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Out of Gondwanaland; the evolutionary history of cooperative breeding and social behaviour among crows, magpies, jays and allies

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Cooperative breeding is comparatively rare among birds on the mainly temperate and boreal Northern Hemisphere. Here we test if the distribution of breeding system reflects a response to latitude in a phylogenetic analysis using correlates with geographical range among the corvids (crows, jays, magpies and allied groups). The corvids trace their ancestry to the predominantly cooperative 'Corvida' branch of oscine passerines from the Australo-Papuan region on the ancient Gondwanaland supercontinent, but we could not confirm the ancestral state of the breeding system within the family, while family cohesion may be ancestral. Initial diversification among pair-breeding taxa that are basal in the corvid phylogeny represented by genera, such as *Pyrrhocorax* and *Dendrocitta*, indicates that the corvid family in its current form could have evolved from pair-breeding ancestors only after they had escaped the Australo-Papuan shield. Within the family, cooperative breeding (alloparental care/family cohesion) is strongly correlated to latitude and its predominance in species maintaining a southerly distribution indicates a secondary evolution of cooperative breeding in the lineage leading away from the basal corvids. Multiple transitions show plasticity in the breeding system, indicating a response to latitude rather than evolutionary inertia. The evolutionary background to the loss of cooperative breeding among species with a northerly distribution is complex and differs between species, indicating a response to a variety of selection forces. Family cohesion where the offspring provide alloparental care is a main route to cooperatively breeding groups among corvids. Some corvid species only lost alloparental care while maintaining coherent family groups. Other species lost family cohesion, and as a corollary they also lost the behaviour, where retained offspring provide alloparental care.

Q2 **Keywords:** Please supply a minimum of three to a maximum of six keywords

1. INTRODUCTION

Recent estimates point to that cooperative breeding involving contribution of more than two birds either as co-breeders or non-breeding extra-birds is more common than previously recognized. For instance, as many as one-quarter of all oscine passerines are currently estimated to reproduce cooperatively (Cockburn 2003). Phylogenetic analyses have recognized a strong role of history predisposing species to breed cooperatively, which is identified as the ancestral state of the breeding system in several avian lineages (Russell 1989; Edwards & Naeem 1993; Cockburn 1996; Nicholls *et al.* 2000; Ligon & Burt 2004). In contrast, ecological context, design and life-history traits conducive to cooperative breeding remains less well understood, with contradictory results for the role of factors like environmental unpredictability (Ford *et al.* 1988; Du Plessis *et al.* 1995) and longevity (Arnold & Owens 1998; Cockburn 2003).

Here we explore the evolutionary history of the breeding system and social behaviour among crows, jays, magpies and allied groups during their range expansion out of an area of origin on the Southern Hemisphere. A historic perspective offers an opportunity to integrate ecological factors and design features that commit extant species to cooperative breeding. Apart from identifying evolutionary stasis or revealing the direction of evolutionary changes, such an analysis may provide clues to the role of ecological conditions driving evolutionary change. Broad-scale comparative analyses can reveal general patterns in covariation between behavioural traits, such as the breeding system and ecological conditions. However, extant species differ not only in the ecological conditions of their environment. As a result of separate evolutionary histories and diversification, lineages differ also in design and associated life-history traits (Ridley 1983; Harvey & Pagel 1991; Winkler 2000). The role of ecology is therefore best seen in clades, which are more homogenous as the result of a more recent shared history. The corvids (Corvini *sensu* Sibley & Monroe 1990; Corvidae *sensu* Dickinson 2003) is a monophyletic group within the oscine passerines, presumably with a relatively

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Late Middle Tertiary origin (Feduccia 1995). The relatively recent origin coupled with a homogenous design within the group makes it suitable for a comparative test.

A main feature of avian cooperative breeding is its relative paucity on the temperate and boreal landmasses of the Northern Hemisphere, reflecting the current geographical distribution within the species-rich Passerida branch of the oscine passerines (Cockburn 2003). Corvids trace their ancestry to the other main branch of the oscine passerine called 'Corvida' by Sibley & Monroe (1990) and consisting of several highly cooperative lineages (Cockburn 1996; Nicholls *et al.* 2000; Ligon & Burt 2004) of Gondwanan origin and currently found mainly in the Australo-Papuan region (Barker *et al.* 2002; Ericson *et al.* 2002). An ancestry among cooperative lineages coupled with a Southern Hemisphere origin offers the opportunity for a comparative analysis of the response in breeding system to latitude. Corvids are suited for such a test in being exceptional among Corvida in the sense that they have dispersed extensively beyond the Australo-Papuan region, while cooperatively breeding birds normally are characterized by a limited dispersal capacity (Cockburn 2003). The corvid family itself may have evolved out of more dispersal prone pair-breeding representatives among cooperative clades (Cockburn 2003) somewhere in Southeast Asia only after their shrike-corvid ancestor had escaped Australo-Papua proper (Barker *et al.* 2004; Ericson *et al.* 2005). Yet, the group is well known for its complex social behaviours that has attracted much attention, and is comparatively well studied (for instance, Brown 1963*a*,*b*, 1970, 1974; Verbeek & Butler 1981; Woolfenden & Fitzpatrick 1984; Severinghaus 1987; Skutch 1987; Brown & Brown 1990; Marzluff & Balda 1990; Richner 1990; Ekman *et al.* 1994; Baglione *et al.* 2002*a*).

2. MATERIAL AND METHODS

The characters of species do not represent evolutionary independent events, but species similarity due to common descent as reflected in a phylogenetic tree has to be controlled for (Harvey & Pagel 1991; Harvey & Purvis 1991). Our analysis focuses on two traits: family cohesion and alloparental care by retained offspring. Both these characters are bivariate, and the DISCRETE v. 1.0.1b software, which provides maximum-likelihood reconstruction of ancestral states and correlated character evolution for discrete characters on a bifurcate phylogeny, is designed to analyse such characters (Pagel 1994, 1997, 1999*a*,*b*). A main advantage of the DISCRETE algorithm is that the analysis of correlated character evolution is not dependent upon the reconstruction of ancestral states, while the maximization process takes its beginning at random points in the phylogeny. The reconstruction of the ancestral distribution of traits in the DISCRETE program can either be 'global' assigning a state to all nodes in the phylogeny or it can be 'local' and find the values for specific nodes (Pagel 1999*b*). A special case of the local reconstruction is to find the states at the roots.

The ancestral state reconstruction and analyses of correlated character evolution were run, including branch lengths calculated from cytochrome *b* using PAUP v. 4.0b10 (Swofford 1998). The phylogeny we use is the hypothesis of Ericson *et al.* (2005) reconstructed from the combined data of one mitochondrial (cytochrome *b*) and two nuclear (rag-1 and myoglobin) genes (figure 1). Branch lengths are in our

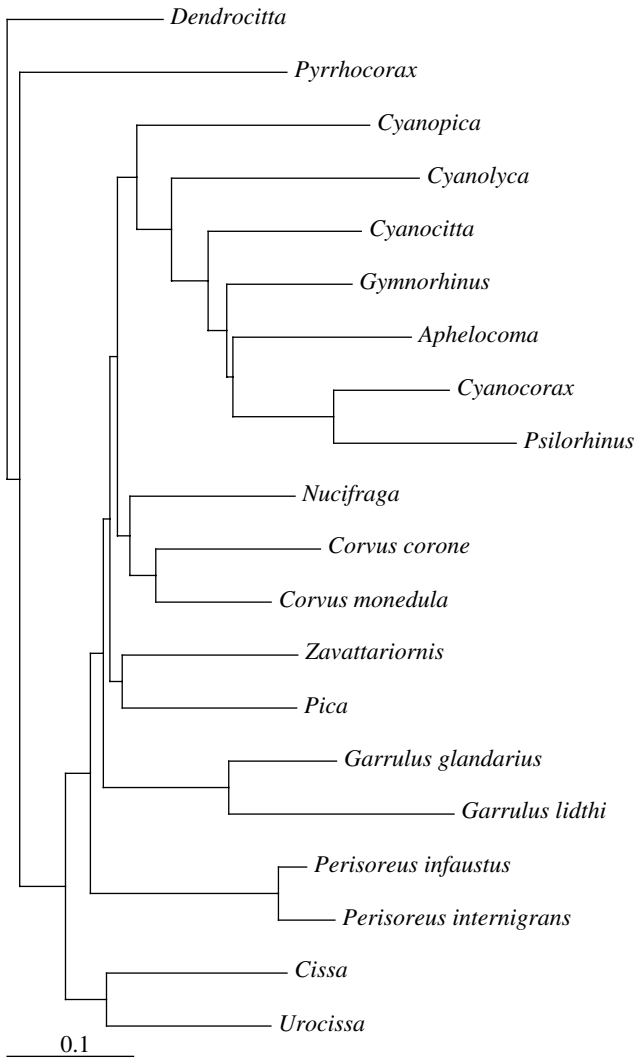

Figure 1. Dataset with branch lengths. Species used in reconstruction of phylogeny—*Dendrocitta formosae*, *Pyrrhocorax pyrrhocorax*, *Cyanopica cyana*, *Cyanolyca viridicyana*, *Cyanocitta cristata*, *Gymnorhinus cyanocephala*, *Aphelocoma coerulescens*, *Cyanocorax chrysops*, *Psilorhinus morio*, *Nucifraga caryocataces*, *Corvus corone*, *Corvus monedula*, *Zavattariornis stresemanni*, *Pica pica*, *Garrulus glandarius*, *Garrulus lidthi*, *Perisoreus infaustus*, *Perisoreus internigrans*, *Cissa chinensis*, *Urocissa erythrorhyncha*.

analysis estimated from cytochrome *b* data. There was no support for the position of *Cyanopica* in the analysis of Ericson *et al.* (2005) and a tree based on cytochrome *b* gene alone gave it a different position in the tree used here. Species included in the analysis are listed in appendix A. Based on molecular data, two monospecific genera (*Platylophus*, *Pseudopodoces*) traditionally considered to be corvids are here excluded (James *et al.* 2002; Ericson *et al.* 2005), leaving 119 species from 23 genera in the group (Madge & Burn 1994). There are 2^n possible assignments of ancestral states in a phylogeny with n nodes, and computations therefore grow fast with the number of species included. Taxa on the same branch and sharing traits contribute only insignificantly to the result in the DISCRETE algorithm (Pagel 1994), and computations could thus be reduced by collapsing nodes for such taxa. Species could be clustered and used as terminal taxa for genera with no known variation in trait combinations. Hence, we clustered congeneric species within the genera *Nucifraga*, *Cissa*, *Urocissa*, *Dendrocitta*,

Pyrrhocorax and *Pica*. For the same reason it was possible to cluster genera on the same branch sharing trait combinations (*Zavattariornis*/*Ptilostomus* and *Cyanocorax*/*Psilorhinus*).

A first test run included within-genus variation in trait combinations among three genera, where we have data on branch length on species level (*Garrulus*, *Corvus*, *Perisoreus*; figure 1). In an extended dataset of a second run, we further included variation on species level within another four genera (*Aphelocoma*, *Cyanocorax*, *Cyanolyca*, *Cyanocitta*), although we did not have data on branch length for species as terminal taxon. For this run we included following species in addition to the taxa in figure 1: *Aphelocoma californica*, *Cyanocorax yncas* (Texas population), *Cyanolyca nana* and *Cyanocitta stelleri* (test for family cohesion only). Species within these four genera were treated as sister groups to their congeners with nodes of branches leading to these species assumed to be located half ways down the branch leading to their congeners. Branch length is taken into account in the DISCRETE algorithm and the role of branch length can be tested through the kappa parameter. A value approaching zero signifies a punctuational mode of evolution, where branch length contributes only insignificantly to the solution, while a kappa value of unity represents a uniform rate of evolution (Pagel 1997). With a kappa value of 0.00054 for the corvids branch length should be of minor significance for the DISCRETE solution, justifying an inclusion of species providing additional information on trait values despite the lack of data on branch length.

The DISCRETE algorithm is based on forward (α) and backward (β) transition rates of a bivariate trait within the phylogeny. These transitions rates for traits can be either different (two-parameter model) or identical (one-parameter model). A two-parameter model can generate paradoxical result and it is justified only if it produces a better fit to the data than a one-parameter model. Else the one-parameter model should be chosen as default (Mooers & Schluter 1999; Pagel 1999*b*). Here there was no support for a better fit from a two-parameter model (likelihood $=-24.6045$; one-parameter model likelihood $=-24.7036$; likelihood ratio $=0.0991$, $p=0.75$) for the corvid data on alloparental care. For the data on family cohesion the two-parameter model (likelihood $=-20.7971$) produced a fit that nearly, but not fully, significantly improved the fit from a one-parameter model (likelihood $=-22.7094$; likelihood ratio $=3.8246$, $p=0.0505$). The ancestral distributions and correlated character evolution were therefore analysed with a one-parameter model ($\alpha=\beta$). Correlated evolution of characters is tested by comparing the likelihood of a model, assuming the traits to be independent (H_0) to one where the evolution of the traits is linked (H_1). The likelihood ratio statistics $=-2$ [(likelihood H_0) $-$ (likelihood H_1)] can be assumed to be χ^2-distributed and the probability of H_1 can be estimated from testing it against a null hypothesis based on transitions rates generated from resampling of the original distribution using the DISCRETE software (Pagel 1997).

3. CHARACTERS

(a) *Breeding system and family cohesion*

The wealth of information on breeding system and social behaviour among corvids is summarized in Brown (1987), Skutch (1987), Madge & Burn (1994) and Cockburn (2003). Primary sources for the data used here are listed in appendix A. Cooperative breeding is conventionally identified from the presence of extra-birds helping to breed (alloparenting), and is as such a bivariate trait in the form required by the DISCRETE program. Delayed offspring dispersal is the main route to become an alloparenting extra-bird among corvids and family cohesion is thus a prerequisite for cooperative breeding (Skutch 1987). We therefore also tested for environmental correlates to family cohesion. As an operative definition, dispersal is conventionally considered to be delayed if mature offspring remain past a breeding season, and identification of retained offspring normally requires colour-banding. Such data on family cohesion are lacking for a couple of less studied genera with tropical and subtropical distribution (*Cissa*, *Dendrocitta*) reported to live in family groups while breeding as pairs (Madge & Burn 1994). We tentatively treated *Cissa* and *Dendrocitta* as having delayed dispersal in the test for family cohesion including cooperatively breeding species and corvid species, where colour-banding identified coherent family groups in the absence of alloparental care. In depth studies of a number of other corvid species have revealed that unassisted pair-breeding is not an uncommon breeding system within coherent families (Verbeek & Butler 1981; Gayou 1986; Eden 1987; Strickland 1991; Ekman *et al.* 1994; Caffrey 2000). We further included Steller's jay (*C. stelleri*), while the offspring maintain a prolonged parent association into the non-breeding season (Brown 1963*b*). To test for the effect of using this more inclusive definition of delayed dispersal, we also ran analyses without *Cissa*, *Dendrocitta* and *C. stelleri*.

(b) *Distribution*

To analyse for any responses in breeding system to the expansion out of their area of origin in Australo-Papuan region (Sibley & Ahlquist 1990; Barker *et al.* 2002; Ericson *et al.* 2002, 2005), the latitudinal distribution of corvids was dichotomized. Species were assigned to the two categories based on the northernmost point of distribution taken to characterize the conditions limiting the expansion northwards. Distributions were taken from Madge & Burn (1994) and references therein. Few terminal taxa had the northern limit of their distribution in the range between around 55 and 60° N, which was used as cut-off points to characterize species with a northern and a southern distribution in our analysis. One group of seven terminal taxa had their distribution limit around 60° N or further north, while the distribution did not reach further north than around 55° N for another group of 15 terminal taxa. This criterion correlated strongly to the midpoint of distribution limits for each species ($r=0.92$, $p<0.0001$).

(c) *Habitat*

The corvids expanded out of the Australo-Papuan region in Mid to Late Tertiary while it was covered with rain Q3 forest (White 1987). The evolutionary history and changes in the breeding system among extant corvids was therefore also tested against habitat. The habitat was represented by forest structure categorized as closed or open which includes habitats ranging from forest edges to clearings, parklands, open brush land and desert.

Table 1. Latitudinal distribution of delayed dispersal and alloparental care within genera or for species to represent within-genera variation.

	breeding system		
species distribution	unassisted biparental care	delayed dispersal, no alloparental care	alloparental care
Northern	*Cyanocitta cristata* *Corvus monedula* *Nucifraga caryocatactes* *Garrulus glandarius*	*Cyanocitta stelleri* *Pica pica* *Perisoreus infaustus*	
Southern	*Cyanolyca nana*	*Cissa chinensis* *Dendrocitta formosae* *Cyanocorax yncas* *Pyrrhocorax*?	*Cyanocorax chrysops* *Cyanolyca viridicyanea* *Corvus corone* (Spain) *Cyanopica cyana* *Garrulus lidthi* *Zavattariornis stresemanni* *Perisoreus internigrans* *Urocissa erythrorhyncha*

4. RESULTS

Alloparental care is known for 27 (32%) corvid species out of 84 with known breeding system. With the exception of *Corvus caurinus* where help is rare (Verbeek & Butler 1981) and the cooperative *Covus corax* (Christensen & Grünkorn 1997), this list is identical to Cockburn (2003). The mating system of cooperatively breeding corvids ranges from monogamous pairs (for instance, Woolfenden & Fitzpatrick 1984) to colonial breeders (Brown 1990; Marzluff & Balda 1990). In addition, 26 solitary breeding species are recorded to live in family groups which in some of these species was be confirmed by in depth studies of colour-banded individuals, while another 24 species are recorded to live solitarily or in pairs. Thus, social cohesion is strong among corvids and a majority of species (69%; 53 out of 77 species with known social system) living in cohesive family groups.

(a) *Latitude effects*

There is a strong association between latitudinal distribution and alloparental care (table 2). A global model without any restrictions on the states at the root and based on the data in table 1 returned a strong association between absence of alloparental care and a northern distribution (likelihood ratio statistics = 12.5652, $p = 0.001$; for test procedure see §2). This result was robust to the inclusion of *C. yncas* (Texas population), *C. nana*, *A. californica* (likelihood ratio = 8.5816, $p = 0.001$; for test procedure see §2), where we lack data on branch length. Inclusion of these three solitary breeders with a southern distribution is conservative, while supporting the null hypothesis that lack of alloparental care is not linked to a northerly distribution.

Likewise a global model without restrictions on states at the root also including *C. yncas* (Texas population), *C. nana* and *A. californica* showed a strong association between latitudinal distribution and family cohesion (likelihood ratio statistics = 15.7766, $p = 0.001$; for test procedure see §2). The relationship between latitude and delayed dispersal remained significant (likelihood ratio = 12.8166, $p = 0.001$; for test procedure see §2) when we included *C. stelleri*, where the offspring retains a prolonged family cohesion (Brown 1963*b*) unlike in its congener

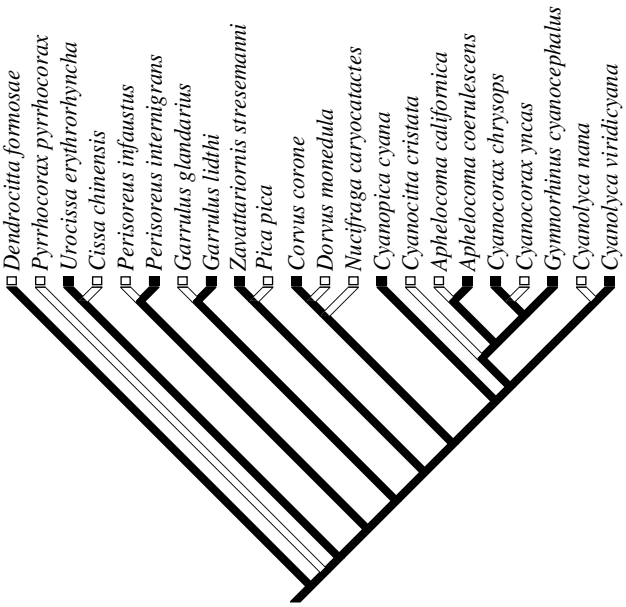

Figure 2. The reconstruction of the ancestral distribution of alloparental care by the DISCRETE software. Dark, alloparental care; light, no alloparental care; strippled, breeding system uncertain.

Cyanocitta cristata. Classifying the Steller jay as having delayed dispersal would be conservative, while it rather supports the null hypothesis that the ancestral state of natal philopatry has been retained at high latitudes. The analysis was robust to reduction in the tree by collapsing nodes for poorly studied species (*Cissa*, *Dendrocitta*) and consistently returned an association between latitude and family cohesion.

(b) *Ancestral states*

The correlation between breeding systems among corvids indicates a loss of alloparental care and delayed dispersal as they expanded their range northwards from having been the ancestral states (Cockburn 1996, 2003; Nicholls *et al.* 2000; Ligon & Burt 2004). Indeed, a global model without root restrictions and including *C. yncas* (Texas population), *C. nana* and *A. californica*, in addition to the terminal taxa in figure 1 returned a reconstruction of the

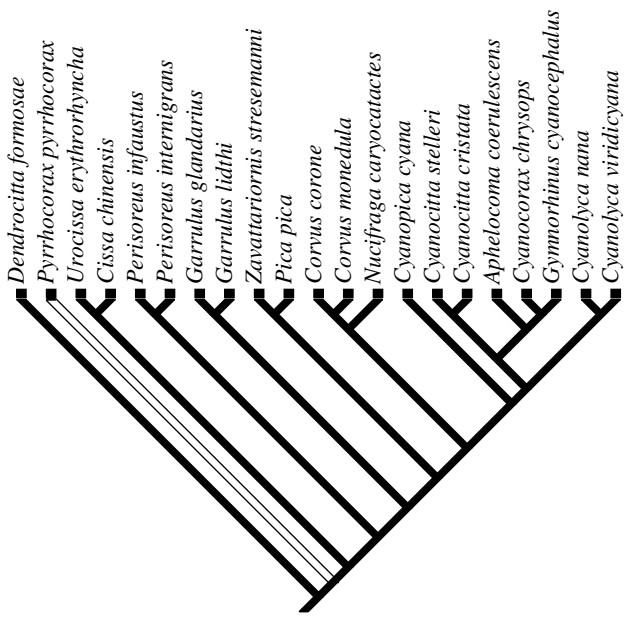

Figure 3. The ancestral distribution of family cohesion (delayed dispersal) by the DISCRETE software. Dark, family cohesion (delayed dispersal); light, no family cohesion among mature birds.

ancestral distribution with alloparental care at all internal nodes except for the one leading to the *Perisoreus* genus (figure 2, likelihood = −27.7255). Yet with a likelihood ratio statistics ≪ 1 in a local model, the character states at the root (alloparental care/no alloparental care) were not identified with significance. The reconstruction was however robust and returned alloparental care as the ancestral state also when nodes were collapsed or data removed for less well-studied genera (e.g. *Cissa*). A corresponding analysis including *C. stelleri* identified family cohesion (delayed dispersal) as the ancestral state at all internal nodes (figure 3, likelihood = −28.4550) and as the state at the root in a local model (likelihood ratio = 5.1932, d.f. = 1, $p = 0.05$). The reconstruction was robust to removing *C. stelleri*, *Cissa* and *Dendrocitta* and collapsing nodes close to the root.

(c) *Correlated evolution and the uncertainty of ancestral states*

To test for that the uncertainty in assignment of the ancestral states of characters, the probability of that alloparental care and delayed dispersal was correlated to latitudinal distribution was investigated further for all four possible combinations of character states at the roots (table 2). Latitude showed a significant association to both delayed dispersal and alloparental care for all combinations of character states at the root verifying that the association is robust to the uncertainty in assignment of ancestral states.

(d) *Habitat*

The analysis could not confirm a forest origin. A global model without root restrictions is consistent with the hypothesis that the ancestral habitat of the corvids was closed forest (likelihood = −36.4608). Yet, a local model could not reconstruct the states at the root with any significant, but both habitat states (closed forest/open forest) are equally likely.

5. DISCUSSION

We analysed cooperative breeding as a two-stage process, where family cohesion (delayed dispersal) is the permissive condition for alloparental care. There would be several caveats in confining the test for environmental correlates to cooperative breeding to species with alloparental care alone. Alloparental care could be selected against in cohesive families, which in the absence of alloparental care would be excluded from cooperative breeders and lumped with species having unassisted uni- or bi-parental care under the conventional definition of cooperative breeding. Apart from separating an understanding of the reasons for family cohesion as part of the explanation for cooperative breeding this could be artificial and misrepresent the processes promoting alloparental care. It would be more reasonable to see the breeding system and the role of extra-birds in cohesive families as the outcome of a parent/offspring conflict, where a solution with the offspring providing no care is just an endpoint to a continuum of different levels of alloparental care (Pruett-Jones 2004). The absence of alloparental care among species living in cohesive family units may hence be equally informative, as its presence to selection forces shaping cooperative breeding (Ekman *et al.* 2001*a*,*b*). Q4

Cooperative breeding is a more frequent breeding system among bird species with a distribution in tropical and subtropical environments on the Southern Hemisphere than in temperate and boreal regions of the Northern Hemisphere (Rowley 1968, 1976; Fry 1977; Brown 1987; Russell 1989). This latitudinal distribution with its inherent correlation between climatic region and breeding system has been a source of ideas for linking environmental factors to the evolution of cooperative breeding (Verbeek 1973; Brown 1974; Ford *et al.* 1988; Ekman & Rosander 1992; Du Plessis *et al.* 1995; Russell *et al.* 2004). Yet, so far the current evidence has identified this pattern as the result of a evolutionary inertia among the species-rich Passerida branch of the oscine passerines and their currently mainly Northern Hemisphere distribution (Cockburn 2003). This conclusion was based on the view that the Passerida conserved their ancestral pair-breeding system as they escaped from their Gondwanan origin via the Australo-Papuan region. This view has been challenged by the discovery of a deep divergence in the Passerida lineage revealing a second escape route out of Gondwanaland over South-Africa suggesting older history in Africa than previously assumed (Barker *et al.* 2004; Beresford *et al.* 2005). Among taxa representing the deep divergence of the African Passerida lineage there are cooperative species (e.g. rockjumpers genus *Chaetops*), calling into question both by which route the Passerida reached the Northern Hemisphere, their ancestral breeding system, and to what extent the Northern Hemisphere predominance of pair-breeding represents evolutionary inertia. Among corvids there could be several explanations to the latitude correlation to breeding system, but in common they are consistent with a response to latitude, where cooperation is selected against with a northerly distribution either because it is lost or it has not evolved secondarily like in congeners with a more southerly distribution.

The corvid family in its current form is likely to have originated outside Australo-Papua (Barker *et al.* 2004; Ericson *et al.* 2005), and low dispersal proneness among cooperative breeders indicates that the initial escape of the

Table 2. Test for correlation between latitude and delayed dispersal (family cohesion; above) and alloparental care by retainede offspring (below) for different states of latitude and trait value at the root.

root latitude (0=south; 1=north)	root delayed dispersal (0=no; 1=yes)	independent evolution log likelihood	dependent evolution log likelihood	likelihood ratio	*p*-value (chi-square test)
0	0	26.7601	22.2532	9.0136	0.01
0	1	26.7362	22.6439	8.1846	0.01
1	0	26.3002	21.9852	8.6300	0.02
1	1	26.2763	22.2880	7.9764	0.02
root latitude (0=south; 1=north)	**root alloparental care (0=no; 1=yes)**	**independent evolution log likelihood**	**dependent evolution log likelihood**	**likelihood ratio**	***p*-value (chi-square test)**
0	0	27.3419	24.8211	5.0416	0.02
0	1	27.3399	24.8450	4.9898	0.02
1	0	27.4979	24.3450	6.2878	0.02
1	1	27.4959	24.8538	5.2840	0.02

corvids lineage from the Australo-Papuan region may well have been by pair-breeding representatives from cooperative clades (Cockburn 2003). The initial diversification among the corvids would then have involved more dispersal prone pair-breeding taxa represented by genera, such as *Dendrocitta* and *Pyrrhocorax*. This initial diversification would then have been followed by a secondary evolution of alloparental care in the lineage leading away from these basal branches. Our global reconstructions could not identify the ancestral state of the breeding system in the corvid family although they trace their ancestry to highly cooperative Corvida lineages (Cockburn 1996, 2003; Nicholls *et al.* 2000; Ligon & Burt 2004). Our difficulties in identifying the ancestral state reflect a labile breeding system among the Corvida, where cooperative breeding has been lost and gained several times (Ligon & Burt 2004).

The reconstruction of ancestral states shows that cooperative breeding among corvids is a highly plastic trait with multiple transitions (figures 2 and 3), but it also indicates a diversity of selection forces involved in the response of the breeding system to latitude. The DISCRETE program did identify family cohesion as ancestral and the absence of cooperation is in several taxa (*C. cristata*, *C. nana*, *A. californica*, genus *Nucifraga*, *Garrulus glandarius/lanceolatus*, and numerous species within genus *Corvus*) associated with loss of family cohesion. In other species, the offspring do not provide alloparental care despite maintaining family cohesion (*Cissa*, *Dendrocitta*, *C. yncas*—Texas population, *Persisoreus infaustus/canadensis*, *Pica pica*, *C. stelleri*). These species maintain a social system that would be permissive to selection for alloparental care. Yet, they do not breed cooperatively. The most likely explanation for this absence of alloparental care among coherent families is that cooperative breeding is selected against. The prevalence of cooperative breeding among congeners with a southern distribution coupled to multiple transitions seems to eliminate evolutionary inertia among an ancestrally non-cooperative breeding system as explanation for its geographical pattern. Multiple transitions in breeding and social system among corvids reflect a highly plastic behaviour, and our results are consistent with an analysis of cooperative breeding in the acrocephaline warblers, where the breeding system was found to be equally labile with links to food abundance and habitat (Leisler *et al.* Q5 2002). This sensitivity of breeding systems to environmental conditions goes well together with family cohesion being responsive to manipulation of feeding conditions as well as the social environment (Komdeur 1992; Baglione *et al.* 2002*b*; Ekman & Griesser 2002; Covas *et al.* 2004), and raises the question whether a consistently cooperative breeding system within entire genera and over their entire ranges reflects should be taken as evidence for evolutionary inertia or a response to selection (Edwards & Naeem 1993).

The corvids evolved in an environment of rain forest (Feduccia 1995), but we found no support for that shifts in breeding system were correlated to an expansion of the distribution into more open habitats. Apart from entering more open habitats the corvids encountered seasonal environments with low ambient temperatures and short days in winter at the expansion of their range onto the Northern Hemisphere. While the offspring may delay dispersal for lack of independent breeding opportunities in a saturated environment (Brown 1969; Komdeur 1992), food-limited survival during temperate and boreal region winters (Jansson *et al.* 1981; Brittingham & Temple 1988) may reduce numbers to an extent that will lift constraints on independent breeding and dispersal (Verbeek 1973; Brown 1974). This can, however, not be the full explanation for the paucity of cooperative breeding, while there is a non-breeding surplus in many Northern Hemisphere populations and still the offspring do not postpone dispersal (Brown 1969). A non-random seasonal timing of natal dispersal on the Northern Hemisphere, where the offspring in species without delayed dispersal almost invariably leave before the energetically challenging winter (Russell *et al.* 2004), rather indicates avoidance of within-family competition driving the offspring to leave thus precluding delayed dispersal. Indeed, when dispersal is delayed it is also associated with relaxed aggression within families as seen in that parents share food with retained offspring in winter, while they deny unrelated group members such unhindered access to food (Scott 1981; Barkan *et al.* 1986; Ekman *et al.* 1994; Pravosudova *et al.* 2000; Dickinson & McGowan 2005). Such a joint one-way effect of adverse climatic conditions on

population saturation and parent behaviour would explain why cooperatively breeding corvids responded with loss of family cohesion (and hence alloparental care) to relaxed population pressure coupled to within-family competition in temperate and boreal climates, while the same condition would have allowed non-cooperative taxa to retain their ancestral breeding system of unassisted pair-breeding in the absence of family cohesion.

6. UNCITED REFERENCE

Q6 Ligon (1971).

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APPENDIX A. Information on social behaviour.

genus/species	
Dendrocitta formosae	Ali & Ripley (1972)
Pyrrhocorax pyrrhocorax	Holyoak (1972)
Urocissa erythrorhyncha	Severinghaus (1987)
Cissa chinensis	Ali & Ripley (1972)
Perisoreus infaustus	Ekman *et al.* (1994), Q8 Lillandt *et al.* (2003)
Perisoreus internigrans	Y.-H. Sun, personal communication
Garrulus lidhti	Bruce (1979)
Garrulus glandarius	Cramp & Perrins (1994)
Pica pica	Eden (1987)
Zavattariornis stresemanni	Q9 Fry *et al.* (2000)
Ptilostomus afer	C. Spottiswoode, personal communication
Nucifraga caryocatactes	Bent (1946), Rolando (1996), Rolando & Caristo (2003)
Corvus monedula	Cramp & Perrins (1994)
Corvus corone (Spain)	Baglione *et al.* (2002*a*)
Cyanopica cyana	Hosono (1983), Canario Q10 *et al.* (2004)
Cyanolyca viridicyanea	Cockburn, personal communication
Cyanolyca nana	Hardy (1971)
Cyanocitta stelleri	Brown (1963*b*)
Cyanocitta cristata	Bent (1946)
Q11 *Psilorhinus morio*	Skutch (1960)
Cyanocorax yncas	Bent (1946); Gayou (1987)
Cyanocorax chrysops	Brown (1974)
Aphelocoma californica	Carmen (2004)
Aphelocoma coerulescens	Woolfenden & Fitzpatrick (1984)

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