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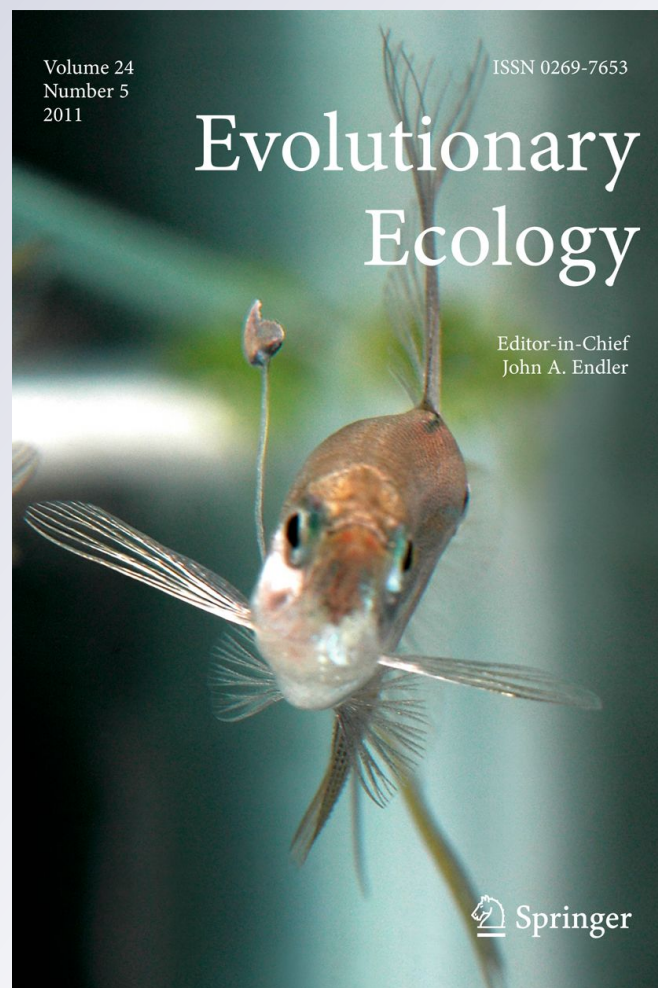
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New phylogenetic information suggests both an increase and at least one loss of cooperative breeding during the evolutionary history of *Aphelocoma* jays

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Abstract Efforts to identify ecological and life history factors associated with cooperative breeding have been largely unsuccessful, and interest is growing in the role of phylogenetic history in determining the distribution of this social system among lineages. In birds, cooperative breeding is distributed non-randomly among lineages, suggesting that phylogenetic inertia may play an important role in determining its distribution. The bird genus *Aphelocoma* has been particularly well studied because, although it is a relatively small genus, it shows broad among-lineage variation in level of cooperation. Previous analyses described an unusual unidirectional pattern of evolutionary loss of cooperation in *Aphelocoma*. Here, historical reconstructions based on new phylogenetic data suggest that evolutionary changes in cooperation have been bidirectional, with at least one gain and at least one loss over relatively recent timescales. This result emphasizes that, although history plays an important role in determining the incidence of cooperative breeding, cooperative behavior can switch relatively quickly in evolutionary time and may be influenced by the ecological context within which particular populations are distributed.

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Introduction

Cooperative breeding occurs when more than two individuals work together to raise the offspring from a single nest or brood. This social system has been documented in many taxa, including insects (Bourke and Franks 1995), mammals (Clutton-Brock 2002), fish (Taborsky 1994), and birds (Brown 1987). Over the past four decades, cooperative breeding has been the focus of considerable analysis and debate because it presents an evolutionary puzzle: why should individuals delay their own dispersal and individual breeding efforts to help to raise young that are not their own offspring? This question can be addressed at several different levels: (1) what are the underlying proximate neurological and physiological mechanisms that maintain cooperative breeding behaviors? (2) what are the evolutionary adaptive functions of these behaviors? Finally, (3) what is the evolutionary history of this trait complex over space and time?

Most research has focused on the second question, attempting to identify relative fitness benefits of cooperation for breeders and helpers (e.g., Emlen 1991; Koenig and Dickinson 2004), and the fitness advantages of cooperative breeding are now well established for many species (Cockburn 1998). In contrast, attempts to identify consistent ecological or life history correlates of cooperative breeding have met with limited success (Woolfenden and Fitzpatrick 1984; Ligon and Burt 2004; Hatchwell 2009). The list of possible factors that have been posited is long and somewhat contradictory: cooperative breeding has been positively associated with ecological constraint (e.g., habitat saturation: Emlen 1982; Komdeur 1992), stable and aseasonal environments (Ford et al. 1988; Arnold and Owens 1999), unpredictable seasonal environments (Du Plessis et al. 1995), tropical environments (Ekman and Ericson 2006), temporal environmental variability (Rubenstein and Lovette 2007), longevity (Arnold and Owens 1998), and delayed maturation (Covas and Griesser 2007).

Among birds, such ecological and life history-related hypotheses have helped to explain patterns of cooperation within particular species or lineages (e.g., Carrion Crow *Corvus corone corone*, Baglione et al. 2002, 2005, 2006; Seychelles Warbler *Acrocephalus sechellensis*, Komdeur 1992; African starlings, Rubenstein and Lovette 2007), but have not been able to predict consistently the distribution of cooperative breeding among taxa (Cockburn 1996). In other words, knowledge of the details of the ecology or life history of a species or population is not sufficient to allow prediction of whether it breeds cooperatively. This point suggests that different levels of analysis (*sensu* Sherman 1988) should be explored, investigating not only why cooperative breeding has evolved in certain taxa (i.e., immediate fitness benefits), but how this behavior has been passed down from generation to generation (i.e., evolutionary history).

Phylogenetic studies have revealed that cooperative breeding is distributed non-randomly in the avian tree of life (Edwards and Naeem 1993; Ligon and Burt 2004; Cockburn 2006), which implies an important role for phylogenetic inertia in determining the presence and absence of cooperative breeding in different lineages. For example, incidence of cooperative breeding is high in passerine lineages that diversified in Australia, particularly the Corvida (Dow 1980; Cockburn 1996; Ligon and Burt 2004). Twenty-four of the 36 (67%) higher taxa (tribe or above) of Corvida include at least one cooperative species

(Cockburn 1996). Because cooperative breeding appears to occur non-randomly within Corvida, comparative analyses within this lineage may be important in elucidating what factors influence its evolution.

Within corvids, the *Aphelocoma* jays have played an important role in this debate, owing to varying levels of cooperation within and among species (Peterson and Burt 1992). This well-studied genus includes species that are plural cooperative (i.e., multiple females within a flock breed with help from non-breeding individuals), singular cooperative (i.e., one breeding female with helpers), and non-cooperative. *Aphelocoma* is part of a larger radiation of New World Jays (Zusi 1987) in which cooperative breeding clusters phylogenetically (Brown 1987). Thus, given the wide range of geographic and ecological contexts in which New World Jays live, phylogenetic inertia has likely played a key role in maintaining cooperative breeding within this larger clade. The only previous detailed phylogenetic analysis of this question concluded somewhat controversially that dominant evolutionary trends within *Aphelocoma* were toward loss of cooperative breeding (Peterson and Burt 1992), although their analyses were based on a rather preliminary phylogenetic hypothesis.

Here, we revisit the question of phylogenetic and evolutionary trends in cooperative breeding in *Aphelocoma* jays based on a more definitive phylogeny with high node support for all relationships bearing on the reconstruction of cooperative breeding, and complete taxon sampling (McCormack et al. 2011). This phylogenetic hypothesis differs from that on which the previous studies were based (Peterson and Burt 1992) in ways that might influence the outcome of analyses. To examine how these revised and improved hypotheses of phylogenetic relationships affect interpretation of social evolution in *Aphelocoma*, here we develop new reconstructions of social evolution in the genus, and interpret results in the context of the time frame indicated by the new time-calibrated phylogeny (McCormack et al. 2011).

Materials and methods

Breeding behavior of *Aphelocoma* jays

New World jays are a lineage within the family Corvidae consisting of 5–7 genera distributed across much of the Americas (Madge and Burn 1994; Bonaccorso and Peterson 2007; Bonaccorso et al. 2010). New World jays are characterized by highly complex social behaviors that are strikingly variable among species. Among the best-studied and variable genera within this group is the genus *Aphelocoma*, which is made up of three species groups (Mexican Jays, Scrub-Jays, and Unicolored Jays) comprising 14 distinct lineages (at least five and as many as 14 species, depending on the species concept employed; see Pitelka 1951; Peterson 1992a; McCormack et al. 2008, 2011). *Aphelocoma* ranges from Central America to the northwestern United States (Fig. 1), inhabiting remarkably diverse habitats, from cloud forest and arid scrub to mangroves (Peterson and Vargas-Barajas 1993; McCormack et al. 2010).

We follow two previous studies of the phylogeny of cooperative breeding in *Aphelocoma* (Peterson and Burt 1992; Brown and Li 1995) by defining cooperative breeding as a categorical variable with three levels: (1) absence of cooperative breeding, (2) singular cooperative breeding (monogamous breeding pair with nonbreeding helpers), and (3) plural cooperative breeding (multiple breeding pairs within the same breeding territory, with nonbreeding helpers). These categories capture the major variation in breeding

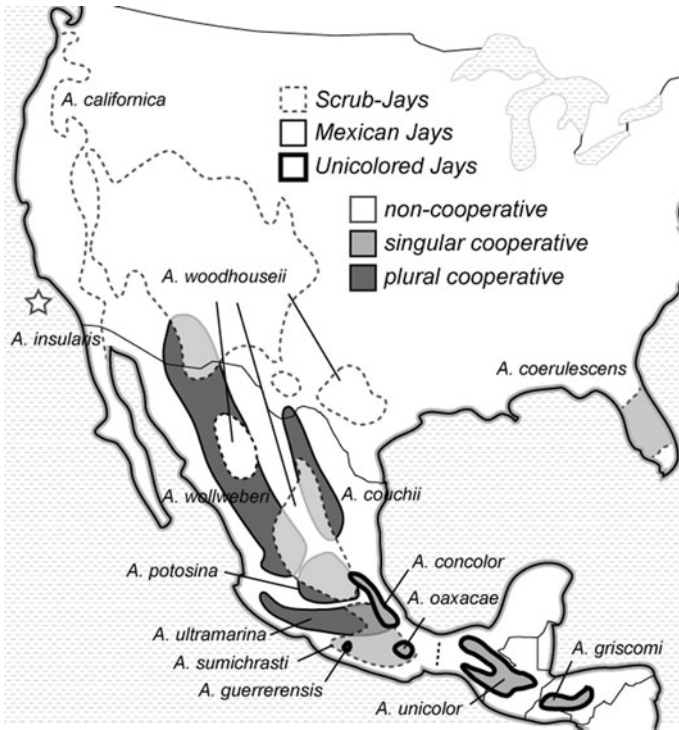


Fig. 1 Geographic distributions of *Aphelocoma* lineages used for character state reconstruction and their level of cooperative breeding. Distinct lineages are referred to by species-level binomials as in McCormack et al. (2011)

behavior detected in previous single-species studies (although it remains unclear whether group-living *A. sumichrasti* populations in Oaxaca have a fully functional cooperative-breeding system including helpers at the nest; Burt and Peterson 1993). For example, plural cooperative breeding occurs in Mexican Jays (McCormack and Brown 2008), whereas Florida Scrub-Jays (*A. coarulescens*) are singular cooperative breeders (Woolfenden and Fitzpatrick 1996). Evidence also suggests that Unicolored Jays (*A. unicolor*) are singular cooperative breeders (Webber and Brown 1994). Cooperative breeding is absent in the other three lineages of Scrub-Jays (*A. californica*, *A. insularis*, and *A. woodhouseii*; Curry et al. 2002).

Phylogenetic hypothesis

We have developed and published detailed analyses toward a definitive phylogenetic hypothesis for *Aphelocoma* based on an mtDNA tree with complete taxon sampling and high node support (McCormack et al. 2011; Fig. 2) that clarified many relationships left unresolved in previous studies. For our trait reconstruction, Steller's Jays *Cyanocitta stelleri* were used as an outgroup based on molecular evidence that *Cyanocitta* is the sister taxon to *Aphelocoma* (Bonaccorso and Peterson 2007), as well as on a unique (across all birds) osteological character found only in these two genera (Curtis and Miller 1938). Neither *Cyanocitta* species (*C. stelleri* and *C. cristata*) shows any cooperative behavior.

first as the most likely scenario, with 66% bootstrap support. Unpublished data from the same analysis indicated that only this topology and one where Mexican Jays diverged first (30% bootstrap support) appeared in the 95% confidence set of topologies. We analyzed our data using both topologies. Since the two likely topologies did not produce conflicting results for ancestral state reconstruction, we present the arrangement (Unicolored Jays diverging first) supported by the majority of bootstrap replicates in the multi-locus tree and with high support by the mtDNA tree.

For completeness, our phylogeny includes every distinct mtDNA lineage of *Aphelocoma*, including multiple divergent lineages within certain clades (e.g., *A. woodhouseii* and *A. arizonae*). Since these lineages always had the same character state for cooperative breeding, their inclusion is not expected to affect the analysis. Additionally, for estimating the timing of switches in cooperative behavior, calibrations like the one we rely on here that use a gene tree likely produce slightly older dates than calibration methods that use species trees (McCormack et al. 2011). For this reason, our calibrated phylogeny may be biased slightly toward older dates, but not in such a way as to substantively alter the conclusions.

Character state reconstruction

We examined the evolution of cooperative breeding only in the ingroup, the *Aphelocoma* jays, and reduced closely-related terminal taxa from McCormack et al. (2011) to single lineages. We used Mesquite 2.6 (Maddison and Maddison 2009) to map current cooperative breeding character states onto the *Aphelocoma* phylogeny under both parsimony and maximum likelihood frameworks. We used both methods since each has different strengths and weaknesses. Parsimony analyses find the ancestral states that minimize the number of steps given the phylogeny and the current distribution of characters. Although parsimony is more widely used in evolutionary reconstructions, it assumes that traits evolve at constant rates and that all character state transitions are equally likely (Cunningham et al. 1998; Pagel 1999; Huelsenbeck et al. 2003); as a consequence, parsimony approaches tend not to perform well when branch lengths are long or rates of character evolution are high, which could be the case in *Aphelocoma*.

Likelihood methods, in contrast, assign character state transitions that are most probable under particular stochastic models of evolution (Schluter et al. 1997; Pagel 1999). One advantage of this method over parsimony is that it takes into account phylogenetic branch lengths and degrees of support for ancestral states much more accurately and explicitly (Cunningham et al. 1998). Reconstructing character states under a likelihood framework assumes that the phylogeny accurately depicts evolutionary time. The phylogeny we used (McCormack et al. 2011) was time-calibrated using a combination of fossils and a molecular clock with the program BEAST 1.5.1 (Drummond and Rambaut 2007), and thus represents the best existing hypothesis for the timing of divergence events in the genus. Cooperative breeding was mapped onto this rate-smoothed phylogeny using branch lengths estimated from BEAST.

Results

Maximum-likelihood character-state reconstructions suggested that singular cooperative breeding is most likely the ancestral trait in *Aphelocoma*, although evidence supporting singular *versus* plural cooperative breeding is not massively different (Fig. 2). Singular

cooperative breeding was approximately 1.5 ($50/35 = 1.42$) times more likely than plural cooperative breeding, and both singular and plural cooperative breeding were at least twice as likely as non-cooperative breeding ($50/15 = 3.3$ and $35/15 = 2.3$, respectively). Parsimony analysis also indicated singular cooperative breeding as the ancestral state.

Moving toward the tips of the tree, parsimony and likelihood methods agreed that breeding behavior has involved at least one gain and at least one loss over the evolutionary history of *Aphelocoma* jays. The two analyses produced results that were largely congruent, but differed somewhat in their ability to assign character states at a few nodes (Fig. 2). Importantly, we found no highly-supported conflict between the two sets of results; the differences were mostly in the inability of either parsimony or likelihood to assign a character state at a particular node or branch. For example, although the maximum-likelihood method assigned nearly equal probability to singular cooperative breeding and non-cooperative breeding to the root node of the Scrub Jay clade (48% non-cooperative, 45% singular cooperative, 6% plural cooperative), the parsimony analysis assigned this node as singular cooperative breeding, suggesting that the Florida Scrub-Jay (*A. coerulescens*) retained cooperative-breeding from an ancestor. Both methods agreed that singular cooperative breeding was maintained in Unicolored Jays, while plural cooperative breeding evolved in the Mexican Jay complex only. Within Scrub-Jays, the likelihood analysis strongly supported a scenario in which cooperative breeding was lost after Florida Scrub-Jays diverged from the rest of Scrub-Jays (non-cooperative breeding was 5.6 ($84/15$) times more likely than singular cooperative breeding), but was then regained in the *A. sumichrasti* lineage. However, parsimony analysis could not assign a state to these internal nodes within the Scrub Jay clade, leaving open the possibility that cooperative breeding was retained for longer in Scrub Jays and then lost twice independently in *A. woodhouseii* and the ancestor of *A. californica* and *A. insularis*.

Discussion

Our study contributes to the growing number of phylogenetic analyses that examine evolutionary gains and losses of social behavior in a variety of taxa (e.g., bees in the family Halictidae and Apidae, Wcislo and Danforth 1997; communally roosting birds, Beauchamp 1999; cooperatively breeding African starlings, Rubenstein and Lovette 2007). The most important conclusion of our study is that cooperative breeding behavior in *Aphelocoma* may have evolved bidirectionally with respect to cooperation, and not unidirectionally as a previous phylogenetic reconstruction suggested (Peterson and Burt 1992). Our analyses suggest that cooperative breeding in this group has increased in some lineages (a transition from singular to plural cooperative breeding in the Mexican Jay group, agreed upon by both likelihood and parsimony, and a possible transition from non- to singular cooperative breeding in Scrub Jays according to likelihood) and has been lost in at least one case (either once early in the history of Scrub Jays according to likelihood, or possibly twice recently in Scrub Jays because parsimony could not assign states to some internal Scrub Jay branches). Our interpretation is based in large part on new phylogenetic information, demonstrating how accurate phylogenies are crucial to understanding the evolution of cooperative breeding (e.g., Edwards and Naeem 1993) and trait evolution in general (e.g., Hackett et al. 2008). Because the phylogeny is taxonomically complete and received high bootstrap support for all major nodes bearing on the reconstruction of cooperative breeding (except the basal node, where results did not differ depending on the particular branching pattern), our results should be considered robust.

A phylogenetic study by Peterson and Burt (1992) suggested unidirectional change toward loss of cooperative breeding in *Aphelocoma*. Their phylogeny—based on a rather uncomfortable parsimony analysis of allozyme distribution among *Aphelocoma* populations (Peterson 1992a)—suggested paraphyly of plural-breeding Mexican Jays, and placed one lineage of Mexican Jays sister to Scrub-Jays, which led to the conclusion that plural breeding was the ancestral trait in the genus. Further, the next two branching events reconstructed in the Scrub-Jay clade involved singular-breeding cooperative lineages of Scrub-Jays (*A. coerulescens* and *A. sumichrasti*), giving the impression that social complexity was reduced successively (Peterson and Burt 1992). In contrast, McCormack et al. (2011) recovered Mexican Jays as a strongly supported monophyletic group, leading to the result supported by both likelihood and parsimony that plural cooperative breeding is a derived trait that arose in this group only once.

The second study to tackle the evolutionary history of sociality in *Aphelocoma* was by Brown and Li (1995), who re-analyzed Peterson's (1992a, b) phylogeny and came to conclusions opposite those of Peterson and Burt (1992). Brown and Li's (1995) results suggested that non-cooperative breeding was the basal trait; however, for reasons explained in detail in Rice et al. (2003), their unorthodox incorporation of adaptive, cooperation-related traits in their character-state matrix indicates that their analyses should be interpreted with caution. Finally, our results also differ from Rice et al.'s (2003) more recent phylogenetic analysis of *Aphelocoma* ecology and behavior. Although the phylogeny they derived was more similar to that of McCormack et al. (2011) than to that of Peterson (1992a, b), their phylogeny indicated that Florida Scrub-Jays were nested within the Scrub Jay complex, forming a clade with the inland populations of Western Scrub-Jays, *A. sumichrasti* and *A. woodhouseii*.

In contrast, McCormack et al. (2011) identified Florida Scrub-Jays as the first-diverging lineage of the Scrub-Jay complex. In addition, the new phylogeny supports a distinct lineage of Scrub Jays from southern Mexico (*A. sumichrasti*) that show some degree of cooperative behavior as nested phylogenetically among non-cooperative lineages of Scrub-Jays. These two phylogenetic differences lead to the conclusion either that cooperative breeding was lost early in the history of Scrub Jays (but after the divergence of *A. coerulescens*) only to be regained recently in *A. sumichrasti* (according to likelihood analysis) or that cooperative breeding was retained for longer in the Scrub Jays and then lost twice independently in *A. woodhouseii* and the ancestor of *A. californica* and *A. insularis*—the parsimony analysis did not support this result, but also could not reject it based on an equivocal state reconstruction for internal Scrub Jay branches. Interestingly, the only behavioral study of *A. sumichrasti* to date (Burt and Peterson 1993) suggests that helpers may not actually assist in feeding young or brood care, perhaps indicating an incomplete transition from non-cooperation to cooperation in this lineage, but detailed information is lacking.

Given the timing of diversification indicated by the calibrated phylogeny of McCormack et al. (2011), switches in cooperative behavior would have occurred beginning in the Miocene, and continuing in the Pliocene and Pleistocene, relatively recently compared to other studies on this subject, which show switching in cooperative behavior over much deeper timescales (e.g., Rubenstein and Lovette 2007). This result suggests that cooperative breeding behavior, although likely governed to some extent by phylogenetic inertia, can change over relatively short evolutionary time scales. It also suggests that, when lost, the necessary architecture for cooperative breeding—be it genetics, life history, or both—remains, facilitating its reemergence. What makes this point particularly interesting is that, to the extent that it has been studied, *Aphelocoma* jays do not appear particularly plastic in

their expression of cooperative breeding at the intraspecific level. For example, the *A. couchii* lineage of Mexican jays shows group living and cooperative behavior throughout a wide array of habitats (J.E.M., pers. observ. 2002–2007; McCormack and Brown 2008; but see some reports to the contrary, e.g., Strahl and Brown 1987), despite the fact that some of these low-elevation habitats are similar to those used by non-cooperative Western Scrub-Jays (McCormack and Smith 2008). One possible exception is *A. sumichrasti*, in which populations from farther west in southern Mexico in the state of Guerrero are likely not group-living (A.T.P., unpubl. data); however, detailed studies of this lineage are lacking, and there is little hard evidence indicating plasticity in levels of cooperation. Hence, the switches observed between cooperative and non-cooperative breeding in *Aphelocoma* do not appear to be part of a flexible continuum of behavior, making it all the more impressive that they have occurred in such quick succession.

Why have these behavioral switches occurred in *Aphelocoma* jays, and particularly within the Western Scrub-Jay complex? Although history is clearly important, for example in the Mexican Jay clade, ecology may be playing a key role. Western Scrub-Jays occur in the most ecologically diverse habitats of any of the major *Aphelocoma* lineages (Peterson and Vargas-Barajas 1993), and are known to have responded evolutionarily to many distinct habitat types (Peterson 1993; Bardwell et al. 2001). Unlike Uicolored Jays and Mexican Jays, many non-cooperative Western Scrub-Jay lineages also live in low-elevation arid habitats, which could facilitate habitat viscosity and lead to overall higher levels of dispersal, conditions that are not thought conducive for cooperative breeding to be maintained (Hamilton 1964; Peterson 1992b). Further, the time-calibrated phylogeny suggests that the loss of cooperative breeding in Western Scrub-Jays occurred sometime from the late Miocene through Pliocene, at a time when the arid scrub landscape preferred by Western Scrub-Jays had recently emerged (Axelrod 1979). Meanwhile, niche models support the view that Mexican Jay geographic ranges remained surprisingly stable during the Last Glacial Maximum (Peterson et al. 2004). As a middle-elevation species confined to a relatively specific niche, habitat saturation could explain the maintenance and further development to plural cooperative breeding in this group. Other factors might also play a role; in the corvid family, for example, cooperative behavior appears to decline with increasing latitude (Ekman and Ericson 2006), a pattern that appears to hold in *Aphelocoma* (Fig. 1). Ultimately, these questions might best be answered through methods that assess how patterns of genetic similarity vary with past and current ecology (e.g., through niche modeling) and whether these patterns associate with the gain or loss of cooperation among *Aphelocoma* sister taxa.

In conclusion, studies like ours that combine novel phylogenetic information with behavioral data are crucially important, since they allow reconstruction of the evolution of social and breeding systems both within and among lineages. Specifically, such studies can help to tease apart the influence of phylogenetic constraints versus historical (and current) ecological conditions on the evolution of complex social behaviors such as cooperative breeding. This insight is particularly true for *Aphelocoma* jays, not only because cooperative breeding behavior within this group is so variable, but because we now have the extensive ecological, behavioral, and phylogenetic data needed to reconstruct trait evolution accurately.

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