversitree: comparative phylogenetic analyses of diversification in R. *Methods Ecol. Evol.* 3:1084–1092.
- FitzJohn, R. G., W. P. Maddison, and S. P. Otto. 2009. Estimating trait-dependent speciation and extinction rates from incompletely resolved phylogenies. *Syst. Biol.* 58:595–611.
- Fritz, S., K. A. Jönsson, J. Fjeldså, and C. Rahbek. 2012. Diversification and biogeographic patterns in four island radiations of passerine birds. *Evolution* 66:179–190.
- Gill, F., and D. Donsker. 2010. IOC world bird names (v 2.7.). Available at <http://www.worldbirdnames.org>.
- Goldberg, E. E., and B. Igić. 2008. On phylogenetic tests of irreversible evolution. *Evolution* 62:2727–2741.
- Goldberg, E. E., L. T. Lancaster, and R. H. Ree. 2011. Phylogenetic inference of reciprocal effects between geographic range evolution and diversification. *Syst. Biol.* 60:451–465.
- Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Anim. Behav.* 28:1140–1162.
- Grimes, L. G. (1976) The occurrence of cooperative breeding behavior in African birds. *Ostrich* 47:1–15.
- Hatchwell, B. J. 2009. The evolution of cooperative breeding in birds: kinship, dispersal and life history. *Philos. T. Roy. Soc. B* 364:3217–3227.
- Heinsohn, R., and M. C. Double. 2004. Cooperate or speciate: new theory for the distribution of passerine birds. *Trends Ecol. Evol.* 19:55–57.
- Jetz, W., and D. R. Rubenstein. 2011. Environmental uncertainty and the global biogeography of cooperative breeding in birds. *Curr. Biol.* 21:72–78.
- Jetz, W., G. H. Thomas, J. B. Joy, K. Hartmann, and A. O. Mooers. 2012. The global diversity of birds in space and time. *Nature* 491:444–448.
- Jönsson, K. A., P. H. Fabre, R. E. Ricklefs, and J. Fjeldså. 2011. Major global radiation of corvid birds originated in the proto-Papuan archipelago. *Proc. Natl. Acad. Sci.* 108:2328–2333.
- Koenig, W., and J. L. Dickinson. 2004. *Ecology and evolution of cooperative breeding in birds*. Cambridge Univ. Press, Cambridge, U. K.
- Komdeur, J. 1992. Importance of habitat saturation and territory quality for evolution of cooperative breeding in the Seychelles warbler. *Nature* 358:493–495.
- Kuhn, T. S., A.Ø. Mooers, and G. H. Thomas. 2011. A simple polytomy resolver for dated phylogenies. *Methods Ecol. Evol.* 2:427–436.
- Lack, D. 1968. *Ecological adaptations for breeding in birds*. Mettuen, London.
- Ligon, J. D., and D. B. Burt. 2004. Evolutionary origins. Pp. 5–34 in W. Koenig, and J. Dickinson, eds. *Ecology and evolution of cooperative breeding in birds*. Cambridge Univ. Press, Cambridge, U.K.
- MacArthur, R. H., and E. O. Wilson. 1967. *The theory of island biogeography*. Princeton Univ. Press, Princeton, NJ.
- Maddison, W. P. 2006. Confounding asymmetries in evolutionary diversification and character change. *Evolution* 44:539–557.
- Maddison, W. P., P. E. Midford, and S. P. Otto. 2007. Estimating a binary character's effect on speciation and extinction. *Syst. Biol.* 56:701–710.
- Mayr, E. 1947. Ecological factors in speciation. *Evolution* 1:263–288.
- Mayr, E., and J. Diamond. 2001. *The birds of Northern Melanesia: speciation, ecology and biogeography*. Oxford Univ. Press, Oxford, U. K.
- Mittelbach, G. G., D. W. Schemske, H. V. Cornell, A. P. Allen, J. M. Brown, M. B. Bush, S. P. Harrison, A. H. Hurlbert, N. Knowlton, H. A. Lessios, et al. 2007. Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecol. Lett.* 10:315–331.
- Moffatt, J. D. 1982. *Territoriality and use of space in the grey-crowned babbler*. Thesis, University of Queensland, Australia.
- Moore, B. R., and M. J. Donoghue. 2007. Correlates of diversification in the plant clade Dipsacales: geographic movements and evolutionary innovations. *Am. Nat.* 170(suppl. 2):28–55.
- Moyle, R. G., C. E. Filardi, C. E. Smith, and J. Diamond. 2009. Explosive Pleistocene diversification and hemispheric expansion of a “great speciator.” *Proc. Natl. Acad. Sci. USA* 106:1863–1868.
- Newton, I. 1989. *Lifetime reproduction in birds*. Academic Press, London.
- Nicholls, J. A., M. C. Double, D. M. Rowell, and R. D. Magrath (2000) The evolution of cooperative and pair breeding in thornbills *Acanthiza* (Pardalotidae). *J. Avian Biol.* 31:165–176.

- Owens, I. P. F., P. M. Bennett, and P. H. Harvey. 1999. Species richness among birds: body size, life history, sexual selection or ecology? *Proc. R. Soc. Lond. B* 266:933–939.
- Pagel, M., and A. Meade. 2006. Bayesian analysis of correlated evolution of discrete characters by reversible-jump Markov Chain Monte Carlo. *Am. Nat.* 167:808–825.
- Paradis E., J. Claude, and K. Strimmer. 2004. APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* 20:289–290.
- Pennell, M. W., L. J. Harmon, and J. C. Uyeda. 2013. Is there room for punctuated equilibrium in macroevolution? *Trends Ecol. Evol.* 29:23–32.
- Phillimore, A. B., and T. D. Price. 2008. Density-dependent cladogenesis in birds. *PLoS Biol.* 6:483–489.
- Phillimore, A. B., R. P. Freckleton, C. D. L. Orme, and I. P. F. Owens. 2006. Ecology predicts large-scale patterns of phylogenetic diversification in birds. *Am. Nat.* 168:220–229.
- Price, S. A., S. S. B. Hopkins, K. K. Smith, and V. L. Roth. 2012. Tempo of trophic evolution and its impact on mammalian diversification. *Proc. Natl. Acad. Sci.* 109:7008–7012.
- Price, T. D. 2008. *Speciation in birds*. Roberts and Co., Boulder, CO.
- Pybus, O. G., and P. H. Harvey. 2000. Testing macro-evolutionary models using incomplete molecular phylogenies. *Proc. R. Soc. Lond. B Biol.* 267:2267–2272.
- R Development Core Team. 2012. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN: 3-900051-07-0. Available at <http://www.R-project.org/>.
- Rabosky, D. L. 2009. Ecological limits and diversification rate: alternative paradigms to explain the variation in species richness among clades and regions. *Ecol. Lett.* 12:735–743.
- . 2010. Extinction rates should not be estimated from molecular phylogenies. *Evolution* 64:1816–1824.
- Rabosky, D. L., and E. E. Goldberg. 2015. Model inadequacy and mistaken inferences of trait-dependent speciation. *Syst. Biol.* 64(2):340–355.
- Rabosky, D. L., and I. J. Lovette. 2008. Density-dependent diversification in North American wood warblers. *Proc. R. Soc. B* 275:2363–2371.
- Rabosky, D. L., G. J. Slater, and M. E. Alfaro. 2012. Clade age and species richness are decoupled across the Eukaryotic tree of life. *PLoS Biol.* 10:e1001381.
- Rahbek, C., and G. R. Graves. 2001. Multiscale assessment of patterns of avian species richness. *Proc. Natl. Acad. Sci. USA* 98:4534–4539.
- Rahbek, C., L. A. Hansen, and J. Fjeldsø. 2012. One degree resolution database of the global distribution of birds. The Natural History Museum of Denmark, Univ. of Copenhagen, Denmark. Available at <http://macroecology.ku.dk/resources/>
- Rambaut, A., M. A. Suchard, D. Xie, and A. J. Drummond. 2013. Tracer v1.5. Available at <http://beast.bio.ed.ac.uk/Tracer>.
- Ricklefs, R. E. 1987. Community diversity—relative roles of local and regional processes. *Science* 235:167–171.
- . 2005. Small clades at the periphery of passerine morphological space. *Am. Nat.* 165:651–659.
- Robinson, D. R., and L. R. Foulds. 1981. Comparison of phylogenetic trees. *Math. Biosci.* 53:131–147.
- Rolland, J., F. Jiguet, K. A. Jønsson, F. L. Condamine, and H. Morlon. 2014. Settling down of seasonal migrants promotes bird diversification. *Proc. R. Soc. B* 281, 20140473.
- Rowley, I. (1976) Co-operative breeding in Australian birds. *Proc. Int. Ornithol. Congr.* 16:657–666.
- Rubenstein, D. R., and Lovette, I. J. 2007. Temporal environmental variability drives the evolution of cooperative breeding in birds. *Curr. Biol.* 17:1414–1419.
- Rusk, C. L., E. L. Walters, and W. D. Koenig. 2013. Cooperative breeding and long-distance dispersal: a test using vagrant records. *PLoS One* 8:e58624. doi:10.1371/journal.pone.0058624.
- Russell, E. M. 1989. Co-operative breeding—a Gondwanan perspective. *Emu* 89:61–62.
- Sanmartín, I., and F. Ronquist. 2004. Southern hemisphere biogeography inferred by event-based models: plant versus animal patterns. *Syst. Biol.* 53:216–243.
- Sol, D., and T. D. Price. 2008. Brain size and the diversification of body size in birds. *Am. Nat.* 172:170–177.
- Sol, D., R. P. Duncan, T. M. Blackburn, P. Cassey, and L. Lefebvre. 2005a. Big brains, enhanced cognition, and response of birds to novel environments. *Proc. Natl. Acad. Sci. USA* 102:5460–5465.
- Sol, D., L. Lefebvre, and J. D. Rodríguez-Tejreiro. 2005b. Brain size, innovative propensity and migratory behavior in temperate Palaearctic birds. *Proc. R. Soc. Lond. B* 272:1433–1441.
- Stephens, P. R., and J. J. Wiens. 2003. Ecological diversification and phylogeny of emydid turtles. *Biol. J. Linn. Soc* 79:577–610.
- Thomas, G. H., R. P. Freckleton, and T. Székely. 2006. Comparative analyses of the influence of developmental mode on phenotypic diversification rates in shorebirds. *Proc. R. Soc. B* 273:1619–1624.
- Tinkle, D. W., H. M. Wilbur, and S. G. Tilley. 1970. Evolutionary strategies in lizard reproduction. *Evolution* 24:55–74.
- Weatherhead, P. J., and M. R. L. Forbes. 1994. Natal philopatry in passerine birds: genetic or ecological influences? *Behav. Ecol.* 5:426–433.
- Weeks, B. C., and S. Claramunt. 2014. Dispersal has inhibited avian diversification in Australasian archipelagoes. *Proc. Roy. Soc. B* 281, 20141257.
- Weir, B. J., and I. W. Rowlands. 1973. Reproductive strategies of mammals. *Annu. Rev. Ecol. Syst.* 4:139–163.
- Weir, J. T. 2006. Divergent timing and patterns of species accumulation in lowland and highland neotropical birds. *Evolution* 60:842–855.
- Whittington P. A., B. M. Dyer, R. J. M. Crawford, and A. J. Williams. 1999. First recorded breeding of Leach’s storm petrel *Oceanodroma leucorhoa* in the Southern Hemisphere, at Dyer Island, South Africa. *Ibis* 141:327–330.
- Winger, B. M., F. K. Barker, and R. H. Ree. 2014. Temperate origins of long-distance seasonal migration in New World songbirds. *Proc. Natl. Acad. Sci. USA* 111:12115–12120.
- Winkler, D. W. 2005. How do migration and dispersal interact? Pp. 401–413 in R. Greenberg and P. P. Marra, eds. *Birds of two worlds*. Johns Hopkins Univ. Press, Baltimore, MD.
- Wolfenden, G. E., and J. W. Fitzpatrick. 1984. *The Florida scrub jay: demography of a cooperative-breeding bird*. Princeton Univ. Press, Princeton, NJ.
- Wyles, J. S., J. G. Kunkel, and A. C. Wilson. 1983. Birds, behavior, and anatomical evolution. *Proc. Natl. Acad. Sci. USA* 80:4394–4397.
- Zack, S. W. 1990. Coupling delayed breeding with short-distance dispersal in cooperatively breeding birds. *Ethology* 86:265–289.
- Zahavi, A. 1975. Mate selection—a selection for a handicap. *J. Theor. Biol.* 53:205–14.

Associate Editor: R. Brumfield  
 Handling Editor: R. Shaw

## Appendix A

### GENERATION OF A SPECIES-LEVEL PHYLOGENY OF THE CORE CORVOIDEA

#### *Taxonomic sampling and sequence data*

We broadly followed the classification of the IOC version 2.7 (Gill and Donsker 2010) to consider a total of 763 species of core Corvoidea, which are listed in Appendix B. To collect suitable candidate genes for the supermatrix assembly, DNA sequences for these same species were downloaded from the EMBL/GenBank/DDBJ databases. Keyword frequency searches were performed to find genes that were sequenced over a large taxonomic range using the species and genus names (Gill and Donsker 2010). With these results, we decided to focus our phylogenetic analyses on seven nuclear (c-MOS, GAPDH, Myo2, ODC, RAG1, RAG2, TGFb2) and four mitochondrial (COI, cytochrome b, ND2, ND3) markers, which have been used extensively to infer core Corvoidea phylogenies (e.g., Cicero and Johnson 2001; Pasquet et al. 2002, 2007; Cibois et al. 2004; Ericson et al. 2005; Filardi and Moyle 2005; Filardi and Smith 2005; Irestedt et al. 2008a, b, 2009; Jönsson et al. 2008a, b, 2010a, b, 2010c, d, 2011, 2012a, b; Norman et al. 2009; Nyári et al. 2009; Fabre et al. 2012, 2013; Fuchs et al. 2012; Kennedy et al. 2012; Reddy et al. 2012; Aggerbeck et al. 2014). For species with little or no genetic coverage across these markers, we generated new sequences of cytochrome b, ND2, and ND3, which have subsequently been deposited on Genbank (accession numbers KP726920–KP726925). Where possible, we selected sequences obtained from the same voucher specimen, otherwise, we used sequences that recovered congruent phylogenetic relationships among the genes, as inferred from phylogenetic inferences using RAxML. A broad selection of outgroup taxa were selected from the remainder of the Passeriformes (Barker et al. 2002; Ericson et al. 2002; Aggerbeck et al. 2014) for which the same genes were available. These outgroup taxa were subsequently pruned from the phylogenies to perform all analyses presented in the main text. A full list of all core Corvoidea sequences used in the final alignment can be found in Table A1. DNA sequences were aligned using the program MAFFT (Katoh et al. 2002), with these alignments subsequently checked by eye using SEAVIEW (Galtier et al. 1996). The final concatenated supermatrix included a total of 12,221 comparable sites (70% missing data).

#### *Phylogenetic analyses*

We first computed maximum-likelihood inference using RAxML 7.2.6 (Stamatakis 2006) under a general time reversible (GTR, Gu et al. 1995) model with a gamma rate distribution ( $\Gamma$ ), implemented on the CIPRES Science Gateway (Miller et al. 2010) for the concatenated dataset. We used 1000 starting trees in this analysis to avoid local optima, with clade support assessed using 10,000 nonparametric bootstrap pseudoreplicates. We

summarized the results by generating a 50% majority rule consensus tree.

#### *Molecular dating and calibrating the tree*

We used a relaxed uncorrelated lognormal distribution as a molecular clock model, implemented in BEAST 1.6.2 (Drummond & Rambaut 2007). Due to the large number of characters in the concatenated supermatrix, and computational issues in launching an unconstrained analysis, we constrained our topology to reflect our consensus tree obtained from the RAxML runs, which facilitated us to obtain convergence in the Bayesian analyses. In this analysis, we used a GTR + I +  $\Gamma$  model of sequence evolution with three partitions: (1) mitochondrial genes, (2) nuclear exons, and (3) nuclear introns. We ran two independent analyses of 800 million generations, sampling trees every 5000 generations, and assuming a Yule speciation process as a tree prior. Diagnostic statistics of these runs were assessed in Tracer (Rambaut and Drummond, 2007), determining convergence success based on the MCMC traces of the parameter estimates, and their effective sample sizes (ESS > 200 representing an acceptable effective sample size). The resulting distribution of trees were summarized in TreeAnnotator (Drummond and Rambaut, 2007) as a maximum clade credibility (MCC) tree, discarding the first 100 million generations as a burn-in.

The majority of passerine phylogenies for which the topologies are calibrated, constrain the root age to determine divergence estimates. This constraint is usually based on the split between Acanthisittidae and all other passerines, dated at 85–82 Mya (Barker et al. 2004) with several studies using the derived dates as secondary calibrations (e.g., Jönsson et al. 2010c; Moyle et al. 2012). These derived dates are very approximate, as this calibration is based on the assumption that the origin of the New Zealand endemic taxon *Acanthisitta* reflects the age of the separation of New Zealand from Australia, which is highly contentious (Worthy et al. 2010; Kennedy et al. 2012). However, choosing appropriate fossil constraints to calibrate deep divergences within passerine phylogenies is difficult due to the highly fragmented nature of their fossil record, and the lack of crown group fossils before the mid-Miocene (Mayr 2005). Despite these uncertainties, in the absence of such constraints, the age estimates become highly unreliable (Ericson et al. 2014). We therefore employed a uniform prior to the root of our tree, using 85 Mya as the upper boundary, and the present day (0 Mya) as the lower boundary. Using the same uniform prior, we employed two extrapolated age estimates derived from the study of Barker et al. (2004): (1) the age of Old World versus New World suboscines at 73.3–0 Mya, and (2) the split between *Menura noveahollandiae* and all other oscines at 66.3–0 Mya.

Additionally, we used alternative fossil/geological calibration points to constrain three further nodes across the tree. The

geological calibration points were as follows: (1) the split between *Coracina newtoni* from Réunion (island age about 2 Mya, see Chevallier and Vatin-Perignon 1982) and *Coracina typica* from Mauritius (island age about 8 Mya, see McDougall and Chamalaun 1969). In using this calibration, we assumed that Mauritius was colonized before the emergence of Réunion, and that Mauritius was the source of colonization of Réunion following the emergence of the latter. To obtain a calibration point based on the split between these two species, we applied a uniform prior with an upper bound at 85 Mya, and a lower bound at 2 Mya (estimated emergence of Réunion). (2) We also followed VanderWerf et al. (2009) and Cibois et al. (2004), in using the divergence between *Chasiempis sandwichensis* from Hawaii (Kauai oldest island age approximately 5.1 Ma; Carson and Clague 1995) and its Southeast Pacific monarch relatives (*Pomarea*) as a geological calibration point. To do this, we employed a uniform prior with a lower bound at 5.1 Mya (representing the emergence of Kauai Island), and an upper bound at 85 Mya. (3) The Most Recent Common Ancestor of *Cyanocitta/Gymnorhinus* was constrained using the age of the fossil *Miocitta* (Becker 1987) from the Miocene (15 Mya), by setting a uniform prior at this node with a range of dates between 85 and 15 Mya. Although we employed the use of multiple calibration points in an attempt to improve the accuracy of our date estimates (Linder et al. 2005), we accept that many uncertainties remain in the dating scheme presented.

#### *Adding species for which DNA data were unavailable to produce a complete species level phylogeny*

Species for which no DNA data were available (159 species) were added as polytomies to the phylogeny following the current taxonomic placement of species (del Hoyo et al. 2005, 2006, 2007, 2008, 2009, 2010). In instances where specific species placements were uncertain, we placed the species randomly within the clade for which it was suggested to be a member. For example, if a species is currently suggested to be a member of the family Rhipiduridae (and we were only confident in the placement of the taxa in question at this taxonomic level), then the polytomy was randomly placed at a node within this group, however, in the majority of cases current taxonomic information allows assignment at much lower levels, that is, among superspecies. We then applied the methods of Kuhn et al. (2011) to randomly resolve these polytomies using the birth–death model to assign branch lengths. This method places constraints on the resolved topology and node ages, leaving the branch lengths of the unresolved polytomies to be permuted. The polytomy resolution was performed using the R package Ape, and BEAST (Paradis et al. 2004; R Development Core Team 2012; Drummond et al. 2012), using an MCMC approach. The MCMC chain was run for 11,100,000 iterations, sampling every 111,000th iteration. Parameter estimates were inspected in Tracer (Rambaut et al. 2013) to assess the burn-in, mixing, and convergence. This process resulted in a pseudoposterior distribution of 100 trees.

Table A1. List of all mitochondrial and nuclear loci sampled for 604 species of the core Corvoidea to generate the supermatrix used for phylogenetic inference.

Species	COI	Cytochrome b	ND2	ND3	c-MOS	GAPDH	Myo2	ODC	RAG1	RAG2	TGFb2
<i>Aegithina tiphia</i>	-	-	X	-	X	X	X	-	X	X	-
<i>Aleadryas rufinucha</i>	-	X	X	-	-	X	X	X	X	-	-
<i>Androphobus viridis</i>	-	-	-	-	-	-	-	X	-	-	-
<i>Aphelocoma californica</i>	X	X	X	X	-	-	-	X	-	-	-
<i>Aphelocoma coerulescens</i>	X	X	X	-	-	-	X	-	-	-	X
<i>Aphelocoma insularis</i>	X	X	X	-	-	-	-	-	-	-	-
<i>Aphelocoma ultramarina</i>	X	X	X	-	-	-	-	X	-	-	-
<i>Aphelocoma unicolor</i>	-	X	X	-	-	-	-	X	-	-	-
<i>Arses insularis</i>	-	-	X	-	-	-	-	-	-	-	-
<i>Arses kaupi</i>	-	-	X	X	-	-	-	-	-	-	-
<i>Arses lorealis</i>	-	-	X	-	-	-	-	-	-	-	-
<i>Arses telescopthalmus</i>	-	-	X	X	-	-	-	-	-	-	-
<i>Artamella viridis</i>	-	-	X	-	-	X	X	X	-	-	-
<i>Artamus cinereus</i>	-	-	X	-	X	X	X	X	-	-	X
<i>Artamus cyanopterus</i>	-	-	X	-	-	X	X	-	X	X	-
<i>Artamus leucorynchus</i>	-	X	X	-	X	-	X	-	X	X	-
<i>Artamus maximus</i>	-	-	-	-	X	X	X	X	-	-	X
<i>Artamus minor</i>	-	-	X	-	-	-	-	-	-	-	-
<i>Artamus personatus</i>	-	-	X	-	-	-	-	-	-	-	-
<i>Artamus superciliosus</i>	-	-	X	-	-	-	-	-	-	-	-
<i>Astrapia mayeri</i>	-	X	-	-	-	X	-	X	-	-	-
<i>Astrapia nigra</i>	-	X	-	-	-	X	-	X	-	-	-
<i>Astrapia rothschildi</i>	-	X	-	-	-	X	-	X	-	-	-
<i>Astrapia splendidissima</i>	-	X	-	-	-	X	-	X	-	-	-
<i>Astrapia stephaniae</i>	-	X	-	-	-	X	-	X	-	-	-
<i>Batis capensis</i>	-	-	-	X	X	X	X	X	X	-	X
<i>Batis crypta</i>	-	X	X	-	X	X	X	X	-	-	X
<i>Batis diops</i>	X	X	X	X	X	X	X	X	X	-	X
<i>Batis minor</i>	-	-	X	X	-	-	X	-	-	-	-
<i>Batis mixta</i>	-	X	X	X	-	-	X	-	X	X	-
<i>Batis molitor</i>	-	-	X	X	X	X	X	X	X	-	X
<i>Batis poensis</i>	-	-	X	-	X	X	X	X	X	-	X
<i>Batis pririt</i>	-	-	X	X	X	X	X	X	X	-	X
<i>Batis soror</i>	-	-	X	X	X	X	X	X	-	-	X
<i>Bias musicus</i>	-	-	X	-	X	X	X	-	X	X	-
<i>Calicalicus madagascariensis</i>	-	-	X	-	X	X	X	X	-	-	-
<i>Calicalicus rufocarpalis</i>	-	-	X	-	-	X	X	X	-	-	-
<i>Calocitta colliei</i>	-	X	X	-	-	-	-	-	-	-	-
<i>Calocitta formosa</i>	-	X	X	-	-	-	X	-	-	-	X
<i>Campephaga flava</i>	-	X	X	-	X	X	X	X	X	-	X
<i>Campephaga petiti</i>	-	-	X	-	X	X	X	X	-	-	-
<i>Campochoera sloetii</i>	-	-	X	-	-	X	X	X	-	-	-
<i>Carterornis chrysomela</i>	X	X	X	-	-	-	X	-	X	X	-
<i>Chaetorhynchus papuensis</i>	-	-	X	X	-	X	X	X	X	X	X
<i>Chasiempis sandwichensis</i>	-	-	X	-	-	-	X	-	-	-	-
<i>Chlorophoneus bocagei</i>	-	-	X	-	-	-	-	-	-	-	-
<i>Chlorophoneus dohertyi</i>	-	X	X	X	-	X	X	-	X	X	-
<i>Chlorophoneus nigrifrons</i>	-	-	X	-	-	-	X	-	-	-	-
<i>Chlorophoneus sulfureopectus</i>	-	-	X	-	X	X	X	X	X	-	X

(Continued)



Continued.

Species	COI	Cytochrome b	ND2	ND3	c-MOS	GAPDH	Myo2	ODC	RAG1	RAG2	TGFb2
<i>Cicinnurus regius</i>	X	X	-	-	-	X	-	X	-	-	-
<i>Cinclosoma punctatum</i>	-	X	-	-	-	-	X	-	X	-	-
<i>Cissa chinensis</i>	-	X	-	-	-	-	X	-	X	-	-
<i>Clytorhynchus hamlini</i>	-	-	X	-	-	-	X	-	-	-	-
<i>Clytorhynchus nigrogularis</i>	-	-	X	-	-	-	-	-	-	-	-
<i>Clytorhynchus pachycephaloides</i>	-	-	X	-	-	-	X	-	-	-	-
<i>Clytorhynchus vitiensis</i>	-	-	X	-	-	-	-	-	-	-	-
<i>Colluricincla boweri</i>	-	-	X	X	-	X	X	X	-	-	-
<i>Colluricincla harmonica</i>	-	X	X	X	-	X	X	X	X	X	-
<i>Colluricincla megarhyncha</i>	-	X	X	X	-	X	X	X	X	-	-
<i>Colluricincla sanghirensis</i>	-	-	X	X	-	X	X	X	-	-	-
<i>Colluricincla umbrina</i>	-	X	X	X	-	-	X	X	-	-	-
<i>Colluricincla woodwardi</i>	-	X	X	X	-	X	X	X	-	-	-
<i>Coloeus dauuricus</i>	X	-	X	X	-	X	-	X	-	-	-
<i>Coloeus monedula</i>	X	X	X	X	-	X	X	X	-	-	-
<i>Coracina abbotti</i>	-	-	-	-	-	X	X	X	-	-	-
<i>Coracina analis</i>	-	-	X	-	-	X	-	X	-	-	-
<i>Coracina atriceps</i>	-	-	-	-	-	X	X	X	-	-	-
<i>Coracina azurea</i>	-	-	X	-	X	X	X	X	-	-	-
<i>Coracina bicolor</i>	-	-	X	-	-	X	X	X	-	-	-
<i>Coracina boyeri</i>	-	-	X	-	-	X	X	X	-	-	-
<i>Coracina caeruleogrisea</i>	-	-	X	-	-	X	X	X	-	-	-
<i>Coracina caesia</i>	-	-	X	-	X	X	X	X	-	-	-
<i>Coracina caledonica</i>	-	-	X	-	X	X	X	X	-	-	-
<i>Coracina ceramensis</i>	-	-	X	-	-	-	-	-	-	-	-
<i>Coracina cinerea</i>	-	-	X	-	X	X	X	X	-	-	-
<i>Coracina coerulescens</i>	-	-	X	-	X	X	X	X	-	-	-
<i>Coracina dispar</i>	-	-	X	-	-	-	-	-	-	-	-
<i>Coracina dohertyi</i>	-	-	X	-	-	X	X	X	-	-	-
<i>Coracina fimbriata</i>	X	X	X	-	-	X	X	X	-	-	-
<i>Coracina graueri</i>	-	-	X	-	-	X	X	X	-	-	-
<i>Coracina holopolia</i>	-	-	X	-	X	X	X	-	-	-	-
<i>Coracina incerta</i>	-	-	X	-	-	X	X	X	-	-	-
<i>Coracina ingens</i>	-	-	X	-	-	-	-	-	-	-	-
<i>Coracina larvata</i>	-	-	-	-	-	X	X	X	-	-	-
<i>Coracina leucopygia</i>	-	-	X	-	-	X	X	X	-	-	-
<i>Coracina lineata</i>	-	X	X	-	X	X	X	X	X	-	-
<i>Coracina longicauda</i>	-	-	X	-	-	X	X	X	-	-	-
<i>Coracina macei</i>	-	-	X	-	X	X	X	X	-	-	-
<i>Coracina maxima</i>	-	-	X	-	-	X	X	X	-	-	-
<i>Coracina mcgregori</i>	-	-	X	-	X	X	X	X	-	-	-
<i>Coracina melanoptera</i>	-	-	X	-	-	X	X	X	-	-	-
<i>Coracina melaschistos</i>	-	X	X	-	X	X	X	X	-	-	-
<i>Coracina mindanensis</i>	-	-	-	-	-	X	X	X	-	-	-
<i>Coracina montana</i>	-	-	X	-	-	X	X	X	-	-	-
<i>Coracina morio</i>	-	-	X	-	-	X	X	X	-	-	-
<i>Coracina newtoni</i>	-	-	X	-	-	X	X	X	-	-	-
<i>Coracina novaehollandiae</i>	-	X	X	-	X	X	X	X	X	X	-

(Continued)

Continued.

Species	COI	Cytochrome b	ND2	ND3	c-MOS	GAPDH	Myo2	ODC	RAG1	RAG2	TGFb2
<i>Coracina ostenta</i>	-	-	X	-	-	X	-	X	-	-	-
<i>Coracina papuensis</i>	-	X	X	-	X	X	X	X	-	-	-
<i>Coracina pectoralis</i>	-	-	X	-	X	X	X	-	-	-	-
<i>Coracina polioptera</i>	-	-	X	-	X	X	X	-	-	-	-
<i>Coracina remota</i>	-	-	X	-	-	X	X	X	-	-	-
<i>Coracina salomonis</i>	-	-	X	-	X	X	X	X	-	-	X
<i>Coracina schistacea</i>	-	-	X	-	-	-	-	-	-	-	-
<i>Coracina striata</i>	-	-	X	-	X	X	X	X	-	-	-
<i>Coracina sula</i>	-	-	X	-	-	-	-	-	-	-	-
<i>Coracina temminckii</i>	-	-	X	-	-	X	X	X	-	-	-
<i>Coracina tenuirostris</i>	-	-	X	-	X	X	X	X	-	-	-
<i>Coracina typica</i>	-	-	X	-	-	X	X	X	-	-	-
<i>Coracina welchmani</i>	-	-	X	-	-	X	X	X	-	-	-
<i>Coracornis raveni</i>	-	-	X	X	-	X	X	X	-	-	-
<i>Corcorax melanorhamphos</i>	-	X	X	X	-	X	X	X	X	X	-
<i>Corvinella corvina</i>	-	-	X	-	-	-	-	-	X	X	-
<i>Corvus albicollis</i>	X	X	X	X	-	-	-	X	-	-	-
<i>Corvus albus</i>	X	X	X	X	-	X	-	X	-	-	-
<i>Corvus bennetti</i>	-	-	X	X	-	X	-	X	-	-	-
<i>Corvus brachyrhynchos</i>	X	X	X	X	X	X	-	X	-	-	-
<i>Corvus capensis</i>	-	-	X	-	-	-	-	-	-	-	-
<i>Corvus caurinus</i>	X	X	X	X	-	X	-	X	-	-	-
<i>Corvus corax</i>	X	X	X	-	-	X	X	X	X	-	X
<i>Corvus cornix</i>	-	-	X	X	-	X	-	X	-	-	-
<i>Corvus corone</i>	X	X	X	-	X	X	X	X	X	X	X
<i>Corvus coronoides</i>	X	X	X	X	-	X	-	X	X	X	-
<i>Corvus crassirostris</i>	-	-	X	X	-	-	-	-	-	-	-
<i>Corvus cryptoleucus</i>	X	X	X	X	-	X	-	X	-	-	-
<i>Corvus culminatus</i>	-	X	X	-	-	X	-	X	X	-	-
<i>Corvus edithae</i>	-	-	X	X	-	-	-	-	-	-	-
<i>Corvus enca</i>	-	-	X	X	-	-	-	-	-	-	-
<i>Corvus florensis</i>	-	-	X	X	-	-	-	-	-	-	-
<i>Corvus frugilegus</i>	X	X	X	X	-	-	X	-	-	-	-
<i>Corvus fuscicapillus</i>	-	-	X	X	-	-	-	-	-	-	-
<i>Corvus hawaiiensis</i>	-	X	X	-	-	-	-	-	-	-	-
<i>Corvus imparatus</i>	-	-	X	-	-	-	-	-	-	-	-
<i>Corvus insularis</i>	-	-	X	X	-	X	-	X	-	-	-
<i>Corvus jamaicensis</i>	-	-	X	X	-	-	-	-	-	-	-
<i>Corvus kubaryi</i>	-	X	X	X	-	-	-	-	-	-	-
<i>Corvus leucognaphalus</i>	-	-	X	X	-	-	-	-	-	-	-
<i>Corvus levaillantii</i>	-	-	X	X	-	-	-	-	-	-	-
<i>Corvus macrorhynchos</i>	X	X	X	X	-	X	-	X	-	-	-
<i>Corvus meeki</i>	-	-	X	X	-	-	-	-	-	-	-
<i>Corvus mellori</i>	-	-	X	X	-	X	-	X	-	-	-
<i>Corvus minutus</i>	-	-	X	X	-	-	-	-	-	-	-
<i>Corvus moneduloides</i>	-	-	X	X	-	-	-	-	-	-	-
<i>Corvus nasicus</i>	-	-	X	X	-	-	-	-	X	-	-
<i>Corvus orru</i>	-	X	X	X	-	X	-	X	X	X	-
<i>Corvus ossifragus</i>	X	-	X	X	-	X	-	X	-	-	-

(Continued)

Continued.

Species	COI	Cytochrome b	ND2	ND3	c-MOS	GAPDH	Myo2	ODC	RAG1	RAG2	TGFb2
<i>Corvus palmarum</i>	-	-	X	X	-	X	-	X	-	-	-
<i>Corvus rhipidurus</i>	-	-	X	X	-	-	-	-	-	-	-
<i>Corvus ruficollis</i>	-	-	X	X	-	-	-	-	-	-	-
<i>Corvus sinaloae</i>	-	-	X	X	-	X	-	X	-	-	-
<i>Corvus splendens</i>	-	-	X	X	-	X	-	X	-	-	-
<i>Corvus tasmanicus</i>	-	-	X	X	-	X	-	X	-	-	-
<i>Corvus torquatus</i>	-	-	X	X	-	-	-	-	-	-	-
<i>Corvus tristis</i>	-	-	X	X	-	-	-	-	-	-	-
<i>Corvus typicus</i>	-	-	X	X	-	-	-	-	-	-	-
<i>Corvus unicolor</i>	-	-	X	X	-	-	-	-	-	-	-
<i>Corvus validus</i>	-	-	X	X	-	-	-	-	-	-	-
<i>Corvus violaceus</i>	-	-	X	X	-	-	-	-	-	-	-
<i>Corvus woodfordi</i>	-	-	X	X	-	X	-	X	-	-	-
<i>Cracticus nigrogularis</i>	X	X	-	-	X	X	X	X	X	-	X
<i>Cracticus quoyi</i>	-	X	X	-	-	X	X	X	X	X	-
<i>Crypsirina temia</i>	-	X	-	-	-	-	-	-	-	-	-
<i>Cyanocitta cristata</i>	X	X	X	-	-	-	X	-	X	X	X
<i>Cyanocitta stelleri</i>	X	X	X	X	-	-	-	-	-	-	-
<i>Cyanocorax affinis</i>	-	X	X	-	-	-	-	-	-	-	X
<i>Cyanocorax beecheii</i>	-	X	X	-	-	-	-	-	-	-	-
<i>Cyanocorax caeruleus</i>	-	X	X	-	-	-	-	-	-	-	-
<i>Cyanocorax cayanus</i>	-	X	X	-	-	-	-	-	-	-	X
<i>Cyanocorax chrysops</i>	X	X	X	-	-	-	X	-	-	-	X
<i>Cyanocorax cristatellus</i>	-	X	X	-	-	-	-	-	-	-	X
<i>Cyanocorax cyanomelas</i>	X	X	X	-	-	-	-	-	-	-	X
<i>Cyanocorax cyanopogon</i>	-	X	X	-	-	-	-	-	-	-	X
<i>Cyanocorax dickeyi</i>	-	X	X	-	-	-	-	-	-	-	X
<i>Cyanocorax heilprini</i>	-	X	X	-	-	-	-	-	-	-	-
<i>Cyanocorax melanocyaneus</i>	-	X	X	-	-	-	-	-	-	-	X
<i>Cyanocorax morio</i>	X	X	X	-	-	-	-	-	-	-	X
<i>Cyanocorax mystacalis</i>	-	X	X	-	-	-	-	-	-	-	X
<i>Cyanocorax sanblasianus</i>	-	X	X	-	-	-	-	-	-	-	-
<i>Cyanocorax violaceus</i>	-	X	X	-	-	-	-	-	-	-	X
<i>Cyanocorax yncas</i>	X	X	X	-	-	-	-	-	-	-	X
<i>Cyanocorax yucatanicus</i>	-	X	X	-	-	-	-	-	-	-	X
<i>Cyanolanius madagascarinus</i>	-	-	X	-	X	X	X	X	-	-	-
<i>Cyanolyca argentigula</i>	-	-	X	-	-	-	-	-	-	-	X
<i>Cyanolyca armillata</i>	-	-	X	-	-	-	-	-	-	-	X
<i>Cyanolyca cucullata</i>	-	-	X	-	-	-	-	-	-	-	X
<i>Cyanolyca mirabilis</i>	-	X	X	-	-	-	-	-	-	-	X
<i>Cyanolyca nana</i>	-	-	X	-	-	-	-	-	-	-	-
<i>Cyanolyca pulchra</i>	-	-	X	-	-	-	-	-	-	-	X
<i>Cyanolyca pumilo</i>	-	-	X	-	-	-	-	-	-	-	X
<i>Cyanolyca turcosa</i>	-	-	X	-	-	-	-	-	-	-	X
<i>Cyanolyca viridicyanus</i>	-	X	X	-	-	-	-	-	-	-	X
<i>Cyanopica cooki</i>	-	X	-	-	-	-	-	-	-	-	-
<i>Cyanopica cyanus</i>	X	X	X	-	-	-	X	-	-	-	-
<i>Cyclarhis gujanensis</i>	X	X	X	X	-	X	X	X	-	-	-
<i>Daphoenositta chrysoptera</i>	-	X	-	-	-	X	X	-	X	X	X
<i>Dendrocitta formosae</i>	-	X	X	-	-	-	-	-	-	-	X

(Continued)

Continued.

Species	COI	Cytochrome b	ND2	ND3	c-MOS	GAPDH	Myo2	ODC	RAG1	RAG2	TGFb2
<i>Dendrocitta frontalis</i>	-	X	X	-	-	X	X	X	X	-	-
<i>Dendrocitta vagabunda</i>	X	X	X	-	-	-	X	-	-	-	-
<i>Dicrurus adsimilis</i>	X	X	X	-	X	-	X	-	X	X	X
<i>Dicrurus aeneus</i>	-	X	X	-	X	-	X	-	-	-	-
<i>Dicrurus aldabranus</i>	-	X	X	-	X	-	X	-	-	-	-
<i>Dicrurus annectans</i>	-	X	X	-	X	-	X	-	-	-	-
<i>Dicrurus atripennis</i>	-	X	X	-	X	-	X	-	-	-	-
<i>Dicrurus balicassius</i>	-	X	X	-	X	-	X	-	-	-	-
<i>Dicrurus bracteatus</i>	-	X	X	-	X	X	X	X	X	-	-
<i>Dicrurus caerulescens</i>	-	X	-	-	-	X	-	-	-	-	-
<i>Dicrurus forficatus</i>	-	X	-	-	X	-	X	-	-	-	-
<i>Dicrurus fuscipennis</i>	-	X	X	-	X	-	X	-	-	-	-
<i>Dicrurus hottentottus</i>	X	X	X	X	X	-	X	-	X	X	X
<i>Dicrurus leucophaeus</i>	-	X	X	-	X	X	X	X	-	-	-
<i>Dicrurus ludwigii</i>	-	X	X	-	X	-	X	-	-	-	-
<i>Dicrurus macrocercus</i>	-	X	X	-	X	-	X	X	-	-	-
<i>Dicrurus megarhynchus</i>	-	X	X	-	X	-	X	-	-	-	-
<i>Dicrurus modestus</i>	-	X	X	-	X	-	X	-	-	-	-
<i>Dicrurus paradiseus</i>	-	X	X	-	X	X	X	-	-	-	-
<i>Dicrurus remifer</i>	-	X	X	-	X	-	X	-	-	-	-
<i>Dicrurus waldenii</i>	-	X	X	-	X	-	X	-	-	-	-
<i>Diphyllodes magnificus</i>	-	X	X	-	-	X	-	X	-	-	-
<i>Diphyllodes respublica</i>	X	X	-	-	-	X	-	X	-	-	-
<i>Drepanornis albertisi</i>	-	X	X	X	-	X	X	X	X	-	-
<i>Drepanornis bruijnii</i>	-	X	-	-	-	X	-	X	-	-	-
<i>Dryoscopus cubla</i>	-	-	X	-	X	X	X	X	X	X	-
<i>Dryoscopus gambensis</i>	-	-	X	X	X	X	X	X	X	-	X
<i>Dyaphorophya castanea</i>	-	-	X	-	X	X	X	X	X	X	X
<i>Dyaphorophya chalybea</i>	-	-	X	-	X	X	X	X	X	-	X
<i>Dyaphorophya concreta</i>	-	-	X	-	-	-	X	-	-	-	-
<i>Dyaphorophya jamesoni</i>	-	-	X	-	X	X	X	X	X	-	X
<i>Dyaphorophya tonsa</i>	-	-	X	-	-	-	X	-	-	-	-
<i>Epimachus fastuosus</i>	-	X	-	-	-	X	-	X	-	-	-
<i>Epimachus meyeri</i>	-	X	-	-	-	X	-	X	-	-	-
<i>Erpornis zantholeuca</i>	-	X	X	X	-	X	X	X	-	-	X
<i>Eulacestoma nigropectus</i>	-	X	X	-	X	X	X	X	X	-	X
<i>Eurocephalus anguitimens</i>	-	-	X	-	-	-	-	-	-	-	-
<i>Euryceros prevostii</i>	-	-	X	-	X	X	-	X	-	-	-
<i>Falcula palliata</i>	-	-	X	-	X	X	-	X	-	-	-
<i>Falcunculus frontatus</i>	-	X	X	-	-	-	X	-	X	X	-
<i>Finschia novaeseelandiae</i>	-	-	X	-	X	-	X	-	X	-	-
<i>Garrulus glandarius</i>	X	X	X	X	-	-	X	X	-	-	-
<i>Garrulus lanceolatus</i>	-	X	X	-	-	X	-	-	-	-	-
<i>Garrulus lidithi</i>	-	X	-	-	-	-	X	-	-	-	-
<i>Grallina bruijnii</i>	-	-	X	X	-	-	-	-	-	-	-
<i>Grallina cyanoleuca</i>	-	X	X	X	-	-	X	-	X	X	-
<i>Gymnorhina tibicen</i>	X	X	X	X	X	X	X	X	X	X	X
<i>Gymnorhinus cyanocephalus</i>	X	X	X	-	-	-	X	-	-	-	X
<i>Hemipus hirundinaceus</i>	-	X	-	-	-	-	-	-	X	X	-

(Continued)

Continued.

Species	COI	Cytochrome b	ND2	ND3	c-MOS	GAPDH	Myo2	ODC	RAG1	RAG2	TGFb2
<i>Hemipus picatus</i>	-	-	X	-	X	X	X	X	X	-	X
<i>Hylophilus poicilotis</i>	-	-	-	-	-	-	-	-	X	X	-
<i>Hypositta corallirostris</i>	-	-	X	-	X	X	X	X	-	-	-
<i>Hypothymis azurea</i>	-	X	X	X	X	X	X	X	-	-	-
<i>Hypothymis coelestis</i>	-	X	X	X	-	X	-	-	-	-	-
<i>Hypothymis helenae</i>	X	X	X	X	-	X	-	-	-	-	-
<i>Hypothymis puella</i>	-	X	X	X	-	X	-	-	-	-	-
<i>Ifrita kowaldi</i>	-	X	X	-	-	-	X	-	X	-	-
<i>Lalage atrovirens</i>	-	-	X	-	-	X	X	X	-	-	-
<i>Lalage leucomela</i>	X	X	X	-	X	X	X	X	X	X	-
<i>Lalage leucopyga</i>	-	-	X	-	-	X	X	X	-	-	-
<i>Lalage leucopygialis</i>	-	-	X	-	-	X	X	X	-	-	-
<i>Lalage maculosa</i>	X	X	X	-	-	-	-	-	-	-	-
<i>Lalage melanoleuca</i>	-	-	X	-	-	X	X	X	-	-	-
<i>Lalage nigra</i>	X	X	X	-	X	X	X	X	-	-	-
<i>Lalage sharpei</i>	-	-	X	-	-	-	-	-	-	-	-
<i>Lalage sueurii</i>	-	-	X	-	-	X	X	X	-	-	-
<i>Lalage tricolor</i>	-	-	X	-	-	X	X	X	-	-	-
<i>Lamprolia victoriae</i>	-	-	-	-	-	X	X	X	-	-	-
<i>Laniarius aethiopicus</i>	-	X	X	-	X	X	X	X	X	-	X
<i>Laniarius atrococcineus</i>	-	-	X	-	-	-	-	-	-	-	-
<i>Laniarius atroflavus</i>	-	-	X	-	-	-	-	-	-	-	-
<i>Laniarius barbarus</i>	-	X	X	-	X	-	X	-	-	-	-
<i>Laniarius bicolor</i>	-	-	X	-	-	-	-	-	-	-	-
<i>Laniarius erlangeri</i>	-	-	X	-	-	-	-	-	-	-	-
<i>Laniarius erythrogaster</i>	-	-	X	-	-	-	-	-	-	-	-
<i>Laniarius ferrugineus</i>	-	-	X	-	-	-	-	-	-	-	-
<i>Laniarius fuelleborni</i>	-	-	X	-	-	-	-	-	-	-	-
<i>Laniarius funebris</i>	-	-	X	-	X	X	X	X	X	-	X
<i>Laniarius leucorhynchus</i>	-	-	-	-	-	-	-	-	-	-	-
<i>Laniarius luehderi</i>	-	X	X	-	X	X	X	X	X	-	X
<i>Laniarius mufumbiri</i>	-	-	X	-	-	-	-	-	-	-	-
<i>Laniarius poensis</i>	-	-	X	-	-	-	-	-	-	-	-
<i>Laniarius ruficeps</i>	-	X	X	-	-	-	-	-	-	-	-
<i>Laniarius sublacteus</i>	-	-	X	-	-	-	-	-	-	-	-
<i>Laniarius turatii</i>	-	X	X	-	-	-	-	-	-	-	-
<i>Lanioturdus torquatus</i>	-	-	X	-	-	-	X	-	X	X	X
<i>Lanius bucephalus</i>	X	X	-	-	-	-	-	-	-	-	-
<i>Lanius cabanisi</i>	-	X	-	-	-	-	-	X	-	-	-
<i>Lanius collaris</i>	-	X	X	-	X	X	X	X	X	-	X
<i>Lanius collurio</i>	X	X	X	X	-	-	X	X	X	-	-
<i>Lanius cristatus</i>	X	X	X	-	X	X	X	-	-	-	-
<i>Lanius dorsalis</i>	-	X	-	-	-	-	-	X	-	-	-
<i>Lanius excubitor</i>	X	X	X	X	-	X	X	X	X	X	X
<i>Lanius excubitoroides</i>	-	X	-	-	-	-	-	X	-	-	-
<i>Lanius isabellinus</i>	X	X	-	-	-	-	X	-	-	-	X
<i>Lanius ludovicianus</i>	X	X	X	X	X	-	X	X	X	-	X
<i>Lanius mackinnoni</i>	-	X	-	-	-	-	-	X	-	-	-
<i>Lanius meridionalis</i>	-	X	-	-	-	-	X	X	-	-	-

(Continued)



Continued.

Species	COI	Cytochrome b	ND2	ND3	c-MOS	GAPDH	Myo2	ODC	RAG1	RAG2	TGFb2
<i>Lanius minor</i>	X	X	-	-	-	-	X	X	-	-	-
<i>Lanius nubicus</i>	-	X	-	-	-	-	X	X	-	-	-
<i>Lanius pallidirostris</i>	-	X	-	-	-	-	-	X	-	-	-
<i>Lanius phoenicuroides</i>	-	X	-	-	-	-	X	X	-	-	-
<i>Lanius schach</i>	X	X	X	-	-	-	-	X	-	-	-
<i>Lanius senator</i>	-	X	X	-	-	-	X	X	-	-	X
<i>Lanius somalicus</i>	-	X	-	-	-	-	-	X	-	-	-
<i>Lanius sphenocercus</i>	-	X	-	-	-	-	-	X	-	-	-
<i>Lanius tephronotus</i>	X	X	-	-	-	-	-	X	-	-	-
<i>Lanius tigrinus</i>	X	X	-	-	-	-	-	-	-	-	-
<i>Lanius vittatus</i>	-	X	X	-	-	X	-	X	X	-	-
<i>Leptopterus chabert</i>	-	-	X	-	X	X	X	X	-	-	-
<i>Lobotos oriolinus</i>	-	-	X	-	-	X	X	X	-	-	-
<i>Lophorina superba</i>	-	X	-	-	-	X	-	X	-	-	-
<i>Lycocorax pyrrhopterus</i>	-	X	-	-	-	X	-	X	-	-	-
<i>Machaerirhynchus flaviventer</i>	-	X	X	-	-	-	-	-	X	-	-
<i>Machaerirhynchus nigripectus</i>	-	-	-	-	X	-	X	X	-	-	X
<i>Malaconotus alius</i>	-	-	X	-	-	-	X	-	-	-	-
<i>Malaconotus blanchoti</i>	-	-	X	-	X	X	X	X	X	-	X
<i>Manucodia ater</i>	-	X	-	-	-	X	X	X	X	X	-
<i>Manucodia chalybatus</i>	-	X	-	-	-	X	-	X	X	X	-
<i>Manucodia comrii</i>	X	X	-	-	-	-	-	-	-	-	-
<i>Manucodia jobiensis</i>	-	X	-	-	-	X	-	X	-	-	-
<i>Mayrornis lessoni</i>	-	-	X	-	-	-	-	-	-	-	-
<i>Mayrornis schistaceus</i>	-	-	X	-	-	-	-	-	-	-	-
<i>Megabyas flammulatus</i>	-	-	X	-	X	X	X	X	X	-	X
<i>Melampitta gigantea</i>	-	X	X	-	-	-	-	-	X	X	-
<i>Melampitta lugubris</i>	-	X	-	-	-	X	X	X	X	X	-
<i>Metabolus rugensis</i>	-	-	X	-	-	-	-	-	-	-	-
<i>Mohoua albicilla</i>	-	-	-	-	X	X	X	-	X	-	-
<i>Mohoua ochrocephala</i>	-	-	X	-	X	-	X	-	X	-	-
<i>Monarcha castaneiventris</i>	-	-	X	X	-	-	X	-	-	-	X
<i>Monarcha cinerascens</i>	-	-	X	-	-	-	X	-	-	-	-
<i>Monarcha frater</i>	-	-	X	-	-	-	X	-	-	-	-
<i>Monarcha godeffroyi</i>	-	-	X	-	-	-	-	-	-	-	-
<i>Monarcha melanopsis</i>	-	X	X	-	-	X	X	X	X	-	-
<i>Monarcha richardsii</i>	-	-	X	-	-	-	-	-	-	-	-
<i>Monarcha rubiensis</i>	-	-	X	-	-	-	-	-	-	-	-
<i>Monarcha takatsukasae</i>	-	-	X	-	-	-	-	-	-	-	-
<i>Myiagra albiventris</i>	-	-	X	X	-	-	-	-	-	-	-
<i>Myiagra alecto</i>	-	X	X	X	-	-	X	-	X	-	-
<i>Myiagra atra</i>	-	-	X	X	-	-	-	-	-	-	-
<i>Myiagra azureocapilla</i>	-	-	X	X	-	-	-	-	-	-	-
<i>Myiagra caledonica</i>	-	X	X	X	-	-	-	-	-	-	-
<i>Myiagra cervinicauda</i>	-	-	X	X	-	-	-	-	-	-	-
<i>Myiagra cyanoleuca</i>	-	X	X	X	-	-	-	-	-	-	-
<i>Myiagra erythrops</i>	-	-	X	X	-	-	-	-	-	-	-
<i>Myiagra ferrocyanea</i>	-	-	X	X	-	-	-	-	-	-	-
<i>Myiagra freycineti</i>	-	-	X	X	-	-	-	-	-	-	-
<i>Myiagra galeata</i>	-	-	X	X	-	-	-	-	-	-	-

(Continued)

Continued.

Species	COI	Cytochrome b	ND2	ND3	c-MOS	GAPDH	Myo2	ODC	RAG1	RAG2	TGFb2
<i>Myiagra hebetior</i>	X	-	X	-	-	-	-	-	-	-	-
<i>Myiagra inquieta</i>	-	-	X	X	-	-	-	-	-	-	-
<i>Myiagra nana</i>	-	-	X	-	-	-	-	-	-	-	-
<i>Myiagra pluto</i>	-	-	X	X	-	-	-	-	-	-	-
<i>Myiagra rubecula</i>	-	-	X	X	-	-	-	-	-	-	-
<i>Myiagra ruficollis</i>	-	-	X	X	-	-	-	-	-	-	-
<i>Myiagra vanikorensis</i>	-	-	X	X	-	-	-	-	-	-	-
<i>Mystacornis crossleyi</i>	-	-	X	-	X	X	X	X	-	-	-
<i>Neolalage banksiana</i>	-	-	X	-	-	-	X	-	-	-	-
<i>Newtonia amphichroa</i>	-	-	X	-	X	X	X	X	-	-	-
<i>Newtonia archboldi</i>	-	-	X	-	X	X	-	X	-	-	-
<i>Newtonia brunneicauda</i>	-	-	X	-	X	X	X	X	-	-	-
<i>Newtonia fanovanae</i>	-	-	X	-	-	-	-	-	-	-	-
<i>Nilaus afer</i>	-	-	X	-	X	X	X	X	X	-	X
<i>Nucifraga caryocatactes</i>	X	X	-	-	-	-	X	-	-	-	-
<i>Nucifraga columbiana</i>	X	X	X	X	-	-	-	-	-	-	-
<i>Nucifraga multipunctata</i>	-	X	X	-	-	X	-	-	-	-	-
<i>Oreocharis arfaki</i>	-	-	-	-	X	X	X	X	-	-	X
<i>Oreoica gutturalis</i>	-	X	X	X	X	X	X	X	X	X	-
<i>Oriolia bernieri</i>	-	-	X	-	X	X	X	X	-	-	-
<i>Oriolus albiloris</i>	-	-	X	X	-	X	-	X	-	-	-
<i>Oriolus auratus</i>	-	-	X	X	-	X	-	X	-	-	-
<i>Oriolus bouroensis</i>	-	-	X	X	-	-	-	-	-	-	-
<i>Oriolus brachyrhynchus</i>	-	-	X	X	-	X	-	X	-	-	-
<i>Oriolus chinensis</i>	-	-	X	X	-	X	-	X	-	-	-
<i>Oriolus chlorocephalus</i>	-	-	X	X	-	X	-	X	-	-	-
<i>Oriolus cruentus</i>	-	-	X	X	-	X	-	X	X	X	-
<i>Oriolus flavocinctus</i>	-	X	X	X	-	X	X	X	X	-	-
<i>Oriolus forsteni</i>	-	-	X	X	-	-	-	-	-	-	-
<i>Oriolus hosii</i>	-	-	X	X	-	-	-	-	-	-	-
<i>Oriolus isabellae</i>	-	-	X	X	-	X	-	X	-	-	-
<i>Oriolus kundoo</i>	-	-	X	-	-	X	-	X	-	-	-
<i>Oriolus larvatus</i>	X	X	X	X	X	X	-	X	X	X	-
<i>Oriolus melanotis</i>	-	-	X	X	-	-	-	-	-	-	-
<i>Oriolus mellianus</i>	-	-	X	-	-	X	-	-	-	-	-
<i>Oriolus monacha</i>	-	-	X	X	-	X	-	X	-	-	-
<i>Oriolus nigripennis</i>	-	-	X	X	-	X	-	X	-	-	-
<i>Oriolus oriolus</i>	X	-	X	X	X	X	X	X	X	-	-
<i>Oriolus percivali</i>	-	-	X	X	-	X	-	X	-	-	-
<i>Oriolus phaeochromus</i>	-	-	X	X	-	-	-	-	-	-	-
<i>Oriolus sagittatus</i>	-	X	X	X	-	X	-	X	-	-	-
<i>Oriolus steerii</i>	-	-	X	X	-	X	-	X	-	-	-
<i>Oriolus szalayi</i>	-	-	X	X	-	X	-	X	-	-	-
<i>Oriolus tenuirostris</i>	-	X	X	-	-	-	-	-	-	-	-
<i>Oriolus traillii</i>	-	-	X	X	-	X	-	X	-	-	-
<i>Oriolus xanthonotus</i>	-	-	X	X	-	X	-	X	X	X	-
<i>Oriolus xanthornus</i>	-	X	X	-	X	X	X	X	-	-	-
<i>Pachycephala albiventris</i>	-	-	X	X	-	X	X	X	-	-	-
<i>Pachycephala arcitorquis</i>	-	-	X	X	-	X	X	X	-	-	-

(Continued)

Continued.

Species	COI	Cytochrome b	ND2	ND3	c-MOS	GAPDH	Myo2	ODC	RAG1	RAG2	TGFb2
<i>Pachycephala aurea</i>	-	-	X	X	-	-	-	-	-	-	-
<i>Pachycephala caledonica</i>	-	-	X	X	-	X	X	X	-	-	-
<i>Pachycephala cinerea</i>	-	-	X	X	-	X	X	X	-	-	-
<i>Pachycephala citreogaster</i>	-	-	X	X	-	X	-	X	-	-	-
<i>Pachycephala flavifrons</i>	-	-	X	X	-	-	-	-	-	-	-
<i>Pachycephala fulvotincta</i>	-	-	X	X	-	-	-	-	-	-	-
<i>Pachycephala graeffii</i>	-	-	X	X	-	-	-	-	-	-	-
<i>Pachycephala griseonota</i>	-	-	X	X	-	-	-	-	-	-	-
<i>Pachycephala hyperythra</i>	-	-	X	X	-	-	X	-	X	X	-
<i>Pachycephala hypoxantha</i>	-	-	X	X	-	X	X	X	-	-	-
<i>Pachycephala implicata</i>	-	-	X	X	-	-	-	-	-	-	-
<i>Pachycephala inornata</i>	-	-	X	X	-	X	X	X	-	-	-
<i>Pachycephala jacquinoti</i>	-	-	X	X	-	-	-	-	-	-	-
<i>Pachycephala lanioides</i>	-	-	X	X	-	X	X	-	-	-	-
<i>Pachycephala lorentzi</i>	-	X	X	X	-	-	X	X	-	-	-
<i>Pachycephala macrorhyncha</i>	-	-	X	X	-	X	-	X	-	-	-
<i>Pachycephala melanura</i>	-	-	X	X	-	X	X	X	-	-	-
<i>Pachycephala mentalis</i>	-	-	X	X	-	-	-	-	-	-	-
<i>Pachycephala modesta</i>	-	-	X	X	-	X	X	X	-	-	-
<i>Pachycephala nudigula</i>	-	-	X	X	-	X	X	X	-	-	-
<i>Pachycephala olivacea</i>	-	X	X	X	-	X	X	X	X	-	-
<i>Pachycephala orioloides</i>	-	-	X	X	-	X	-	X	-	-	-
<i>Pachycephala orpheus</i>	-	-	X	X	-	-	-	-	-	-	-
<i>Pachycephala pectoralis</i>	-	X	X	X	-	X	X	X	X	-	-
<i>Pachycephala phaionota</i>	-	-	X	X	-	-	X	-	-	-	-
<i>Pachycephala philippinensis</i>	-	-	X	X	-	X	X	X	-	-	-
<i>Pachycephala rufiventris</i>	-	-	X	X	-	X	X	X	-	-	-
<i>Pachycephala schlegelii</i>	-	X	X	X	-	X	X	X	-	-	-
<i>Pachycephala simplex</i>	-	X	X	X	-	X	X	X	-	-	-
<i>Pachycephala soror</i>	X	X	X	X	X	X	X	X	X	X	-
<i>Pachycephala sulfuriventer</i>	-	-	X	X	-	X	X	X	-	-	-
<i>Paradigalla brevicauda</i>	-	X	-	-	-	X	-	X	-	-	-
<i>Paradigalla carunculata</i>	-	X	-	-	-	X	-	X	-	-	-
<i>Paradisaea apoda</i>	-	X	-	-	-	X	-	X	-	-	-
<i>Paradisaea decora</i>	-	X	-	-	-	-	-	-	-	-	-
<i>Paradisaea guilielmi</i>	-	X	-	-	-	X	-	X	-	-	-
<i>Paradisaea minor</i>	-	X	-	-	-	X	-	X	-	-	-
<i>Paradisaea raggiana</i>	-	X	X	-	X	X	-	X	X	X	-
<i>Paradisaea rubra</i>	X	X	-	-	-	X	-	X	-	-	-
<i>Paradisaea rudolphi</i>	-	X	-	-	-	X	-	X	-	-	-
<i>Paramythia montium</i>	-	-	-	-	-	-	X	X	X	X	-
<i>Parotia carolae</i>	-	X	-	-	-	X	-	X	-	-	-
<i>Parotia helenae</i>	-	X	-	-	-	X	-	X	-	-	-
<i>Parotia lawesii</i>	-	X	-	-	-	X	-	X	-	-	-
<i>Parotia sefilata</i>	-	X	-	-	-	X	-	X	-	-	-
<i>Parotia wahnesi</i>	-	X	-	-	-	X	-	X	-	-	-
<i>Peltops blainvillii</i>	-	X	X	-	X	X	X	X	X	-	X
<i>Pericrocotus brevirostris</i>	-	-	X	-	-	X	-	X	-	-	-
<i>Pericrocotus cantonensis</i>	-	-	X	-	-	X	X	X	-	-	-

(Continued)

Continued.

Species	COI	Cytochrome b	ND2	ND3	c-MOS	GAPDH	Myo2	ODC	RAG1	RAG2	TGFb2
<i>Pericrocotus cinnamomeus</i>	X	X	X	-	X	X	X	X	-	-	-
<i>Pericrocotus divaricatus</i>	X	-	X	-	X	X	X	X	-	-	-
<i>Pericrocotus erythropygius</i>	-	-	X	-	X	X	X	X	-	-	-
<i>Pericrocotus ethologus</i>	-	-	X	-	X	X	X	X	X	X	-
<i>Pericrocotus flammeus</i>	-	-	X	-	X	X	X	X	-	-	-
<i>Pericrocotus igneus</i>	-	-	X	-	-	X	X	X	-	-	-
<i>Pericrocotus lansbergei</i>	-	-	X	-	-	X	-	X	-	-	-
<i>Pericrocotus miniatus</i>	-	-	X	-	-	X	-	X	-	-	-
<i>Pericrocotus roseus</i>	-	-	X	-	-	X	-	X	-	-	-
<i>Pericrocotus solaris</i>	-	X	X	-	-	X	X	X	-	-	-
<i>Pericrocotus speciosus</i>	-	X	X	-	-	X	-	-	-	-	-
<i>Pericrocotus tegimae</i>	-	-	X	-	-	X	-	X	-	-	-
<i>Perisoreus canadensis</i>	X	X	X	-	-	-	-	-	-	-	X
<i>Perisoreus infaustus</i>	X	X	-	-	-	-	X	-	-	-	-
<i>Perisoreus internigrans</i>	-	X	-	-	-	-	-	-	-	-	-
<i>Philentoma pyrhoptera</i>	-	-	X	-	X	X	X	X	X	X	X
<i>Philentoma velata</i>	-	-	X	-	X	X	X	X	X	-	X
<i>Phonygammus keraudrenii</i>	X	X	-	-	-	X	-	X	-	-	-
<i>Pica hudsonia</i>	X	X	X	X	-	-	-	-	-	-	-
<i>Pica nuttalli</i>	X	-	-	-	-	-	-	-	-	-	-
<i>Pica pica</i>	X	X	X	X	X	X	X	-	X	X	-
<i>Pitohui cristatus</i>	-	X	X	X	-	X	X	X	X	X	-
<i>Pitohui dichrous</i>	-	X	X	X	-	X	X	X	-	-	-
<i>Pitohui ferrugineus</i>	-	X	X	X	-	X	X	X	X	-	-
<i>Pitohui incertus</i>	-	X	X	-	-	-	-	-	-	-	-
<i>Pitohui kirhocephalus</i>	-	X	X	X	-	X	X	-	-	-	-
<i>Pitohui nigrescens</i>	-	X	X	X	-	X	X	X	X	-	-
<i>Pityriasis gymnocephala</i>	-	-	X	-	X	X	X	X	X	X	X
<i>Platylophus galericulatus</i>	-	-	-	-	-	X	X	X	-	-	-
<i>Platysmurus leucopterus</i>	-	X	-	-	-	-	-	-	-	-	-
<i>Platysteira albifrons</i>	-	-	X	-	-	-	-	-	-	-	-
<i>Platysteira cyanea</i>	-	X	X	-	X	X	X	X	X	-	X
<i>Platysteira laticincta</i>	-	-	X	-	-	-	X	-	-	-	-
<i>Platysteira peltata</i>	-	-	X	-	X	X	X	X	X	-	X
<i>Podoces biddulphi</i>	-	X	-	-	-	-	-	-	-	-	-
<i>Podoces hendersoni</i>	X	X	-	-	-	-	X	-	-	-	-
<i>Pomarea iphis</i>	-	X	X	-	-	-	X	-	-	-	-
<i>Pomarea mendozae</i>	-	X	-	-	-	-	-	-	-	-	-
<i>Pomarea whitneyi</i>	-	X	-	-	-	-	-	-	-	-	-
<i>Prionops plumatus</i>	X	X	-	X	-	-	-	-	X	X	-
<i>Prionops retzii</i>	-	-	X	-	X	X	X	X	X	-	X
<i>Prionops scopifrons</i>	-	-	X	-	X	X	X	X	X	-	X
<i>Pseudobias wardi</i>	X	X	X	X	X	X	X	X	X	X	X
<i>Psophodes olivaceus</i>	-	X	X	-	X	X	X	X	X	-	X
<i>Pteridophora alberti</i>	-	X	-	-	-	X	-	X	-	-	-
<i>Pteruthius aenobarbus</i>	-	X	-	-	-	-	-	-	-	-	-
<i>Pteruthius flaviscapis</i>	-	X	X	-	-	X	-	X	X	-	-
<i>Pteruthius melanotis</i>	-	X	X	-	-	X	X	X	X	X	-
<i>Pteruthius rufiventer</i>	-	X	X	-	-	-	-	-	-	-	-

(Continued)

Continued.

Species	COI	Cytochrome b	ND2	ND3	c-MOS	GAPDH	Myo2	ODC	RAG1	RAG2	TGFb2
<i>Pteruthius xanthochlorus</i>	-	X	X	-	-	-	-	-	X	X	-
<i>Ptiloris intercedens</i>	-	X	-	-	-	X	-	X	-	-	-
<i>Ptiloris magnificus</i>	-	X	X	-	X	X	X	X	X	X	X
<i>Ptiloris paradiseus</i>	-	X	-	-	-	X	-	X	-	-	-
<i>Ptiloris victoriae</i>	-	X	-	-	X	X	X	X	-	-	-
<i>Ptilorrhoea caerulea</i>	-	-	-	-	-	-	-	-	X	X	-
<i>Ptilorrhoea leucosticta</i>	-	X	-	-	-	X	X	X	X	-	-
<i>Ptilostomus afer</i>	X	X	-	-	-	-	X	-	-	-	-
<i>Pyrrhonorax graculus</i>	X	X	X	-	-	X	-	X	X	-	-
<i>Pyrrhonorax pyrrhonorax</i>	X	X	X	-	-	X	X	X	X	-	-
<i>Rhagologus leucostigma</i>	-	X	X	-	-	X	X	X	X	-	X
<i>Rhipidura albicollis</i>	-	X	X	X	X	X	X	-	-	-	X
<i>Rhipidura albiscapa</i>	-	X	X	X	-	-	X	-	X	-	X
<i>Rhipidura albolimbata</i>	-	-	X	X	-	-	-	-	-	-	X
<i>Rhipidura atra</i>	-	-	X	X	-	-	-	-	-	-	X
<i>Rhipidura aureola</i>	-	-	X	X	-	-	-	-	-	-	X
<i>Rhipidura brachyrhyncha</i>	-	-	X	X	-	-	-	-	-	-	X
<i>Rhipidura cockerelli</i>	X	X	X	X	-	-	-	-	-	-	X
<i>Rhipidura cyaniceps</i>	-	X	X	X	-	X	X	X	-	-	X
<i>Rhipidura dahli</i>	-	-	X	X	-	-	-	-	-	-	X
<i>Rhipidura dedemi</i>	-	-	X*	-	-	-	-	-	-	-	-
<i>Rhipidura diluta</i>	-	-	X	X	-	-	-	-	-	-	X
<i>Rhipidura dryas</i>	-	-	X	X	-	-	-	-	-	-	X
<i>Rhipidura fuliginosa</i>	-	-	X	X	-	X	X	X	-	-	X
<i>Rhipidura fuscorufa</i>	-	-	X	X	-	-	-	-	-	-	X
<i>Rhipidura hyperythra</i>	-	-	X	X	-	-	-	-	X	X	X
<i>Rhipidura javanica</i>	X	X	X	X	-	-	-	-	-	-	X
<i>Rhipidura leucophrys</i>	X	X	X	X	-	-	-	-	-	-	X
<i>Rhipidura leucothorax</i>	-	-	X	X	-	-	-	-	-	-	X
<i>Rhipidura nigrocinnamomea</i>	-	-	X	X	-	-	-	-	-	-	X
<i>Rhipidura perlata</i>	X	X	X	X	-	-	-	-	-	-	X
<i>Rhipidura phasiana</i>	-	-	X	X	-	-	-	-	-	-	X
<i>Rhipidura rennelliana</i>	X	X	X	X	-	-	-	-	-	-	X
<i>Rhipidura rufidorsa</i>	-	-	X	X	-	-	-	-	-	-	X
<i>Rhipidura rufifrons</i>	X	X	X	X	-	X	X	X	X	-	X
<i>Rhipidura rufiventris</i>	-	-	X	X	-	-	-	-	-	-	X
<i>Rhipidura superciliaris</i>	-	-	X	X	-	-	-	-	-	-	X
<i>Rhipidura superflua</i>	-	-	X*	-	-	-	-	-	-	-	-
<i>Rhipidura tenebrosa</i>	-	-	X	X	-	-	-	-	-	-	X
<i>Rhipidura teysmanni</i>	-	-	X	X	-	-	-	-	-	-	X
<i>Rhipidura threnothorax</i>	X	X	X	X	-	-	-	-	-	-	X
<i>Rhipidura verreauxi</i>	-	-	X	X	-	-	-	-	-	-	X
<i>Rhodophoneus cruentus</i>	-	-	X	-	-	-	X	-	-	-	-
<i>Schetba rufa</i>	X	X	X	X	-	X	X	X	X	-	-
<i>Seleucidis melanoleucus</i>	-	X	-	-	-	X	-	X	-	-	-
<i>Semioptera wallacii</i>	-	X	-	-	-	X	-	X	-	-	-
<i>Sphecotheres vieilloti</i>	-	X	X	X	-	X	X	X	X	X	-
<i>Strepera graculina</i>	-	X	-	-	-	-	-	-	X	X	-
<i>Strepera versicolor</i>	-	-	X	-	X	-	X	-	X	-	X

(Continued)



Continued.

Species	COI	Cytochrome b	ND2	ND3	c-MOS	GAPDH	Myo2	ODC	RAG1	RAG2	TGFb2
<i>Struthidea cinerea</i>	-	X	X	-	-	-	X	-	X	X	-
<i>Symposiachrus axillaris</i>	-	-	X	-	X	-	X	-	X	X	-
<i>Symposiachrus barbatus</i>	-	-	X	-	-	-	X	-	-	-	-
<i>Symposiachrus bimaculatus</i>	-	-	X*	-	-	-	-	-	-	-	-
<i>Symposiachrus everetti</i>	-	-	X	-	-	-	-	-	-	-	-
<i>Symposiachrus guttula</i>	-	-	X	-	-	-	X	-	-	-	-
<i>Symposiachrus infelix</i>	-	-	X	-	-	-	-	-	-	-	-
<i>Symposiachrus leucurus</i>	-	-	X	-	-	-	-	-	-	-	-
<i>Symposiachrus loricatus</i>	-	-	X	-	-	-	-	-	-	-	-
<i>Symposiachrus manadensis</i>	-	-	X	-	-	-	X	-	-	-	-
<i>Symposiachrus menckei</i>	-	-	X*	-	-	-	-	-	-	-	-
<i>Symposiachrus mundus</i>	-	-	X	-	-	-	-	-	-	-	-
<i>Symposiachrus trivirgatus</i>	-	-	X	-	-	-	-	-	-	-	-
<i>Symposiachrus verticalis</i>	-	-	X	-	-	-	-	-	-	-	-
<i>Symposiachrus vidua</i>	-	-	X	X	-	-	-	-	-	-	-
<i>Tchagra australis</i>	-	-	X	-	-	-	X	-	X	-	-
<i>Tchagra senegalus</i>	-	-	X	-	X	X	X	-	X	X	-
<i>Telophorus zeylonus</i>	-	-	X	-	X	X	X	X	X	-	X
<i>Temnurus temnurus</i>	-	X	-	-	-	-	X	-	-	-	-
<i>Tephrodornis pondicerianus</i>	X	-	X	-	X	X	X	X	X	-	X
<i>Tephrodornis virgatus</i>	-	X	X	-	-	X	-	X	X	X	-
<i>Terpsiphone atrocaudata</i>	X	X	X	X	-	X	-	-	-	-	-
<i>Terpsiphone atrochalybeia</i>	-	X	X	X	-	X	-	-	-	-	-
<i>Terpsiphone batesi</i>	-	X	X	X	-	X	-	-	-	-	-
<i>Terpsiphone bedfordi</i>	-	X	X	X	-	X	-	-	-	-	-
<i>Terpsiphone bourbonnensis</i>	-	X	X	X	-	-	-	-	-	-	-
<i>Terpsiphone cinnamomea</i>	X	X	X	X	-	X	-	-	-	-	-
<i>Terpsiphone corvina</i>	-	X*	X*	X*	-	-	-	-	-	-	-
<i>Terpsiphone cyanescens</i>	-	X	X	X	-	X	-	-	-	-	-
<i>Terpsiphone mutata</i>	-	X	X	X	-	-	X	-	-	-	-
<i>Terpsiphone paradisi</i>	X	X	X	-	X	X	X	-	-	-	-
<i>Terpsiphone rufiventer</i>	-	X	X	X	-	X	-	-	-	-	-
<i>Terpsiphone rufocinerea</i>	X	X	X	X	-	X	-	-	-	-	-
<i>Terpsiphone smithii</i>	-	-	X	X	-	X	-	-	-	-	-
<i>Terpsiphone viridis</i>	-	X	X	-	X	X	X	X	-	-	-
<i>Trochocercus cyanomelas</i>	-	X	X	-	-	-	X	-	-	-	-
<i>Trochocercus nitens</i>	-	X	X	-	-	-	X	-	-	-	-
<i>Turnagra capensis</i>	-	X	X	X	-	X	X	X	-	-	-
<i>Tylas eduardi</i>	X	X	X	X	X	X	X	X	X	-	-
<i>Urocissa erythrorhyncha</i>	X	X	X	-	-	X	X	X	X	-	-
<i>Urocissa flavirostris</i>	-	X	X	-	-	-	-	-	-	-	-
<i>Vanga curvirostris</i>	X	X	X	X	X	X	X	X	X	X	-
<i>Vireo altiloquus</i>	X	X	-	-	-	-	-	-	-	-	-
<i>Vireo atricapilla</i>	-	-	X	-	-	-	-	-	-	-	-
<i>Vireo bellii</i>	X	X	-	-	-	-	-	-	-	-	-
<i>Vireo cassinii</i>	X	X	-	-	-	-	-	-	-	-	-
<i>Vireo flavifrons</i>	-	X	-	-	-	-	-	-	-	-	-
<i>Vireo flavoviridis</i>	X	-	-	-	-	X	X	X	-	-	-
<i>Vireo gilvus</i>	X	X	X	X	-	-	-	-	-	-	-

(Continued)

Continued.

Species	COI	Cytochrome b	ND2	ND3	c-MOS	GAPDH	Myo2	ODC	RAG1	RAG2	TGFb2
<i>Vireo griseus</i>	X	X	-	-	-	-	-	-	-	-	-
<i>Vireo huttoni</i>	X	X	-	-	-	-	X	-	X	-	-
<i>Vireo latimeri</i>	X	X	X	-	X	-	-	-	-	-	-
<i>Vireo leucophrys</i>	-	X	X	-	-	-	-	-	-	-	-
<i>Vireo olivaceus</i>	X	X	X	-	-	X	X	X	X	X	-
<i>Vireo philadelphicus</i>	X	X	-	-	X	-	-	-	X	X	-
<i>Vireo plumbeus</i>	-	X	X	-	-	-	-	-	-	-	-
<i>Vireo solitarius</i>	X	X	X	X	-	-	-	-	-	-	-
<i>Vireo vicinior</i>	X	X	-	-	-	-	-	-	-	-	-
<i>Vireolanius leucotis</i>	X	X	X	X	-	X	X	X	-	-	-
<i>Vireolanius melitophrys</i>	X	X	-	X	-	-	-	-	X	-	-
<i>Xenopirostris damii</i>	X	X	X	X	X	X	X	X	-	-	-
<i>Xenopirostris pollenii</i>	-	-	X	-	X	X	X	X	-	-	-
<i>Xenopirostris xenopirostris</i>	X	X	X	-	X	X	X	X	X	X	-
<i>Zavattariornis stresemanni</i>	-	X	-	-	-	-	-	-	-	-	-

X indicates sequences downloaded from Genbank, while X\* indicates sequences generated for the current study.

LITERATURE CITED

Aggerbeck, M., J. Fjeldså, L. Christidis, P. H. Fabre, and K. A. Jönsson. 2014. Resolving deep lineage divergences in the core corvid passerine birds supports a proto-Papuan island origin. *Mol. Phylogenet. Evol.* 70:272–285.

Akaike, H. 1974. A new look at the statistical model identification. *IEEE Trans. Automat. Contr.* 19:716–723

Barker, F. K., G. F. Barrowclough, and J. G. Groth. 2002. A phylogenetic hypothesis for passerine birds: taxonomic and biogeographic implications of an analysis of nuclear DNA sequence data. *Proc. R. Soc. Lond. B* 269:295–308.

Barker, F. K., A. Cibois, P. Schikler, J. Feinstein, and J. Cracraft. 2004. Phylogeny and diversification of the largest avian radiation. *Proc. Natl. Acad. Sci. USA* 105:12145–12149.

Becker, J. J. 1987. Neogene avian localities of North America. Smithsonian Institution Press, Washington, DC.

Carson, H. L., and D. A. Clague. 1995. Geology and biogeography of the Hawaiian Islands. Pp. 14–29 in W.L. Wagner and V. A. Funk, eds. *Hawaiian biogeography, evolution on a hot spot archipelago*. Smithsonian Institution Press, Washington, DC.

Chevallier, L., and N. Vatin-Perignon. 1982. Volcano-structural evolution of Piton des Neiges, Reunion Island, Indian Ocean. *Bull. Volc.* 45:285–298.

Cibois, A., J.-C. Thibault, and E. Pasquet. 2004. Biogeography of eastern Polynesian Monarchs (Pomarea): an endemic genus close to extinction. *Condor* 106:837–851.

Cicero, C., and N. K. Johnson. 2001. Higher-level phylogeny of New World vireos (Aves: Vireonidae) based on sequences of multiple mitochondrial DNA genes. *Mol. Phyl. Evol.* 20:27–40.

Darriba, D., G. L. Taboada, R. Doallo, and D. Posada. 2012. jModelTest2: more models, new heuristics and parallel computing. *Nat. Methods* 9:772.

del Hoyo, J., A. Elliot, and D. A. Christie. 2005–2010. *Handbook of the birds of the world*. Vol. 10–15. Lynx Edicions, Barcelona, Spain.

Drummond, A. J., and A. Rambaut. 2007. BEAST: Bayesian evolutionary analysis by sampling trees. *BMC. Evol. Biol.* 7:214.

Ericson, P. G. P., L. Christidis, A. Cooper, M. Irestedt, J. Jackson, U. S. Johansson, and J. A. Norman. 2002. A Gondwanan origin of passerine birds supported by DNA sequences of the endemic New Zealand wrens. *Proc. R. Soc. Lond. B* 269:235–241.

Ericson, P. G. P., A. L. Jansén, U. S. Johansson, and J. Ekman. 2005. Inter-generic relationships of crows, jays, magpies and allied groups (Aves: Corvidae) based on nucleotide sequence data. *J. Avian Biol.* 36:222–234.

Ericson, P. G. P., S. Klopstein, M. Irestedt, J. M. T. Nguyen, and J. A. Nylander. 2014. Dating the diversification of the major lineages of the Passeriformes (Aves). *BMC Evol. Biol.* 14:8.

Fabre, P. H., M. Irestedt, J. Fjeldså, R. Bristol, J. J. Groombridge, M. Irham, and K. A. Jönsson. 2012. Dynamic colonization exchanges between continents and islands drive diversification in paradise-flycatchers (Terpsiphone, Monarchidae). *J. Biogeogr.* 39:1900–1918.

Fabre, P. H., M. Moltzen, J. Fjeldså, M. Irestedt, J. P. Lessard, and K. A. Jönsson. 2013. Multiple waves of colonization by monarch flycatchers (Myiagra, Monarchidae) across the Indo-Pacific and their implications for coexistence and speciation. *J. Biogeogr.* 41:274–286.

Filardi, C. E., and R. G. Moyle. 2005. Single origin of a pan-Pacific bird group and upstream colonization of Australasia. *Nature* 438:216–219.

Filardi, C. E., and C. E. Smith. 2005. Molecular phylogenetics of monarch flycatchers (genus *Monarcha*) with emphasis on Solomon Island endemics. *Mol. Phyl. Evol.* 37: 776–788.

Fuchs, J., M. Irestedt, J. Fjeldså, A. Couloux, E. Pasquet, and R. C. K. Bowie. 2012. Molecular phylogeny of African bush-shrikes and allies: tracing the biogeographic history of an explosive radiation of corvid birds. *Mol. Phylogenet. Evol.* 64:93–105.

Galtier, N., M. Gouy, and C. Gautier. 1996. SEAVIEW and PHYLO\_WIN: two graphic tools for sequence alignment and molecular phylogeny. *Comput. Appl. Biosci.* 12:543–548.

Gill, F., and D. Donsker. 2010. IOC world bird names (v 2.7). Available at <http://www.worldbirdnames.org>.

Gu, X., J.-X. Fu, and W.-H. Li. 1995. Maximum likelihood estimation of the heterogeneity of substitution rate among nucleotide sites. *Mol. Biol. Evol.* 12:546–557.

Irestedt, M., J. Fuchs, K. A. Jönsson, J. I. Ohlson, E. Pasquet, and P. G. P. Ericson. 2008. The systematic affinity of the enigmatic Lamprolia victoriae (Aves: Passeriformes)—an example of avian dispersal between

- New Guinea and Fiji over Miocene intermittent land bridges? *Mol. Phylogenet. Evol.* 48:1218–1222.
- Irestedt, M., K. A. Jønsson, J. Fjeldså, L. Christidis, and P. G. P. Ericson. 2009. An unexpectedly long history of sexual selection in birds-of-paradise. *BMC Evol. Biol.* 9:235.
- Jønsson, K. A., R. C. K. Bowie, J. A. Norman, L. Christidis, and J. Fjeldså. 2008a. Polyphyletic origin of toxic Pitohui birds suggests widespread occurrence of toxicity in corvid birds. *Biol. Lett.* 4:71–74.
- Jønsson, K. A., M. Irestedt, J. Fuchs, P. G. P. Ericson, L. Christidis, R. C. K. Bowie, J. A. Norman, E. Pasquet, and J. Fjeldså. 2008b. Explosive avian radiations and multi-directional dispersal across Wallacea: evidence from the Campephagidae and other Crown Corvida (Aves). *Mol. Phylogenet. Evol.* 47:221–236.
- Jønsson, K. A., R. C. K. Bowie, R. G. Moyle, L. Christidis, J. A. Norman, B. W. Benz, and J. Fjeldså. 2010a. Historical biogeography of an Indo-Pacific passerine bird family (Pachycephalidae): different colonization patterns in the Indonesian and Melanesian archipelagos. *J. Biogeogr.* 37:245–257.
- Jønsson, K. A., R. C. K. Bowie, R. G. Moyle, M. Irestedt, L. Christidis, J. A. Norman, and J. Fjeldså. 2010b. Phylogeny and biogeography of Oriolidae (Aves: Passeriformes). *Ecography* 33:232–241.
- Jønsson, K. A., R. C. K. Bowie, J. A. A. Nylander, L. Christidis, J. A. Norman, and J. Fjeldså. 2010c. Biogeographical history of cuckoo-shrikes (Aves: Passeriformes): transoceanic colonization of Africa from Australo-Papua. *J. Biogeogr.* 37:1767–1781.
- Jønsson, K. A., M. Irestedt, P. G. P. Ericson, and J. Fjeldså. 2010d. A molecular phylogeny of minivets (Passeriformes: Campephagidae: Pericrocotus): implications for biogeography and convergent plumage evolution. *Zool. Scr.* 39:1–8.
- Jønsson, K. A., P. H. Fabre, R. E. Ricklefs, and J. Fjeldså. 2011. A major global radiation of corvid birds originated in the proto-Papuan archipelago. *Proc. Natl. Acad. Sci. USA* 108:2328–2333.
- Jønsson, K. A., P. H. Fabre, S. A. Fritz, R. S. Etienne, R. E. Ricklefs, T. B. Jørgensen, J. Fjeldså, C. Rahbek, P. G. P. Ericson, F. Woog, et al. 2012a. Ecological and evolutionary determinants for the adaptive radiation of the Madagascan vangas. *Proc. Natl. Acad. Sci. USA* 109:6620–6625.
- Jønsson, K. A., P. H. Fabre, and M. Irestedt. 2012b. Brains, tools, innovation and biogeography in crows and ravens. *BMC Evol. Biol.* 12:72.
- Katoh, K., K. Misawa, K. Kuma, and T. Miyata. 2002. MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. *Nucleic Acids Res.* 30:3059–3066.
- Kennedy, J. D., J. T. Weir, J. M. Hooper, D. T. Tietze, J. Martens and T. D. Price. 2012. Ecological limits on diversification of the Himalayan core Corvoidea. *Evolution* 66:2599–2613.
- Kuhn, T. S., A. Ø. Mooers, and G. H. Thomas. 2011. A simple polytomy resolver for dated phylogenies. *Methods Ecol. Evol.* 2:427–436.
- Linder, H. P., C. R. Hardy, and F. Rutschmann. 2005. Taxon sampling effects in molecular clock dating: an example from the African Restionaceae. *Mol. Phyl. Evol.* 35:569–582.
- Mayr, G. 2005. The Paleogene fossil record of birds in Europe. *Biol. Rev.* 80:515–542.
- McDougall, I., and F. H. Chamalaun. 1969. Isotopic dating and geomagnetic polarity studies on volcanic rocks from Mauritius, Indian Ocean. *Geol. Soc. Am. Bull.* 80:1419–442.
- Miller, M.A., W. Pfeiffer, and T. Schwartz. 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. Pp. 1–8 *in* Proceedings of the gateway computing environments workshop (GCE), New Orleans, LA.
- Moyle, R. G., M. J. Andersen, C. H. Oliveros, F. Steinheimer, and S. Reddy. 2012. Phylogeny and biogeography of the core babblers (Aves: Timaliidae). *Syst. Biol.* 61:631–651.
- Norman, J. A., P. G. P. Ericson, K. A. Jønsson, J. Fjeldså, and L. Christidis. 2009. A multi-gene phylogeny reveals novel relationships for aberrant genera of Australo-Papuan core Corvoidea and polyphyly of the Pachycephalidae and Psophodidae (Aves: Passeriformes). *Mol. Phylogenet. Evol.* 52:488–497.
- Nyári, Á. R. S., B. W. Benz, K. A. Jønsson, J. Fjeldså, and R. G. Moyle. 2009. Phylogenetic relationships of fantails (Aves: Rhipiduridae). *Zool. Scr.* 38:553–561.
- Paradis E., J. Claude, and K. Strimmer. 2004. APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* 20:289–290.
- Pasquet, E., A. Cibois, F. Baillon, and C. Érard. 2002. What are African monarchs (Aves, Passeriformes)? A phylogenetic analysis of mitochondrial genes. *C. R. Biol* 325:107–118.
- Pasquet, E., J.-M. Pons, J. Fuchs, C. Cruaud, and V. Bretagnolle. 2007. Evolutionary history and biogeography of the drongos (Dicruridae), a tropical Old World clade of corvid passerines. *Mol. Phyl. Evol.* 45:158–167.
- R Development Core Team. 2012. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN: 3-900051-07-0. Available at <http://www.R-project.org/>.
- Rambaut, A., and A. J. Drummond. 2007. Tracer version 1.4. Available at <http://beast.bio.ed.ac.uk/Tracer>.
- Reddy, S., A. Driskell, D. L. Rabosky, S. J. Hackett, and T. S. Schulenberg. 2012. Diversification and the adaptive radiation of the vangas of Madagascar. *Proc. R. Soc. B.* 279:2062–2071.
- Stamatakis, A. 2006. RAXML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* 22:2688–2690.
- VanderWerf, E. A., L. C. Young, N. W. Yeung, and D. B. Carlon. 2009. Stepping stone speciation in Hawaii's flycatchers: molecular divergence supports new island endemics within the elepaio. *Conserv. Genet.* 11:1283–1289.
- Worthy, T. H., S. J. Hand, J. M. T. Nguyen, A. J. D. Tennyson, J. P. Worthy, P. Scofield, W. E. Boles, and M. Archer. 2010. Biogeographical and phylogenetic implications of an early Miocene wren (Aves: Passeriformes: Acanthisittidae) from New Zealand. *J. Vert. Paleo.* 30:479–498.

## Appendix B

### CHARACTER DATA HIGHLIGHTING KNOWN AND INFERRED BREEDING SYSTEMS, ISLAND/CONTINENTAL DISTRIBUTION, AND DISPERSAL MODES FOR THE 763 SPECIES OF THE CORE CORVOIDEA

#### Data description

Systematics—Species of the core Corvoidea considered in this study, for which the taxonomy generally follows the IOC version 2.7.

Known breeding system—Breeding systems for all species of core Corvoidea as summarized by Cockburn (2003, 2006). Uniparental denotes species in which only one parent assists in feeding of young. Pair denotes species in which both parents assist in the feeding of young. Cooperative denotes species in which a reasonable amount of broods (>10%) are fed by more than two individuals. Unknown represents those species in which a breeding system cannot be assigned on the basis of field observations alone.

**Inferred breeding system**—In cases where breeding system was unknown, assignment of breeding system was inferred from the closest relatives in the phylogeny. However, for 18 species, breeding systems were unable to be inferred and classified as unknown, due to lack of field data and a large phylogenetic distance from their closest relatives.

**Distribution**—Using a broad definition, we characterized species as being an island endemic if its distribution is restricted to one or several oceanic islands. Islands that are closer to continental landmasses, but separated by deep-water channels were also regarded as islands in this sense. Consequently, several Indo-Pacific islands, including Lubang, Sibutu, Sangihe, Talaud, Kofiau, Numfor, Biak, and the D'Entrecasteaux islands, were treated as islands in the analyses. On the other hand, Yapen, the Louisiade, Raja Ampat, Sula, Sulu, and Togian archipelagos were treated as belonging to continental landmasses as these

islands are separated from continents by fairly shallow seas. Similarly, several large and old landmasses, and/or archipelagos that were connected during the low sea levels of the Pleistocene (Madagascar, the Greater Sundas, Japan, Taiwan, Sri Lanka, the Philippines, New Guinea, and New Zealand) were treated as continental.

**Migration**—Resident species are those in which all populations are sedentary year-round, or only perform occasional, altitudinal, and/or local movements. Migratory species are those that perform regular seasonal movement (generally >1000 km). Species in which some populations are resident while others are migratory were treated as migratory.

**Sources**—For all species, sources generally follow the species and family accounts from the Handbook of the Birds of the World (2005, 2006, 2007, 2008, 2009) and Cockburn (2006), except where otherwise stated.

Species	Known breeding system	Inferred breeding system	Island/ Continental	Migratory status	Sources
<i>Aegithina lafresnaye</i>	Unknown	Pair	Continental	Resident	
<i>Aegithina nigrolutea</i>	Pair	Pair	Continental	Resident	
<i>Aegithina tiphia</i>	Pair	Pair	Continental	Resident	
<i>Aegithina viridissima</i>	Pair	Pair	Continental	Resident	
<i>Aleadryas rufinucha</i>	Unknown	Pair	Continental	Resident	
<i>Androphobus viridis</i>	Unknown	Pair	Continental	Resident	
<i>Aphelocoma californica</i>	Cooperative	Cooperative	Continental	Resident	
<i>Aphelocoma coerulescens</i>	Cooperative	Cooperative	Continental	Resident	
<i>Aphelocoma insularis</i>	Pair	Pair	Island	Resident	
<i>Aphelocoma ultramarina</i>	Cooperative	Cooperative	Continental	Resident	
<i>Aphelocoma unicolor</i>	Cooperative	Cooperative	Continental	Resident	
<i>Arses insularis</i>	Unknown	Pair	Continental	Resident	
<i>Arses kaupi</i>	Pair	Pair	Continental	Resident	
<i>Arses lorealis</i>	Pair	Pair	Continental	Resident	
<i>Arses telescopthalmus</i>	Pair	Pair	Continental	Resident	
<i>Artamella viridis</i>	Pair	Pair	Continental	Resident	
<i>Artamus cinereus</i>	Cooperative	Cooperative	Widespread	Resident	Higgins et al. (2006)
<i>Artamus cyanopterus</i>	Cooperative	Cooperative	Continental	Migratory	Higgins et al. (2006)
<i>Artamus fuscus</i>	Unknown	Cooperative	Continental	Resident	
<i>Artamus insignis</i>	Unknown	Cooperative	Island	Resident	
<i>Artamus leucorhynchus</i>	Cooperative	Cooperative	Widespread	Migratory	Higgins et al. (2006)
<i>Artamus maximus</i>	Cooperative	Cooperative	Continental	Resident	
<i>Artamus mentalis</i>	Cooperative	Cooperative	Island	Resident	
<i>Artamus minor</i>	Cooperative	Cooperative	Continental	Migratory	Higgins et al. (2006)
<i>Artamus monachus</i>	Unknown	Cooperative	Continental	Resident	
<i>Artamus personatus</i>	Pair	Pair	Continental	Migratory	Higgins et al. (2006)
<i>Artamus superciliosus</i>	Pair	Pair	Continental	Migratory	Higgins et al. (2006)
<i>Astrapia mayeri</i>	Uniparental	Uniparental	Continental	Resident	
<i>Astrapia nigra</i>	Unknown	Uniparental	Continental	Resident	
<i>Astrapia rothschildi</i>	Uniparental	Uniparental	Continental	Resident	
<i>Astrapia splendidissima</i>	Uniparental	Uniparental	Continental	Resident	
<i>Astrapia stephaniae</i>	Uniparental	Uniparental	Continental	Resident	
<i>Batis capensis</i>	Cooperative	Cooperative	Continental	Resident	
<i>Batis crypta</i>	Unknown	Unknown	Continental	Resident	
<i>Batis diops</i>	Unknown	Cooperative	Continental	Resident	
<i>Batis fratrum</i>	Cooperative	Cooperative	Continental	Resident	
<i>Batis ituriensis</i>	Unknown	Unknown	Continental	Resident	
<i>Batis margaritae</i>	Unknown	Unknown	Continental	Resident	
<i>Batis minima</i>	Unknown	Unknown	Continental	Resident	
<i>Batis minor</i>	Pair	Pair	Continental	Resident	
<i>Batis minulla</i>	Unknown	Unknown	Continental	Resident	
<i>Batis mixta</i>	Unknown	Unknown	Continental	Resident	
<i>Batis molitor</i>	Cooperative	Cooperative	Continental	Resident	
<i>Batis orientalis</i>	Unknown	Unknown	Continental	Resident	
<i>Batis perkeo</i>	Unknown	Unknown	Continental	Resident	
<i>Batis pririt</i>	Pair	Pair	Continental	Resident	
<i>Batis poensis</i>	Unknown	Pair	Continental	Resident	
<i>Batis senegalensis</i>	Pair	Pair	Continental	Resident	
<i>Batis soror</i>	Cooperative	Cooperative	Continental	Resident	
<i>Bias musicus</i>	Cooperative	Cooperative	Continental	Resident	

(Continued)



Continued.

Species	Known breeding system	Inferred breeding system	Island/ Continental	Migratory status	Sources
<i>Bocagia minuta</i>	Unknown	Pair	Continental	Resident	
<i>Calicalicus madagascariensis</i>	Pair	Pair	Continental	Resident	
<i>Calicalicus rufocarpalis</i>	Unknown	Pair	Continental	Resident	
<i>Calocitta colliei</i>	Cooperative	Cooperative	Continental	Resident	
<i>Calocitta formosa</i>	Cooperative	Cooperative	Continental	Resident	
<i>Campephaga flava</i>	Pair	Pair	Continental	Migratory	
<i>Campephaga petiti</i>	Unknown	Pair	Continental	Resident	
<i>Campephaga phoenicea</i>	Pair	Pair	Continental	Migratory	
<i>Campephaga quiscalina</i>	Pair	Pair	Continental	Resident	
<i>Campochoaera sloetii</i>	Unknown	Cooperative	Continental	Resident	
<i>Carterornis chrysomela</i>	Pair	Pair	Widespread	Resident	
<i>Carterornis leucotis</i>	Pair	Pair	Continental	Resident	
<i>Carterornis pileatus</i>	Unknown	Pair	Island	Resident	
<i>Chaetorhynchus papuensis</i>	Unknown	Pair	Continental	Resident	
<i>Chasiempis sandwichensis</i>	Unknown	Pair	Island	Resident	
<i>Chlorophoneus bocagei</i>	Unknown	Pair	Continental	Resident	
<i>Chlorophoneus dohertyi</i>	Unknown	Pair	Continental	Resident	
<i>Chlorophoneus kupeensis</i>	Unknown	Pair	Continental	Resident	
<i>Chlorophoneus multicolor</i>	Unknown	Pair	Continental	Resident	
<i>Chlorophoneus nigrifrons</i>	Unknown	Pair	Continental	Resident	
<i>Chlorophoneus olivaceus</i>	Pair	Pair	Continental	Resident	
<i>Chlorophoneus quadricolor</i>	Unknown	Pair	Continental	Resident	
<i>Chlorophoneus sulfureopectus</i>	Pair	Pair	Continental	Resident	
<i>Chlorophoneus viridis</i>	Pair	Pair	Continental	Resident	
<i>Cicinnurus regius</i>	Uniparental	Uniparental	Continental	Resident	
<i>Cinclosoma ajax</i>	Unknown	Unknown	Continental	Resident	
<i>Cinclosoma castaneothorax</i>	Cooperative	Cooperative	Continental	Resident	
<i>Cinclosoma castanotum</i>	Cooperative	Cooperative	Continental	Resident	
<i>Cinclosoma cinnamomeum</i>	Cooperative	Cooperative	Continental	Resident	
<i>Cinclosoma punctatum</i>	Pair	Pair	Continental	Resident	
<i>Cissa chinensis</i>	Pair	Pair	Continental	Resident	
<i>Cissa hypoleuca</i>	Unknown	Pair	Continental	Resident	
<i>Cissa thalassina</i>	Unknown	Pair	Continental	Resident	
<i>Clytorhynchus hamlini</i>	Unknown	Pair	Island	Resident	
<i>Clytorhynchus nigrogularis</i>	Unknown	Pair	Island	Resident	
<i>Clytorhynchus pachycephaloides</i>	Pair	Pair	Island	Resident	
<i>Clytorhynchus vitiensis</i>	Unknown	Pair	Island	Resident	
<i>Colluricincla boweri</i>	Pair	Pair	Continental	Resident	
<i>Colluricincla harmonica</i>	Pair	Pair	Continental	Resident	
<i>Colluricincla megarhyncha</i>	Pair	Pair	Widespread	Resident	
<i>Colluricincla sanghirensis</i>	Pair	Pair	Island	Resident	
<i>Colluricincla umbrina</i>	Unknown	Pair	Continental	Resident	
<i>Colluricincla woodwardi</i>	Unknown	Pair	Continental	Resident	
<i>Coloelus dauuricus</i>	Pair	Pair	Continental	Migratory	
<i>Coloelus monedula</i>	Pair	Pair	Continental	Migratory	
<i>Coracina abbotti</i>	Unknown	Pair	Continental	Resident	
<i>Coracina analis</i>	Unknown	Pair	Island	Resident	

(Continued)

Continued.

Species	Known breeding system	Inferred breeding system	Island/ Continental	Migratory status	Sources
<i>Coracina atriceps</i>	Unknown	Pair	Island	Resident	
<i>Coracina azurea</i>	Unknown	Pair	Continental	Resident	
<i>Coracina bicolor</i>	Unknown	Pair	Widespread	Resident	
<i>Coracina boyeri</i>	Pair	Pair	Continental	Resident	
<i>Coracina caeruleogrisea</i>	Unknown	Pair	Continental	Resident	
<i>Coracina caesia</i>	Pair	Pair	Continental	Resident	
<i>Coracina caledonica</i>	Pair	Pair	Island	Resident	
<i>Coracina ceramensis</i>	Unknown	Pair	Island	Resident	
<i>Coracina cinerea</i>	Unknown	Pair	Continental	Resident	
<i>Coracina coerulescens</i>	Unknown	Pair	Continental	Resident	
<i>Coracina cucullata</i>	Unknown	Pair	Island	Resident	
<i>Coracina dispar</i>	Unknown	Pair	Island	Resident	
<i>Coracina dohertyi</i>	Unknown	Pair	Island	Resident	
<i>Coracina fimbriata</i>	Unknown	Pair	Widespread	Resident	
<i>Coracina fortis</i>	Unknown	Pair	Island	Resident	
<i>Coracina graueri</i>	Unknown	Pair	Continental	Resident	
<i>Coracina holopolia</i>	Unknown	Pair	Island	Resident	
<i>Coracina incerta</i>	Unknown	Pair	Continental	Resident	
<i>Coracina ingens</i>	Unknown	Pair	Island	Resident	
<i>Coracina insperata</i>	Unknown	Pair	Island	Resident	
<i>Coracina javensis</i>	Unknown	Pair	Continental	Resident	
<i>Coracina larvata</i>	Unknown	Pair	Continental	Resident	
<i>Coracina leucopygia</i>	Unknown	Pair	Continental	Resident	
<i>Coracina lineata</i>	Pair	Pair	Widespread	Resident	
<i>Coracina longicauda</i>	Pair	Pair	Continental	Resident	
<i>Coracina macei</i>	Unknown	Pair	Widespread	Resident	
<i>Coracina maxima</i>	Cooperative	Cooperative	Continental	Resident	
<i>Coracina mcgregori</i>	Unknown	Pair	Continental	Resident	
<i>Coracina melanoptera</i>	Pair	Pair	Continental	Migratory	
<i>Coracina melas</i>	Unknown	Pair	Continental	Resident	
<i>Coracina melaschistos</i>	Unknown	Pair	Continental	Migratory	Robson (2008) and King and Dickinson (2008)
<i>Coracina mindanensis</i>	Unknown	Pair	Continental	Resident	
<i>Coracina monacha</i>	Unknown	Pair	Island	Resident	
<i>Coracina montana</i>	Unknown	Pair	Continental	Resident	
<i>Coracina morio</i>	Unknown	Pair	Widespread	Resident	
<i>Coracina nesiotis</i>	Unknown	Pair	Island	Resident	
<i>Coracina newtoni</i>	Pair	Pair	Island	Resident	
<i>Coracina novaehollandiae</i>	Pair	Pair	Widespread	Migratory	Higgins et al. (2006)
<i>Coracina ostenta</i>	Pair	Pair	Continental	Resident	
<i>Coracina papuensis</i>	Pair	Pair	Widespread	Resident	Higgins et al. (2006)
<i>Coracina parvula</i>	Unknown	Pair	Island	Resident	
<i>Coracina pectoralis</i>	Pair	Pair	Continental	Resident	
<i>Coracina personata</i>	Unknown	Pair	Island	Resident	

(Continued)

Continued.

Species	Known breeding system	Inferred breeding system	Island/ Continental	Migratory status	Sources
<i>Coracina polioptera</i>	Unknown	Pair	Continental	Resident	
<i>Coracina remota</i>	Unknown	Pair	Island	Resident	Coates and Peckover (2001)
<i>Coracina salomonis</i>	Unknown	Pair	Island	Resident	
<i>Coracina schistacea</i>	Unknown	Pair	Island	Resident	
<i>Coracina schisticeps</i>	Unknown	Pair	Widespread	Resident	
<i>Coracina striata</i>	Pair	Pair	Widespread	Resident	
<i>Coracina sula</i>	Unknown	Pair	Island	Resident	
<i>Coracina temminckii</i>	Unknown	Pair	Continental	Resident	
<i>Coracina tenuirostris</i>	Pair	Pair	Widespread	Migratory	Higgins et al. (2006)
<i>Coracina typica</i>	Pair	Pair	Island	Resident	
<i>Coracina welchmani</i>	Unknown	Pair	Island	Resident	
<i>Coracornis raveni</i>	Unknown	Pair	Continental	Resident	
<i>Corcorax melanorhamphos</i>	Cooperative	Cooperative	Continental	Resident	
<i>Corvinella corvina</i>	Cooperative	Cooperative	Continental	Resident	
<i>Corvus albicollis</i>	Pair	Pair	Continental	Resident	
<i>Corvus albus</i>	Pair	Pair	Widespread	Resident	
<i>Corvus bennetti</i>	Pair	Pair	Continental	Resident	Higgins et al. (2006)
<i>Corvus brachyrhynchos</i>	Cooperative	Cooperative	Continental	Migratory	
<i>Corvus capensis</i>	Pair	Pair	Continental	Resident	
<i>Corvus caurinus</i>	Pair	Pair	Continental	Resident	
<i>Corvus corax</i>	Pair	Pair	Widespread	Resident	
<i>Corvus cornix</i>	Pair	Pair	Widespread	Migratory	
<i>Corvus corone</i>	Cooperative	Cooperative	Widespread	Migratory	
<i>Corvus coronoides</i>	Pair	Pair	Continental	Resident	
<i>Corvus crassirostris</i>	Pair	Pair	Continental	Resident	
<i>Corvus cryptoleucus</i>	Pair	Pair	Continental	Migratory	
<i>Corvus culminatus</i>	Pair	Pair	Continental	Resident	Rasmussen and Anderton (2005) and Ali and Ripley (1972)
<i>Corvus edithae</i>	Pair	Pair	Continental	Resident	
<i>Corvus enca</i>	Unknown	Pair	Widespread	Resident	
<i>Corvus florensis</i>	Unknown	Pair	Island	Resident	
<i>Corvus frugilegus</i>	Pair	Pair	Continental	Migratory	
<i>Corvus fuscicapillus</i>	Unknown	Pair	Continental	Resident	
<i>Corvus hawaiiensis</i>	Pair	Pair	Island	Resident	
<i>Corvus imparatus</i>	Unknown	Cooperative	Continental	Resident	
<i>Corvus insularis</i>	Pair	Pair	Island	Resident	
<i>Corvus jamaicensis</i>	Unknown	Unknown	Island	Resident	
<i>Corvus kubaryi</i>	Pair	Pair	Island	Resident	
<i>Corvus leucognathus</i>	Unknown	Unknown	Island	Resident	

(Continued)

Continued.

Species	Known breeding system	Inferred breeding system	Island/ Continental	Migratory status	Sources
<i>Corvus leuillanti</i>	Pair	Pair	Widespread	Resident	Rasmussen and Anderton (2005) and Ali and Ripley (1972)
<i>Corvus macrorhynchos</i>	Pair	Pair	Widespread	Resident	Rasmussen and Anderton (2005) and Ali and Ripley (1972)
<i>Corvus meeki</i>	Unknown	Pair	Island	Resident	
<i>Corvus mellori</i>	Pair	Pair	Continental	Resident	
<i>Corvus minutus</i>	Pair	Pair	Island	Resident	
<i>Corvus moneduloides</i>	Pair	Pair	Island	Resident	
<i>Corvus nasicus</i>	Unknown	Unknown	Island	Resident	
<i>Corvus orru</i>	Pair	Pair	Widespread	Resident	
<i>Corvus ossifragus</i>	Pair	Pair	Continental	Resident	McGowan (2001)
<i>Corvus palmarum</i>	Pair	Pair	Island	Resident	Latta et al. (2006)
<i>Corvus rhipidurus</i>	Pair	Pair	Continental	Resident	
<i>Corvus ruficollis</i>	Pair	Pair	Widespread	Resident	
<i>Corvus sinaloae</i>	Cooperative	Cooperative	Continental	Resident	
<i>Corvus splendens</i>	Pair	Pair	Widespread	Resident	Rasmussen and Anderton (2005), Ali and Ripley (1972), and Madge and Burn (1999)
<i>Corvus tasmanicus</i>	Pair	Pair	Continental	Resident	
<i>Corvus torquatus</i>	Pair	Pair	Continental	Migratory	
<i>Corvus tristis</i>	Unknown	Pair	Widespread	Resident	
<i>Corvus typicus</i>	Unknown	Pair	Continental	Resident	
<i>Corvus unicolor</i>	Unknown	Pair	Island	Resident	
<i>Corvus validus</i>	Unknown	Pair	Island	Resident	
<i>Corvus violaceus</i>	Unknown	Pair	Island	Resident	
<i>Corvus woodfordi</i>	Unknown	Pair	Island	Resident	
<i>Cracticus argenteus</i>	Unknown	Cooperative	Continental	Resident	
<i>Cracticus cassicus</i>	Cooperative	Cooperative	Widespread	Resident	
<i>Cracticus louisianensis</i>	Unknown	Cooperative	Continental	Resident	
<i>Cracticus mentalis</i>	Unknown	Cooperative	Continental	Resident	
<i>Cracticus nigrogularis</i>	Cooperative	Cooperative	Continental	Resident	
<i>Cracticus quoyi</i>	Pair	Pair	Continental	Resident	
<i>Cracticus torquatus</i>	Cooperative	Cooperative	Continental	Resident	
<i>Crypsirina cucullata</i>	Unknown	Pair	Continental	Resident	
<i>Crypsirina temia</i>	Pair	Pair	Continental	Resident	
<i>Cyanocitta cristata</i>	Pair	Pair	Continental	Migratory	
<i>Cyanocitta stelleri</i>	Pair	Pair	Continental	Resident	
<i>Cyanocorax affinis</i>	Cooperative	Cooperative	Continental	Resident	

(Continued)

Continued.

Species	Known breeding system	Inferred breeding system	Island/ Continental	Migratory status	Sources
<i>Cyanocorax beecheii</i>	Cooperative	Cooperative	Continental	Resident	
<i>Cyanocorax caeruleus</i>	Cooperative	Cooperative	Continental	Resident	
<i>Cyanocorax cayanus</i>	Cooperative	Cooperative	Continental	Resident	
<i>Cyanocorax chrysops</i>	Cooperative	Cooperative	Continental	Resident	
<i>Cyanocorax cristatellus</i>	Cooperative	Cooperative	Continental	Resident	
<i>Cyanocorax cyanomelas</i>	Unknown	Cooperative	Continental	Resident	
<i>Cyanocorax cyanopogon</i>	Unknown	Cooperative	Continental	Resident	
<i>Cyanocorax dickeyi</i>	Cooperative	Cooperative	Continental	Resident	
<i>Cyanocorax heilprini</i>	Unknown	Cooperative	Continental	Resident	
<i>Cyanocorax luxuosus</i>	Pair	Pair	Continental	Resident	
<i>Cyanocorax melanocyaneus</i>	Cooperative	Cooperative	Continental	Resident	
<i>Cyanocorax morio</i>	Cooperative	Cooperative	Continental	Resident	
<i>Cyanocorax mystacalis</i>	Unknown	Cooperative	Continental	Resident	
<i>Cyanocorax sanblasianus</i>	Cooperative	Cooperative	Continental	Resident	
<i>Cyanocorax violaceus</i>	Cooperative	Cooperative	Continental	Resident	
<i>Cyanocorax yncas</i>	Cooperative	Cooperative	Continental	Resident	
<i>Cyanocorax yucatanicus</i>	Cooperative	Cooperative	Continental	Resident	
<i>Cyanolanius madagascarinus</i>	Unknown	Pair	Widespread	Resident	
<i>Cyanolyca argentigula</i>	Unknown	Pair	Continental	Resident	
<i>Cyanolyca armillata</i>	Unknown	Cooperative	Continental	Resident	
<i>Cyanolyca cucullata</i>	Unknown	Cooperative	Continental	Resident	
<i>Cyanolyca mirabilis</i>	Unknown	Pair	Continental	Resident	
<i>Cyanolyca nana</i>	Pair	Pair	Continental	Resident	
<i>Cyanolyca pulchra</i>	Unknown	Cooperative	Continental	Resident	
<i>Cyanolyca pumilo</i>	Unknown	Pair	Continental	Resident	
<i>Cyanolyca turcosa</i>	Unknown	Cooperative	Continental	Resident	
<i>Cyanolyca viridicyanus</i>	Cooperative	Cooperative	Continental	Resident	
<i>Cyanopica cooki</i>	Cooperative	Cooperative	Continental	Resident	
<i>Cyanopica cyanus</i>	Cooperative	Cooperative	Continental	Resident	
<i>Cyclarhis gujanensis</i>	Pair	Pair	Continental	Resident	
<i>Cyclarhis nigrirostris</i>	Unknown	Pair	Continental	Resident	
<i>Daphoenositta chrysoptera</i>	Cooperative	Cooperative	Continental	Resident	
<i>Daphoenositta miranda</i>	Cooperative	Cooperative	Continental	Resident	
<i>Daphoenositta papuensis</i>	Cooperative	Cooperative	Continental	Resident	
<i>Dendrocitta bayleyi</i>	Pair	Pair	Island	Resident	
<i>Dendrocitta cinerascens</i>	Unknown	Pair	Continental	Resident	
<i>Dendrocitta formosae</i>	Pair	Pair	Continental	Resident	
<i>Dendrocitta frontalis</i>	Pair	Pair	Continental	Resident	
<i>Dendrocitta leucogastra</i>	Pair	Pair	Continental	Resident	
<i>Dendrocitta occipitalis</i>	Unknown	Pair	Continental	Resident	
<i>Dendrocitta vagabunda</i>	Pair	Pair	Continental	Resident	
<i>Dicrurus adsimilis</i>	Pair	Pair	Continental	Resident	
<i>Dicrurus aeneus</i>	Pair	Pair	Continental	Resident	
<i>Dicrurus aldabranus</i>	Unknown	Pair	Island	Resident	
<i>Dicrurus andamanensis</i>	Pair	Pair	Island	Resident	

(Continued)



Continued.

Species	Known breeding system	Inferred breeding system	Island/ Continental	Migratory status	Sources
<i>Dicrurus annectans</i>	Pair	Pair	Continental	Migratory	Rasmussen and Anderton (2005), Ali and Ripley (1972)
<i>Dicrurus atripennis</i>	Unknown	Pair	Continental	Resident	
<i>Dicrurus balicassius</i>	Unknown	Pair	Widespread	Resident	
<i>Dicrurus bracteatus</i>	Pair	Pair	Widespread	Migratory	
<i>Dicrurus caerulescens</i>	Pair	Pair	Continental	Resident	
<i>Dicrurus forficatus</i>	Pair	Pair	Widespread	Resident	
<i>Dicrurus fuscipennis</i>	Pair	Pair	Island	Resident	
<i>Dicrurus hottentottus</i>	Pair	Pair	Widespread	Migratory	
<i>Dicrurus leucophaeus</i>	Unknown	Pair	Widespread	Migratory	
<i>Dicrurus ludwigii</i>	Unknown	Pair	Continental	Resident	
<i>Dicrurus macrocercus</i>	Cooperative	Cooperative	Continental	Migratory	
<i>Dicrurus megarhynchus</i>	Unknown	Pair	Island	Resident	
<i>Dicrurus modestus</i>	Unknown	Pair	Widespread	Resident	
<i>Dicrurus montanus</i>	Unknown	Pair	Continental	Resident	
<i>Dicrurus paradiseus</i>	Pair	Pair	Widespread	Resident	
<i>Dicrurus remifer</i>	Pair	Pair	Continental	Resident	
<i>Dicrurus waldenii</i>	Unknown	Pair	Island	Resident	
<i>Diphylloides magnificus</i>	Uniparental	Uniparental	Continental	Resident	
<i>Diphylloides respublica</i>	Uniparental	Uniparental	Continental	Resident	
<i>Drepanornis albertisi</i>	Uniparental	Uniparental	Continental	Resident	
<i>Drepanornis bruijnii</i>	Uniparental	Uniparental	Continental	Resident	
<i>Dryoscopus angolensis</i>	Unknown	Pair	Continental	Resident	
<i>Dryoscopus cubla</i>	Pair	Pair	Continental	Resident	
<i>Dryoscopus gambensis</i>	Unknown	Pair	Continental	Resident	
<i>Dryoscopus pringlii</i>	Unknown	Pair	Continental	Resident	
<i>Dryoscopus sabinii</i>	Unknown	Pair	Continental	Resident	
<i>Dryoscopus senegalensis</i>	Pair	Pair	Continental	Resident	
<i>Dyaphorophya blissetti</i>	Cooperative	Cooperative	Continental	Resident	
<i>Dyaphorophya castanea</i>	Cooperative	Cooperative	Continental	Resident	
<i>Dyaphorophya chalybea</i>	Cooperative	Cooperative	Continental	Resident	
<i>Dyaphorophya concreta</i>	Unknown	Cooperative	Continental	Resident	
<i>Dyaphorophya jamesoni</i>	Unknown	Cooperative	Continental	Resident	
<i>Dyaphorophya tonsa</i>	Cooperative	Cooperative	Continental	Resident	
<i>Epimachus fastuosus</i>	Uniparental	Uniparental	Continental	Resident	
<i>Epimachus meyeri</i>	Uniparental	Uniparental	Continental	Resident	
<i>Erpornis zantholeuca</i>	Cooperative	Cooperative	Continental	Resident	
<i>Eulacestoma nigropectus</i>	Unknown	Unknown	Continental	Resident	
<i>Eurocephalus anguitimens</i>	Cooperative	Cooperative	Continental	Resident	
<i>Eurocephalus rueppelli</i>	Cooperative	Cooperative	Continental	Resident	
<i>Euryceros prevostii</i>	Pair	Pair	Continental	Resident	
<i>Eutrichomyias rowleyi</i>	Unknown	Pair	Island	Resident	
<i>Falculea palliata</i>	Unknown	Pair	Continental	Resident	

(Continued)

Continued.

Species	Known breeding system	Inferred breeding system	Island/ Continental	Migratory status	Sources
<i>Falcunculus frontatus</i>	Cooperative	Cooperative	Continental	Resident	
<i>Finschia novaeseelandiae</i>	Cooperative	Cooperative	Continental	Resident	
<i>Garrulus glandarius</i>	Pair	Pair	Continental	Resident	
<i>Garrulus lanceolatus</i>	Pair	Pair	Continental	Resident	
<i>Garrulus lidhi</i>	Cooperative	Cooperative	Island	Resident	
<i>Grallina bruijni</i>	Pair	Pair	Continental	Resident	
<i>Grallina cyanoleuca</i>	Pair	Pair	Continental	Resident	Higgins et al. (2006)
<i>Gymnorhina tibicen</i>	Cooperative	Cooperative	Continental	Resident	
<i>Gymnorhinus cyanocephalus</i>	Cooperative	Cooperative	Continental	Resident	
<i>Hemipus hirundinaceus</i>	Pair	Pair	Widespread	Resident	
<i>Hemipus picatus</i>	Pair	Pair	Continental	Resident	
<i>Hylophilus aurantifrons</i>	Pair	Pair	Continental	Resident	
<i>Hylophilus brunneiceps</i>	Unknown	Pair	Continental	Resident	
<i>Hylophilus decurtatus</i>	Pair	Pair	Continental	Resident	
<i>Hylophilus flavipes</i>	Pair	Pair	Continental	Resident	
<i>Hylophilus hypoxanthus</i>	Unknown	Pair	Continental	Resident	
<i>Hylophilus muscicapinus</i>	Unknown	Pair	Continental	Resident	
<i>Hylophilus ochraceiceps</i>	Pair	Pair	Continental	Resident	
<i>Hylophilus olivaceus</i>	Unknown	Pair	Continental	Resident	
<i>Hylophilus pectoralis</i>	Unknown	Pair	Continental	Resident	
<i>Hylophilus poicilotis</i>	Pair	Pair	Continental	Resident	
<i>Hylophilus sclateri</i>	Unknown	Pair	Continental	Resident	
<i>Hylophilus semibrunneus</i>	Unknown	Pair	Continental	Resident	
<i>Hylophilus semicinereus</i>	Unknown	Pair	Continental	Resident	
<i>Hylophilus thoracicus</i>	Unknown	Pair	Continental	Resident	
<i>Hypositta corallirostris</i>	Unknown	Pair	Continental	Resident	
<i>Hypothymis azurea</i>	Pair	Pair	Widespread	Resident	
<i>Hypothymis coelestis</i>	Unknown	Pair	Continental	Resident	
<i>Hypothymis helenae</i>	Unknown	Pair	Continental	Resident	
<i>Hypothymis puella</i>	Unknown	Pair	Continental	Resident	
<i>Ifrita kowaldi</i>	Unknown	Unknown	Continental	Resident	
<i>Lalage atrovirens</i>	Unknown	Pair	Widespread	Resident	
<i>Lalage aurea</i>	Unknown	Pair	Island	Resident	
<i>Lalage leucomela</i>	Pair	Pair	Widespread	Resident	Higgins et al. (2006)
<i>Lalage leucopyga</i>	Unknown	Pair	Island	Resident	
<i>Lalage leucopygialis</i>	Unknown	Pair	Continental	Resident	
<i>Lalage maculosa</i>	Unknown	Pair	Island	Resident	
<i>Lalage melanoleuca</i>	Unknown	Pair	Continental	Resident	
<i>Lalage moesta</i>	Unknown	Pair	Island	Resident	
<i>Lalage nigra</i>	Pair	Pair	Widespread	Resident	
<i>Lalage sharpei</i>	Unknown	Pair	Island	Resident	
<i>Lalage sueurii</i>	Unknown	Pair	Widespread	Resident	
<i>Lalage tricolor</i>	Pair	Pair	Continental	Migratory	Higgins et al. (2006)
<i>Lamprolia victoriae</i>	Pair	Pair	Island	Resident	
<i>Laniarius aethiopicus</i>	Pair	Pair	Continental	Resident	
<i>Laniarius amboimensis</i>	Unknown	Pair	Continental	Resident	
<i>Laniarius atrococcineus</i>	Pair	Pair	Continental	Resident	
<i>Laniarius atroflavus</i>	Pair	Pair	Continental	Resident	

(Continued)

Continued.

Species	Known breeding system	Inferred breeding system	Island/ Continental	Migratory status	Sources
<i>Laniarius barbarus</i>	Unknown	Pair	Continental	Resident	
<i>Laniarius bicolor</i>	Pair	Pair	Continental	Resident	
<i>Laniarius brauni</i>	Unknown	Pair	Continental	Resident	
<i>Laniarius erlangeri</i>	Unknown	Pair	Continental	Resident	
<i>Laniarius erythrogaster</i>	Unknown	Pair	Continental	Resident	
<i>Laniarius ferrugineus</i>	Pair	Pair	Continental	Resident	
<i>Laniarius fuelleborni</i>	Unknown	Pair	Continental	Resident	
<i>Laniarius funebris</i>	Pair	Pair	Continental	Resident	
<i>Laniarius leucorhynchus</i>	Unknown	Pair	Continental	Resident	
<i>Laniarius luehderi</i>	Pair	Pair	Continental	Resident	
<i>Laniarius mufumbiri</i>	Unknown	Pair	Continental	Resident	
<i>Laniarius poensis</i>	Unknown	Pair	Continental	Resident	
<i>Laniarius ruficeps</i>	Unknown	Pair	Continental	Resident	
<i>Laniarius sublacteus</i>	Unknown	Pair	Continental	Resident	
<i>Laniarius turatii</i>	Unknown	Pair	Continental	Resident	
<i>Lanioturdus torquatus</i>	Pair	Pair	Continental	Resident	
<i>Lanius bucephalus</i>	Pair	Pair	Widespread	Migratory	
<i>Lanius cabanisi</i>	Cooperative	Cooperative	Continental	Resident	
<i>Lanius collaris</i>	Pair	Pair	Continental	Resident	
<i>Lanius collurio</i>	Pair	Pair	Continental	Migratory	
<i>Lanius collurioides</i>	Pair	Pair	Continental	Migratory	
<i>Lanius cristatus</i>	Pair	Pair	Continental	Migratory	
<i>Lanius dorsalis</i>	Unknown	Pair	Continental	Resident	
<i>Lanius excubitor</i>	Pair	Pair	Continental	Migratory	
<i>Lanius excubitoroides</i>	Cooperative	Cooperative	Continental	Resident	
<i>Lanius gubernator</i>	Unknown	Pair	Continental	Resident	
<i>Lanius isabellinus</i>	Pair	Pair	Continental	Migratory	
<i>Lanius ludovicianus</i>	Pair	Pair	Widespread	Migratory	Yosef (1996)
<i>Lanius mackinnoni</i>	Unknown	Pair	Continental	Resident	
<i>Lanius meridionalis</i>	Pair	Pair	Widespread	Resident	Harris and Franklin (2000), Rasmussen and Anderton (2005), and Ali and Ripley (1972)
<i>Lanius minor</i>	Pair	Pair	Continental	Migratory	
<i>Lanius newtoni</i>	Unknown	Pair	Island	Resident	
<i>Lanius nubicus</i>	Pair	Pair	Continental	Migratory	
<i>Lanius pallidirostris</i>	Pair	Pair	Continental	Migratory	Harris and Franklin (2000), Rasmussen and Anderton (2005), and Ali and Ripley (1972)
<i>Lanius phoenicuroides</i>	Pair	Pair	Continental	Migratory	
<i>Lanius schach</i>	Pair	Pair	Widespread	Migratory	
<i>Lanius senator</i>	Pair	Pair	Continental	Migratory	
<i>Lanius somalicus</i>	Unknown	Pair	Continental	Resident	

(Continued)

Continued.

Species	Known breeding system	Inferred breeding system	Island/ Continental	Migratory status	Sources
<i>Lanius souzae</i>	Unknown	Pair	Continental	Resident	Dowsett-Lemaire and Dowsett (2006)
<i>Lanius sphenocercus</i>	Pair	Pair	Continental	Migratory	
<i>Lanius tephronotus</i>	Pair	Pair	Continental	Migratory	
<i>Lanius tigrinus</i>	Pair	Pair	Continental	Migratory	
<i>Lanius validirostris</i>	Unknown	Pair	Continental	Resident	
<i>Lanius vittatus</i>	Pair	Pair	Continental	Migratory	
<i>Leptopterus chabert</i>	Cooperative	Cooperative	Continental	Resident	
<i>Lobotos lobatus</i>	Unknown	Pair	Continental	Resident	
<i>Lobotos oriolinus</i>	Unknown	Pair	Continental	Resident	
<i>Lophorina superba</i>	Uniparental	Uniparental	Continental	Resident	
<i>Lycocorax pyrrhopterus</i>	Unknown	Pair	Island	Resident	
<i>Machaerirhynchus flaviventer</i>	Pair	Pair	Continental	Resident	
<i>Machaerirhynchus nigripectus</i>	Unknown	Pair	Continental	Resident	
<i>Malaconotus alius</i>	Unknown	Pair	Continental	Resident	
<i>Malaconotus blanchoti</i>	Pair	Pair	Continental	Resident	
<i>Malaconotus cruentus</i>	Pair	Pair	Continental	Resident	
<i>Malaconotus gladiator</i>	Unknown	Pair	Continental	Resident	
<i>Malaconotus lagdeni</i>	Pair	Pair	Continental	Resident	
<i>Malaconotus monteiri</i>	Unknown	Pair	Continental	Resident	
<i>Manucodia ater</i>	Pair	Pair	Continental	Resident	
<i>Manucodia chalybatus</i>	Pair	Pair	Continental	Resident	
<i>Manucodia comrii</i>	Unknown	Pair	Island	Resident	
<i>Manucodia jobiensis</i>	Unknown	Pair	Continental	Resident	
<i>Mayrornis lessoni</i>	Unknown	Pair	Island	Resident	
<i>Mayrornis schistaceus</i>	Unknown	Pair	Island	Resident	
<i>Mayrornis versicolor</i>	Unknown	Pair	Island	Resident	
<i>Megabyas flammulatus</i>	Cooperative	Cooperative	Continental	Resident	
<i>Melampitta gigantea</i>	Unknown	Pair	Continental	Resident	
<i>Melampitta lugubris</i>	Pair	Pair	Continental	Resident	
<i>Metabolus rugensis</i>	Unknown	Pair	Island	Resident	
<i>Mohoua albicilla</i>	Cooperative	Cooperative	Continental	Resident	
<i>Mohoua ochrocephala</i>	Cooperative	Cooperative	Continental	Resident	
<i>Monarcha barbatus</i>	Unknown	Pair	Island	Resident	
<i>Monarcha castaneiventris</i>	Unknown	Pair	Island	Resident	
<i>Monarcha cinerascens</i>	Unknown	Pair	Widespread	Resident	
<i>Monarcha erythrostickus</i>	Unknown	Pair	Island	Resident	
<i>Monarcha frater</i>	Pair	Pair	Continental	Migratory	
<i>Monarcha godeffroyi</i>	Unknown	Pair	Island	Resident	
<i>Monarcha melanopsis</i>	Pair	Pair	Continental	Migratory	Higgins et al. (2006)
<i>Monarcha richardsii</i>	Unknown	Pair	Island	Resident	
<i>Monarcha rubiensis</i>	Unknown	Pair	Widespread	Resident	
<i>Monarcha takatsukasae</i>	Unknown	Pair	Island	Resident	
<i>Myiagra albiventris</i>	Unknown	Pair	Island	Resident	
<i>Myiagra alecto</i>	Pair	Pair	Widespread	Resident	
<i>Myiagra atra</i>	Unknown	Pair	Island	Resident	
<i>Myiagra azureocapilla</i>	Unknown	Pair	Island	Resident	
<i>Myiagra caledonica</i>	Pair	Pair	Island	Resident	

(Continued)

Continued.

Species	Known breeding system	Inferred breeding system	Island/ Continental	Migratory status	Sources
<i>Myiagra cervinicauda</i>	Unknown	Pair	Island	Resident	
<i>Myiagra cyanoleuca</i>	Pair	Pair	Continental	Migratory	Higgins et al. (2006)
<i>Myiagra erythroptera</i>	Unknown	Pair	Island	Resident	
<i>Myiagra ferrocyanea</i>	Unknown	Pair	Island	Resident	
<i>Myiagra freycineti</i>	Unknown	Pair	Island	Resident	
<i>Myiagra galeata</i>	Unknown	Pair	Island	Resident	
<i>Myiagra hebetior</i>	Unknown	Pair	Island	Resident	
<i>Myiagra inquieta</i>	Pair	Pair	Continental	Resident	
<i>Myiagra nana</i>	Unknown	Pair	Continental	Resident	
<i>Myiagra oceanica</i>	Unknown	Pair	Island	Resident	
<i>Myiagra pluto</i>	Unknown	Pair	Island	Resident	
<i>Myiagra rubecula</i>	Pair	Pair	Widespread	Migratory	
<i>Myiagra ruficollis</i>	Pair	Pair	Widespread	Resident	
<i>Myiagra vanikorensis</i>	Unknown	Pair	Island	Resident	
<i>Mystacornis crossleyi</i>	Pair	Pair	Continental	Resident	
<i>Neolalage banksiana</i>	Unknown	Pair	Island	Resident	
<i>Newtonia amphichroa</i>	Unknown	Cooperative	Continental	Resident	
<i>Newtonia archboldi</i>	Unknown	Cooperative	Continental	Resident	
<i>Newtonia brunneicauda</i>	Unknown	Cooperative	Continental	Resident	
<i>Newtonia fanovanae</i>	Unknown	Cooperative	Continental	Resident	
<i>Nilaus afer</i>	Pair	Pair	Continental	Resident	
<i>Nucifraga caryocatactes</i>	Pair	Pair	Widespread	Resident	
<i>Nucifraga columbiana</i>	Pair	Pair	Continental	Resident	
<i>Nucifraga multipunctata</i>	Pair	Pair	Continental	Resident	
<i>Oreocharis arfaki</i>	Unknown	Pair	Continental	Resident	
<i>Oreoica gutturalis</i>	Pair	Pair	Continental	Resident	
<i>Oriolia bernieri</i>	Cooperative	Cooperative	Continental	Resident	
<i>Oriolus albiloris</i>	Unknown	Pair	Continental	Resident	
<i>Oriolus auratus</i>	Pair	Pair	Continental	Migratory	Fry et al. (2000)
<i>Oriolus bouroensis</i>	Unknown	Pair	Island	Resident	
<i>Oriolus brachyrhynchus</i>	Pair	Pair	Continental	Resident	
<i>Oriolus chinensis</i>	Pair	Pair	Widespread	Migratory	
<i>Oriolus chlorocephalus</i>	Unknown	Pair	Continental	Resident	
<i>Oriolus crassirostris</i>	Unknown	Pair	Island	Resident	
<i>Oriolus cruentus</i>	Unknown	Pair	Continental	Resident	
<i>Oriolus flavocinctus</i>	Pair	Pair	Widespread	Resident	
<i>Oriolus forsteni</i>	Unknown	Pair	Island	Resident	
<i>Oriolus hosii</i>	Unknown	Pair	Continental	Resident	
<i>Oriolus isabellae</i>	Unknown	Pair	Continental	Resident	
<i>Oriolus kundoo</i>	Unknown	Pair	Continental	Migratory	Rasmussen and Anderton (2005) and Ali and Ripley (1972)
<i>Oriolus larvatus</i>	Pair	Pair	Continental	Resident	
<i>Oriolus melanotis</i>	Unknown	Pair	Island	Resident	
<i>Oriolus mellianus</i>	Unknown	Pair	Continental	Migratory	
<i>Oriolus monacha</i>	Unknown	Pair	Continental	Resident	
<i>Oriolus nigripennis</i>	Unknown	Pair	Continental	Resident	

(Continued)



Continued.

Species	Known breeding system	Inferred breeding system	Island/ Continental	Migratory status	Sources
<i>Oriolus oriolus</i>	Pair	Pair	Continental	Migratory	
<i>Oriolus percivali</i>	Unknown	Pair	Continental	Resident	
<i>Oriolus phaeochromus</i>	Unknown	Pair	Island	Resident	
<i>Oriolus sagittatus</i>	Pair	Pair	Continental	Migratory	
<i>Oriolus steerii</i>	Unknown	Pair	Continental	Resident	
<i>Oriolus szalayi</i>	Pair	Pair	Continental	Resident	
<i>Oriolus tenuirostris</i>	Unknown	Pair	Continental	Migratory	
<i>Oriolus traillii</i>	Pair	Pair	Continental	Migratory	
<i>Oriolus xanthonotus</i>	Unknown	Pair	Widespread	Resident	
<i>Oriolus xanthornus</i>	Pair	Pair	Widespread	Migratory	
<i>Pachycephala albiventris</i>	Unknown	Pair	Continental	Resident	
<i>Pachycephala arctitorquis</i>	Unknown	Pair	Island	Resident	
<i>Pachycephala aurea</i>	Unknown	Pair	Continental	Resident	
<i>Pachycephala caledonica</i>	Pair	Pair	Island	Resident	
<i>Pachycephala citreogaster</i>	Pair	Pair	Island	Resident	
<i>Pachycephala flavifrons</i>	Unknown	Pair	Island	Resident	
<i>Pachycephala fulvotincta</i>	Pair	Pair	Widespread	Resident	
<i>Pachycephala graeffii</i>	Pair	Pair	Island	Resident	
<i>Pachycephala griseonota</i>	Unknown	Pair	Island	Resident	
<i>Pachycephala grisola</i>	Unknown	Pair	Widespread	Resident	
<i>Pachycephala homeyeri</i>	Unknown	Pair	Widespread	Resident	
<i>Pachycephala hyperythra</i>	Unknown	Pair	Continental	Resident	
<i>Pachycephala hypoxantha</i>	Unknown	Pair	Continental	Resident	
<i>Pachycephala implicata</i>	Unknown	Pair	Island	Resident	
<i>Pachycephala inornata</i>	Pair	Pair	Continental	Resident	
<i>Pachycephala jacquinoti</i>	Unknown	Pair	Island	Resident	
<i>Pachycephala johni</i>	Unknown	Pair	Island	Resident	
<i>Pachycephala lanioides</i>	Pair	Pair	Continental	Resident	
<i>Pachycephala lorentzi</i>	Unknown	Pair	Continental	Resident	
<i>Pachycephala macrorhyncha</i>	Pair	Pair	Island	Resident	
<i>Pachycephala melanura</i>	Pair	Pair	Widespread	Resident	
<i>Pachycephala mentalis</i>	Pair	Pair	Island	Resident	
<i>Pachycephala meyeri</i>	Unknown	Pair	Continental	Resident	
<i>Pachycephala modesta</i>	Unknown	Pair	Continental	Resident	
<i>Pachycephala monacha</i>	Unknown	Pair	Continental	Resident	
<i>Pachycephala nudigula</i>	Unknown	Pair	Island	Resident	
<i>Pachycephala olivacea</i>	Pair	Pair	Continental	Resident	
<i>Pachycephala orioloides</i>	Pair	Pair	Island	Resident	
<i>Pachycephala orpheus</i>	Unknown	Pair	Island	Resident	
<i>Pachycephala pectoralis</i>	Pair	Pair	Widespread	Resident	
<i>Pachycephala phaionota</i>	Unknown	Pair	Island	Resident	
<i>Pachycephala philippinensis</i>	Unknown	Pair	Continental	Resident	
<i>Pachycephala rufiventris</i>	Pair	Pair	Widespread	Migratory	
<i>Pachycephala rufogularis</i>	Pair	Pair	Continental	Resident	
<i>Pachycephala schlegelii</i>	Unknown	Pair	Continental	Resident	
<i>Pachycephala simplex</i>	Unknown	Pair	Widespread	Resident	
<i>Pachycephala soror</i>	Unknown	Pair	Widespread	Resident	
<i>Pachycephala sulfuriventer</i>	Unknown	Pair	Continental	Resident	

(Continued)

Continued.

Species	Known breeding system	Inferred breeding system	Island/ Continental	Migratory status	Sources
<i>Pachycephala vitiensis</i>	Pair	Pair	Island	Resident	
<i>Paradigalla brevicauda</i>	Uniparental	Uniparental	Continental	Resident	
<i>Paradigalla carunculata</i>	Unknown	Uniparental	Continental	Resident	
<i>Paradisaea apoda</i>	Uniparental	Uniparental	Continental	Resident	
<i>Paradisaea decora</i>	Uniparental	Uniparental	Island	Resident	
<i>Paradisaea guilielmi</i>	Uniparental	Uniparental	Continental	Resident	
<i>Paradisaea minor</i>	Uniparental	Uniparental	Continental	Resident	
<i>Paradisaea raggiana</i>	Uniparental	Uniparental	Continental	Resident	
<i>Paradisaea rubra</i>	Uniparental	Uniparental	Continental	Resident	
<i>Paradisaea rudolphi</i>	Uniparental	Uniparental	Continental	Resident	
<i>Paramythia montium</i>	Pair	Pair	Continental	Resident	
<i>Parotia berlepschi</i>	Unknown	Uniparental	Continental	Resident	
<i>Parotia carolae</i>	Uniparental	Uniparental	Continental	Resident	
<i>Parotia helenae</i>	Unknown	Uniparental	Continental	Resident	
<i>Parotia lawesii</i>	Uniparental	Uniparental	Continental	Resident	
<i>Parotia sefilata</i>	Uniparental	Uniparental	Continental	Resident	
<i>Parotia wahnesi</i>	Uniparental	Uniparental	Continental	Resident	
<i>Peltops blainvillii</i>	Unknown	Pair	Continental	Resident	
<i>Peltops montanus</i>	Unknown	Pair	Continental	Resident	
<i>Pericrocotus brevirostris</i>	Unknown	Pair	Continental	Resident	
<i>Pericrocotus cantonensis</i>	Unknown	Pair	Continental	Migratory	
<i>Pericrocotus cinnamomeus</i>	Cooperative	Cooperative	Widespread	Resident	
<i>Pericrocotus divaricatus</i>	Pair	Pair	Widespread	Migratory	
<i>Pericrocotus erythropygus</i>	Pair	Pair	Continental	Resident	
<i>Pericrocotus ethologus</i>	Pair	Pair	Continental	Migratory	
<i>Pericrocotus flammeus</i>	Unknown	Cooperative	Continental	Resident	Rasmussen and Anderton (2005) and Ali and Ripley (1971)
<i>Pericrocotus igneus</i>	Unknown	Cooperative	Widespread	Resident	
<i>Pericrocotus lansbergei</i>	Unknown	Pair	Island	Resident	
<i>Pericrocotus miniatus</i>	Unknown	Pair	Continental	Resident	
<i>Pericrocotus roseus</i>	Pair	Pair	Continental	Migratory	
<i>Pericrocotus solaris</i>	Cooperative	Cooperative	Continental	Resident	
<i>Pericrocotus speciosus</i>	Unknown	Pair	Widespread	Resident	Rasmussen and Anderton (2005) and Ali and Ripley (1971)
<i>Pericrocotus tegimae</i>	Unknown	Pair	Island	Resident	
<i>Perisoreus canadensis</i>	Pair	Pair	Continental	Resident	
<i>Perisoreus infaustus</i>	Pair	Pair	Continental	Resident	
<i>Perisoreus internigrans</i>	Cooperative	Cooperative	Continental	Resident	
<i>Philentoma pyrhoptera</i>	Unknown	Pair	Continental	Resident	
<i>Philentoma velata</i>	Unknown	Pair	Continental	Resident	
<i>Phonygammus keraudrenii</i>	Pair	Pair	Widespread	Resident	
<i>Pica hudsonia</i>	Pair	Pair	Continental	Resident	
<i>Pica nuttalli</i>	Pair	Pair	Continental	Resident	

(Continued)

Continued.

Species	Known breeding system	Inferred breeding system	Island/ Continental	Migratory status	Sources
<i>Pica pica</i>	Pair	Pair	Continental	Resident	
<i>Pitohui cristatus</i>	Unknown	Pair	Continental	Resident	
<i>Pitohui dichrous</i>	Cooperative	Cooperative	Continental	Resident	
<i>Pitohui ferrugineus</i>	Cooperative	Cooperative	Continental	Resident	
<i>Pitohui incertus</i>	Unknown	Cooperative	Continental	Resident	
<i>Pitohui kirhocephalus</i>	Unknown	Cooperative	Continental	Resident	
<i>Pitohui nigrescens</i>	Unknown	Unknown	Continental	Resident	
<i>Pityriasis gymnocephala</i>	Cooperative	Cooperative	Continental	Resident	Smythies and Davison (1999)
<i>Platylophus galericulatus</i>	Unknown	Unknown	Continental	Resident	
<i>Platysmurus leucopterus</i>	Pair	Pair	Continental	Resident	
<i>Platysteira albifrons</i>	Unknown	Pair	Continental	Resident	
<i>Platysteira cyanea</i>	Pair	Pair	Continental	Resident	
<i>Platysteira laticincta</i>	Unknown	Cooperative	Continental	Resident	
<i>Platysteira peltata</i>	Cooperative	Cooperative	Continental	Resident	
<i>Podoces biddulphi</i>	Unknown	Pair	Continental	Resident	
<i>Podoces hendersoni</i>	Unknown	Pair	Continental	Resident	
<i>Podoces panderi</i>	Pair	Pair	Continental	Resident	
<i>Podoces pleskei</i>	Unknown	Pair	Continental	Resident	
<i>Pomarea dimidiata</i>	Cooperative	Cooperative	Island	Resident	
<i>Pomarea iphis</i>	Pair	Pair	Island	Resident	
<i>Pomarea mendozae</i>	Pair	Pair	Island	Resident	
<i>Pomarea nigra</i>	Unknown	Pair	Island	Resident	
<i>Pomarea whitneyi</i>	Pair	Pair	Island	Resident	
<i>Prionops alberti</i>	Cooperative	Cooperative	Continental	Resident	
<i>Prionops caniceps</i>	Cooperative	Cooperative	Continental	Resident	
<i>Prionops gabela</i>	Cooperative	Cooperative	Continental	Resident	
<i>Prionops plumatus</i>	Cooperative	Cooperative	Continental	Resident	
<i>Prionops polioliophus</i>	Cooperative	Cooperative	Continental	Resident	
<i>Prionops retzii</i>	Cooperative	Cooperative	Continental	Resident	
<i>Prionops rufiventris</i>	Unknown	Cooperative	Continental	Resident	
<i>Prionops scopifrons</i>	Cooperative	Cooperative	Continental	Resident	
<i>Pseudobias wardi</i>	Unknown	Pair	Continental	Resident	
<i>Psophodes cristatus</i>	Pair	Pair	Continental	Resident	
<i>Psophodes nigrogularis</i>	Pair	Pair	Continental	Resident	
<i>Psophodes occidentalis</i>	Pair	Pair	Continental	Resident	
<i>Psophodes olivaceus</i>	Pair	Pair	Continental	Resident	
<i>Pteridophora alberti</i>	Uniparental	Uniparental	Continental	Resident	
<i>Pteruthius aenobarbus</i>	Unknown	Pair	Continental	Resident	
<i>Pteruthius flaviscapis</i>	Pair	Pair	Continental	Resident	
<i>Pteruthius melanotis</i>	Pair	Pair	Continental	Resident	
<i>Pteruthius rufiventer</i>	Unknown	Pair	Continental	Resident	
<i>Pteruthius xanthochlorus</i>	Unknown	Pair	Continental	Resident	
<i>Ptiloris intercedens</i>	Unknown	Uniparental	Continental	Resident	
<i>Ptiloris magnificus</i>	Uniparental	Uniparental	Continental	Resident	
<i>Ptiloris paradiseus</i>	Uniparental	Uniparental	Continental	Resident	
<i>Ptiloris victoriae</i>	Uniparental	Uniparental	Continental	Resident	

(Continued)

Continued.

Species	Known breeding system	Inferred breeding system	Island/ Continental	Migratory status	Sources
<i>Ptilorhoa caeruleus</i>	Unknown	Pair	Continental	Resident	
<i>Ptilorhoa castanonota</i>	Unknown	Pair	Continental	Resident	
<i>Ptilorhoa leucosticta</i>	Pair	Pair	Continental	Resident	
<i>Ptilostomus afer</i>	Cooperative	Cooperative	Continental	Resident	
<i>Pyrrhonorax graculus</i>	Pair	Pair	Continental	Resident	
<i>Pyrrhonorax pyrrhonorax</i>	Pair	Pair	Widespread	Resident	
<i>Rhagologus leucostigma</i>	Unknown	Unknown	Continental	Resident	
<i>Rhipidura albicollis</i>	Pair	Pair	Continental	Resident	
<i>Rhipidura albiscapa</i>	Unknown	Pair	Widespread	Migratory	
<i>Rhipidura albolimbata</i>	Pair	Pair	Continental	Resident	
<i>Rhipidura atra</i>	Pair	Pair	Continental	Resident	
<i>Rhipidura aureola</i>	Pair	Pair	Continental	Resident	
<i>Rhipidura brachyrhyncha</i>	Unknown	Pair	Continental	Resident	
<i>Rhipidura cockerelli</i>	Unknown	Pair	Island	Resident	
<i>Rhipidura cyaniceps</i>	Unknown	Pair	Continental	Resident	
<i>Rhipidura dahli</i>	Unknown	Pair	Island	Resident	
<i>Rhipidura dedemi</i>	Unknown	Pair	Island	Resident	
<i>Rhipidura diluta</i>	Unknown	Pair	Island	Resident	
<i>Rhipidura drownei</i>	Unknown	Pair	Island	Resident	
<i>Rhipidura dryas</i>	Unknown	Pair	Widespread	Resident	
<i>Rhipidura euryura</i>	Unknown	Pair	Continental	Resident	
<i>Rhipidura fuliginosa</i>	Pair	Pair	Widespread	Resident	
<i>Rhipidura fuscorufa</i>	Unknown	Pair	Island	Resident	
<i>Rhipidura hyperythra</i>	Unknown	Pair	Continental	Resident	
<i>Rhipidura javanica</i>	Pair	Pair	Widespread	Resident	
<i>Rhipidura kubaryi</i>	Unknown	Pair	Island	Resident	
<i>Rhipidura lepida</i>	Unknown	Pair	Island	Resident	
<i>Rhipidura leucophrys</i>	Pair	Pair	Widespread	Resident	
<i>Rhipidura leucothorax</i>	Pair	Pair	Widespread	Resident	
<i>Rhipidura maculipectus</i>	Unknown	Pair	Continental	Resident	
<i>Rhipidura malaitae</i>	Unknown	Pair	Island	Resident	
<i>Rhipidura matthiae</i>	Unknown	Pair	Island	Resident	
<i>Rhipidura nebulosa</i>	Unknown	Pair	Island	Resident	
<i>Rhipidura nigrocinnamomea</i>	Unknown	Pair	Continental	Resident	
<i>Rhipidura opistherythra</i>	Unknown	Pair	Island	Resident	
<i>Rhipidura perlata</i>	Unknown	Pair	Continental	Resident	
<i>Rhipidura personata</i>	Unknown	Pair	Island	Resident	
<i>Rhipidura phasiana</i>	Unknown	Pair	Continental	Resident	
<i>Rhipidura phoenicura</i>	Unknown	Pair	Continental	Resident	
<i>Rhipidura rennelliana</i>	Unknown	Pair	Island	Resident	
<i>Rhipidura rufidorsa</i>	Unknown	Pair	Continental	Resident	
<i>Rhipidura rufifrons</i>	Pair	Pair	Widespread	Migratory	Higgins et al. (2006)
<i>Rhipidura rufiventris</i>	Pair	Pair	Widespread	Resident	
<i>Rhipidura semirubra</i>	Unknown	Pair	Island	Resident	
<i>Rhipidura superciliaris</i>	Unknown	Pair	Continental	Resident	
<i>Rhipidura superflua</i>	Unknown	Pair	Island	Resident	
<i>Rhipidura tenebrosa</i>	Unknown	Pair	Island	Resident	

(Continued)

Continued.

Species	Known breeding system	Inferred breeding system	Island/ Continental	Migratory status	Sources
<i>Rhipidura teysmanni</i>	Unknown	Pair	Continental	Resident	
<i>Rhipidura threnothorax</i>	Unknown	Pair	Continental	Resident	
<i>Rhipidura verreauxi</i>	Pair	Pair	Island	Resident	
<i>Rhodophoneus cruentus</i>	Unknown	Pair	Continental	Resident	
<i>Schetba rufa</i>	Cooperative	Cooperative	Continental	Resident	
<i>Seleucidis melanoleucus</i>	Uniparental	Uniparental	Continental	Resident	
<i>Semioptera wallacii</i>	Uniparental	Uniparental	Island	Resident	
<i>Sphecotheres vieilloti</i>	Cooperative	Cooperative	Widespread	Resident	Higgins et al. (2006)
<i>Sphecotheres viridis</i>	Unknown	Cooperative	Island	Resident	
<i>Strepera fuliginosa</i>	Pair	Pair	Continental	Resident	Higgins et al. (2006)
<i>Strepera graculina</i>	Pair	Pair	Continental	Resident	Higgins et al. (2006)
<i>Strepera versicolor</i>	Pair	Pair	Continental	Resident	Higgins et al. (2006)
<i>Struthidea cinerea</i>	Cooperative	Cooperative	Continental	Resident	
<i>Symposiachrus axillaris</i>	Unknown	Pair	Widespread	Resident	
<i>Symposiachrus bimaculatus</i>	Unknown	Pair	Island	Resident	
<i>Symposiachrus boanensis</i>	Unknown	Pair	Island	Resident	
<i>Symposiachrus brehmii</i>	Unknown	Pair	Island	Resident	
<i>Symposiachrus browni</i>	Unknown	Pair	Island	Resident	
<i>Symposiachrus everetti</i>	Unknown	Pair	Island	Resident	
<i>Symposiachrus guttula</i>	Pair	Pair	Widespread	Resident	
<i>Symposiachrus infelix</i>	Unknown	Pair	Island	Resident	
<i>Symposiachrus julianae</i>	Unknown	Pair	Island	Resident	
<i>Symposiachrus leucurus</i>	Unknown	Pair	Island	Resident	
<i>Symposiachrus loricatus</i>	Unknown	Pair	Island	Resident	
<i>Symposiachrus manadensis</i>	Unknown	Pair	Continental	Resident	
<i>Symposiachrus menckei</i>	Unknown	Pair	Island	Resident	
<i>Symposiachrus mundus</i>	Unknown	Pair	Island	Resident	
<i>Symposiachrus sacerdotum</i>	Unknown	Pair	Island	Resident	
<i>Symposiachrus trivirgatus</i>	Pair	Pair	Widespread	Migratory	
<i>Symposiachrus verticalis</i>	Unknown	Pair	Island	Resident	
<i>Symposiachrus vidua</i>	Unknown	Pair	Island	Resident	
<i>Tchagra australis</i>	Pair	Pair	Continental	Resident	
<i>Tchagra jamesi</i>	Pair	Pair	Continental	Resident	
<i>Tchagra senegalus</i>	Pair	Pair	Continental	Resident	
<i>Tchagra tchagra</i>	Pair	Pair	Continental	Resident	
<i>Telophorus zeylonus</i>	Pair	Pair	Continental	Resident	
<i>Temnurus temnurus</i>	Unknown	Pair	Continental	Resident	
<i>Tephrodornis virgatus</i>	Pair	Pair	Continental	Resident	Rasmussen and Anderton (2005) and Ali and Ripley (1971)
<i>Tephrodornis pondicerianus</i>	Pair	Pair	Continental	Resident	Rasmussen and Anderton (2005) and Ali and Ripley (1971)
<i>Terpsiphone atrocaudata</i>	Pair	Pair	Widespread	Migratory	
<i>Terpsiphone atrochalybeia</i>	Pair	Pair	Island	Resident	

(Continued)

Continued.

Species	Known breeding system	Inferred breeding system	Island/ Continental	Migratory status	Sources
<i>Terpsiphone batesi</i>	Unknown	Pair	Continental	Resident	
<i>Terpsiphone bedfordi</i>	Unknown	Pair	Continental	Resident	
<i>Terpsiphone bourbonnensis</i>	Pair	Pair	Island	Resident	
<i>Terpsiphone cinnamomea</i>	Pair	Pair	Widespread	Resident	
<i>Terpsiphone corvina</i>	Pair	Pair	Island	Resident	
<i>Terpsiphone cyanescens</i>	Unknown	Pair	Continental	Resident	
<i>Terpsiphone mutata</i>	Pair	Pair	Widespread	Resident	
<i>Terpsiphone paradisi</i>	Pair	Pair	Widespread	Migratory	
<i>Terpsiphone rufiventer</i>	Pair	Pair	Widespread	Resident	
<i>Terpsiphone rufocinerea</i>	Pair	Pair	Continental	Resident	
<i>Terpsiphone smithii</i>	Unknown	Pair	Island	Resident	
<i>Terpsiphone viridis</i>	Pair	Pair	Continental	Migratory	
<i>Trochocercus cyanomelas</i>	Pair	Pair	Continental	Resident	
<i>Trochocercus nitens</i>	Pair	Pair	Continental	Resident	
<i>Turnagra capensis</i>	Unknown	Unknown	Continental	Resident	Higgins et al. (2006)
<i>Tylas eduardi</i>	Unknown	Pair	Continental	Resident	
<i>Urocissa caerulea</i>	Cooperative	Cooperative	Continental	Resident	
<i>Urocissa erythrorhyncha</i>	Unknown	Cooperative	Continental	Resident	
<i>Urocissa flavirostris</i>	Unknown	Cooperative	Continental	Resident	
<i>Urocissa ornata</i>	Unknown	Cooperative	Continental	Resident	
<i>Urocissa whiteheadi</i>	Unknown	Cooperative	Continental	Resident	
<i>Urolestes melanoleucus</i>	Cooperative	Cooperative	Continental	Resident	Dowsett et al. (2008)
<i>Vanga curvirostris</i>	Pair	Pair	Continental	Resident	
<i>Vireo altiloquus</i>	Unknown	Pair	Widespread	Migratory	
<i>Vireo approximans</i>	Unknown	Pair	Island	Resident	
<i>Vireo atricapilla</i>	Pair	Pair	Continental	Migratory	
<i>Vireo bairdi</i>	Unknown	Pair	Island	Resident	
<i>Vireo bellii</i>	Pair	Pair	Continental	Migratory	
<i>Vireo brevipennis</i>	Unknown	Pair	Continental	Resident	
<i>Vireo caribaeus</i>	Pair	Pair	Island	Resident	
<i>Vireo carmioli</i>	Unknown	Pair	Continental	Resident	
<i>Vireo cassinii</i>	Pair	Pair	Continental	Migratory	
<i>Vireo crassirostris</i>	Unknown	Pair	Island	Resident	
<i>Vireo flavifrons</i>	Pair	Pair	Continental	Migratory	
<i>Vireo flavoviridis</i>	Pair	Pair	Widespread	Migratory	
<i>Vireo gilvus</i>	Pair	Pair	Continental	Migratory	
<i>Vireo gracilirostris</i>	Unknown	Pair	Island	Resident	
<i>Vireo griseus</i>	Pair	Pair	Continental	Migratory	
<i>Vireo gundlachii</i>	Pair	Pair	Island	Resident	
<i>Vireo huttoni</i>	Pair	Pair	Continental	Resident	
<i>Vireo hypochryseus</i>	Unknown	Pair	Widespread	Resident	
<i>Vireo latimeri</i>	Pair	Pair	Island	Resident	
<i>Vireo leucophrys</i>	Unknown	Pair	Continental	Resident	
<i>Vireo magister</i>	Pair	Pair	Widespread	Resident	
<i>Vireo masteri</i>	Unknown	Pair	Continental	Resident	
<i>Vireo modestus</i>	Unknown	Pair	Island	Resident	
<i>Vireo nanus</i>	Unknown	Pair	Island	Resident	

(Continued)



Continued.

Species	Known breeding system	Inferred breeding system	Island/ Continental	Migratory status	Sources
<i>Vireo nelsoni</i>	Pair	Pair	Continental	Resident	
<i>Vireo olivaceus</i>	Pair	Pair	Continental	Migratory	
<i>Vireo osburni</i>	Unknown	Pair	Island	Resident	
<i>Vireo pallens</i>	Unknown	Pair	Widespread	Resident	
<i>Vireo philadelphicus</i>	Pair	Pair	Continental	Migratory	
<i>Vireo plumbeus</i>	Pair	Pair	Continental	Migratory	
<i>Vireo solitarius</i>	Pair	Pair	Continental	Migratory	
<i>Vireo vicinior</i>	Pair	Pair	Continental	Migratory	
<i>Vireolanius eximius</i>	Unknown	Pair	Continental	Resident	
<i>Vireolanius leucotis</i>	Unknown	Pair	Continental	Resident	
<i>Vireolanius melitophrys</i>	Unknown	Pair	Continental	Resident	
<i>Vireolanius pulchellus</i>	Unknown	Pair	Continental	Resident	
<i>Xenopirostris damii</i>	Pair	Pair	Continental	Resident	
<i>Xenopirostris pollenii</i>	Pair	Pair	Continental	Resident	
<i>Xenopirostris xenopirostris</i>	Unknown	Pair	Continental	Resident	
<i>Zavattariornis stresemanni</i>	Cooperative	Cooperative	Continental	Resident	

## LITERATURE CITED

- Ali, S., and S. D. Ripley. 1971. Handbook of the Birds of India and Pakistan. Oxford Univ. Press, Bombay. Vol. 6. 245 p.
- Ali, S., and S. D. Ripley. 1972. Handbook of the Birds of India and Pakistan. Oxford Univ. Press, Bombay. Vol. 7. 276 p.
- Boles, W. E. 2006. Family Rhipiduridae (fantails). Pp. 200–242 in J. del Hoyo, A. Elliott, and D. Christie, eds. Handbook of the birds of the world. Vol. 11. Old world flycatchers to old world warblers. Lynx Edicions, Barcelona.
- . 2007a. Family Eupetidae (Jewel-babblers and allies). Pp. 348–373 in J. del Hoyo, A. Elliott, and D. Christie, eds. Handbook of the birds of the world. Vol. 12. Picathartes to tits and chickadees. Lynx Edicions, Barcelona.
- . 2007b. Family Pachycephalidae (whistlers). Pp. 374–437 in J. del Hoyo, A. Elliott, and D. Christie, eds. Handbook of the birds of the world. Vol. 12. Picathartes to tits and chickadees. Lynx Edicions, Barcelona.
- Brewer, D., and R. Orenstein. 2010. Species accounts of Vireonidae. Pp. 415–439 in J. del Hoyo, A. Elliott, and David A. Christie, eds. Handbook of the birds of the world. Vol. 15. Weavers to new world warblers. Lynx Edicions, Barcelona.
- Clement, P., P. A. Gregory, and C. W. Moeliker. 2006. Species accounts of Monarchidae. Pp. 280–329 in J. del Hoyo, A. Elliott, and D. Christie, eds. Handbook of the birds of the world. Vol. 11. Old world flycatchers to old world warblers. Lynx Edicions, Barcelona.
- Coates, B. J., and W. S. Peckover. 2001. Birds of New Guinea and the Bismarck Archipelago. A photographic guide. Dove Publications, Alderley. 272 p.
- Cockburn, A. 2006. Prevalence of different modes of parental care in birds. Proc. R. Soc. Lond. B 273:1375–1383.
- Collar, N. J., and P. Clement. 2007. Family Timaliidae (babblers). Pp. 70–291 in J. del Hoyo, A. Elliott, and D. Christie, eds. Handbook of the birds of the world. Vol. 12. Picathartes to tits and chickadees. Lynx Edicions, Barcelona.
- dos Anjos, L., 2009. Family Corvidae (crows). Pp. 494–640 in J. del Hoyo, A. Elliott, and D. Christie, eds. Handbook of the birds of the world. Vol. 14. Bush-shrikes to Old World sparrows. Lynx Edicions, Barcelona.
- Dowsett, R. J., D. R. Aspinwall, and F. Dowsett-Lemaire. 2008. The birds of Zambia. Tauraco Press & Aves, Liège. 606 p.
- Dowsett-Lemaire, F., and R. J. Dowsett. 2006. The birds of Malawi. Tauraco Press and Aves, Liège. 556 p.
- Fry, C. H., S. Keith and E. K. Urban 2000: The birds of Africa, Vol. VI.-Academic Press, London.
- Frith, C. B., and D. W. Frith. 2009. Family Paradisaeidae (birds-of-paradise). Pp. 404–492 in J. del Hoyo, A. Elliott, and D. Christie, eds. Handbook of the birds of the world. Vol. 14. Bush-shrikes to Old World sparrows. Lynx Edicions, Barcelona.
- Gregory, P. A. 2007. Family Acanthizidae (thornbills). Pp. 544–611 in J. del Hoyo, A. Elliott, and D. Christie, eds. Handbook of the birds of the world. Vol. 12. Picathartes to tits and chickadees. Lynx Edicions, Barcelona.
- Harris, T., and K. Franklin. 2000. Shrikes & bush-shrikes. Including wood-shrikes, helmet-shrikes, flycatcher-shrikes, philentomas, batises and wattle-eyes. Christopher Helm, London. 392 p.
- Higgins, P. J., J. M. Peter, and S. J. Cowling. 2006. Handbook of Australian, New Zealand & Antarctic Birds. Vol. 7: boatbill to starlings. Part A: boatbill to larks. Oxford Univ. Press, Melbourne. 1055 p.
- King, B. F., and Edward C. Dickinson. 1980. A field guide to the birds of south-east Asia. Covering Burma, Malaya, Thailand, Cambodia, Vietnam, Laos and Hong Kong, Collins, London. 480 p.
- Latta, S., C. Rimmer, A. Keith, J. Wiley, H. Raffaele, K. McFarland, and E. Fernandez. 2006. Field guide to the birds of the Dominican Republic & Haiti. Christopher Helm, London. 258 p.
- Madge, S., and H. Burn. 1999. Crows & jays. Christopher Helm Publishers, London. 192 p.
- McGowan, K. J. 2001. Corvus ossifragus—fish crow. Birds N. Am. 589:1–27.
- Noske, R. A. 2007. Family Neosittidae (sittellas). Pp. 628–641 in J. del Hoyo, A. Elliott, and D. Christie, eds. Handbook of the birds of the world. Vol. 12. Picathartes to tits and chickadees. Lynx Edicions, Barcelona.
- Rasmussen, P. C., and J. C. Anderton. 2005. Birds of South Asia. The ripley guide. Vol. 2: attributes and status. Smithsonian Institution and Lynx Editions, Washington, DC, and Barcelona. 683 p.
- Robson, C. 2008. A field guide to the birds of south-east Asia. New Holland Publishers, London. 544 p.
- Rocamora, G. J., and D. Yeatman-Berthelot. 2009. Family Dicruridae (dron-gos). Pp. 172–226 in J. del Hoyo, A. Elliott, and D. Christie, eds.

- Handbook of the birds of the world. Vol. 14. Bush-shrikes to Old World sparrows. Lynx Edicions, Barcelona.
- Rowley, C. R., and E. M. Russell. 2009a. Family Artamidae (woodswallows). Pp. 286–307 in J. del Hoyo, A. Elliott, and D. Christie, eds. Handbook of the birds of the world. Vol. 14. Bush-shrikes to Old World sparrows. Lynx Edicions, Barcelona.
- . 2009b. Family Struthideidae (Australian mudnesters). Pp. 272–285 in J. del Hoyo, A. Elliott, and D. Christie, eds. Handbook of the birds of the world. Vol. 14. Bush-shrikes to Old World sparrows. Lynx Edicions, Barcelona.
- Russell, E. M., and I. C. R. Rowley. 2009. Family Cracticidae (butcherbirds). Pp. 308–342 in J. del Hoyo, A. Elliott, and D. Christie, eds. Handbook of the birds of the world. Vol. 14. Bush-shrikes to Old World Sparrows. Lynx Edicions, Barcelona.
- Sheldon, F. H., and R. G. Moyle. 2009. Family Pityriaseidae (bristlehead). Pp. 344–348 in J. del Hoyo, A. Elliott, and D. Christie, eds. Handbook of the birds of the world. Vol. 14. Bush-shrikes to Old World sparrows. Lynx Edicions, Barcelona.
- Smythies, B. E., and G. W. H. Davison. 1999. The birds of Borneo. Natural History Publications (Borneo) Sdn. Bhd., Kota Kinabalu, Malaysia. 853 p.
- Taylor, P. B. 2005. Family:Campehagidae (cuckoo-shrikes). Pp. 40–122 in J. del Hoyo, A. Elliott, and D. Christie, eds. Handbook of the birds of the world. Vol. 10. Cuckoo-shrikes to thrushes. Lynx Edicions, Barcelona.
- Tingay, S. R., and A. Tingay. 2009. Family Grallinidae (mudlarks). Pp. 258–271 in J. del Hoyo, A. Elliott, and D. Christie, eds. Handbook of the birds of the world. Vol. 14. Bush-shrikes to Old World sparrows. Lynx Edicions, Barcelona.
- Walther, B. A., and P. J. Jones. 2008. Family oriolidae (orioles). Pp. 692–731 in J. del Hoyo, A. Elliott, and D. Christie, eds. Handbook of the birds of the world. Vol. 13. Penduline-tits to Shrikes. Lynx Edicions, Barcelona.
- Wells, D. R. 2005. Family: Aegithinidae (ioras). Pp. 278–290 in J. del Hoyo, A. Elliott, and D. Christie, eds. Handbook of the birds of the world. Vol. 10. Cuckoo-shrikes to thrushes. Lynx Edicions, Barcelona.
- Yosef, R. 2008. Family Laniidae (Shrikes). Pp. 732–796 in J. del Hoyo, A. Elliott, and D. Christie, eds. Handbook of the birds of the world. Vol. 13. Penduline-tits to shrikes. Lynx Edicions, Barcelona.
- . 1996. *Lanius ludovicianus*—loggerhead shrike. *Birds N. Am.* 231:1–28.

## Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

**Table S1.** Model fitting and parameter estimates of three-state diversification models in MuSSE performed on a posterior distribution of trees based on molecular data only.

**Table S2.** Likelihood and Bayes factors of evolutionary models in which breeding systems are suggested to be dependently or independently related to island distribution and migratory behavior, as implemented in BayesTraits.

**Table S3.** Model fitting and parameter estimates of the region-dependent diversification models in GeoSSE performed on a posterior distribution of trees based on molecular data only.

**Figure S1.** Posterior probability distributions of parameter rate estimates generated from a BiSSE analysis examining the effect of breeding system (pair and cooperative) on lineage diversification and transitions, using an MCMC approach.

**Figure S2.** Posterior probability distributions of parameter rate estimates generated from a BiSSE analysis examining the effect of breeding system (pair and cooperative) on lineage diversification and transitions, using an MCMC approach.

**Figure S3.** Posterior probability distributions of parameter rate estimates generated from a MuSSE analysis examining the effect of breeding system (pair, cooperative, and uniparental) on lineage diversification and transitions, using an MCMC approach.

**Figure S4.** Posterior probability distributions of parameter rate estimates generated from a MuSSE analysis examining the effect of breeding system (pair, cooperative, and uniparental) on lineage diversification and transitions, using an MCMC approach.

**Figure S5.** Posterior probability distributions of parameter rate estimates generated from a MuSSE analysis examining the effect of breeding system (pair, cooperative, and uniparental) on lineage diversification and transitions, using an MCMC approach.

**Figure S6.** Ancestral reconstruction of breeding system generated with the multistate speciation and extinction (MuSSE) model implemented using an MCMC approach.

**Figure S7.** Posterior probability distributions of parameter rate estimates generated from a GeoSSE analysis examining the effect of island and continental dwelling on lineage diversification and transitions, using an MCMC approach.

**Figure S8.** Global maps of breeding species richness of each 1° × 1° grid cell for pair breeders (left panel), cooperative breeders (center panel), and all breeding systems combined (right panel).

**Figure S9.** *Left panel:* Global maps showing studentized residuals of linear models examining the relationship between species richness of 1° × 1° grid cells, among pair breeders ~ pair and cooperative breeders combined. Red and blue colors highlight areas where cooperative and 1015 pair breeders are overrepresented respectively. *Right panel:* Species richness among 1° × 1° 1016 grid cells for all pair and cooperative breeders combined.