

# Phylogeny, specialization, and brood parasite–host coevolution: some possible pitfalls of parsimony

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Coevolutionary hypotheses (COEV) predict that parasitic birds become more specialized in host selection over time as more host species evolve defenses. A contrasting model, PHYLO, suggests that brood parasites exhibit a phylogenetic trajectory toward increasing generalization because there is a positive correlation between present-day numbers of host species and the branching order of parasitic cowbird species in a DNA-based phylogeny. However, this apparent phylogenetic pattern does not conflict with COEV, as some have concluded. Assuming allopatric speciation, which is supported by an area cladogram, COEV predicts a correlation between branching order and host number because the potential hosts of the earliest cowbirds to branch off have had the greatest amount of time to evolve defenses. Although PHYLO is more parsimonious than COEV, the difference is trivial, with the latter requiring only one more evolutionary change in the entire cowbird clade to produce the pattern that exists today. Support for COEV over PHYLO comes from brood parasitic cuckoos, which are much more specialized than parasitic cowbirds and represent an older clade, as shown by new DNA data. Cuckoos also have lower interspecific variance in host numbers than do cowbirds, which conflicts with PHYLO. Unlike COEV, which assumes that the number of hosts a parasite uses is related at least as much to present ecological conditions as to phylogenetic history, PHYLO assumes that current host numbers reflect historical character states. However, host number is labile, with as much variation within as between species. Nor are published host numbers reliable measures of parasite host selectivity, as they are due in part to researcher effort and range size. Although the comparative approach can provide insights into evolutionary history, some coevolved features may be too dynamic to retain a phylogenetic signature, and, in the case of parasitic birds, neither PHYLO nor COEV can be invalidated, although the latter is more consistent with available evidence. Strict adherence to parsimony may often be inappropriate when assessing coevolved characters. *Key words:* brood parasitism, coevolution, cowbirds, cuckoos, generalist, parsimony, phylogenetic reconstruction, specialist. [*Behav Ecol* 13:1–10 (2002)]

A commonly addressed issue in studies of parasite–host evolution is the large range in the numbers of host species used by various parasites (Thompson, 1994). Birds that are obligate brood parasites and the species that serve as their hosts are especially interesting in this regard because of the large range in number of host species, 1 to > 200, used by different parasitic birds. Accordingly, parasitic birds and their hosts have been the subject of numerous recent studies dealing with parasite–host coevolution (Davies and Brooke, 1989a,b; Lotem et al., 1992, 1995; Marchetti et al., 1998; Rothstein, 1990; Sealy, 1996; Soler and Møller, 1990, 1996) and have been the subject of several books (Davies, 2000; Johnsgard, 1997; Ortega, 1998; Rothstein and Robinson, 1998). In this article, we contrast two conflicting hypotheses dealing with the evolution of host use in parasitic birds. The first hypothesis is that parasitic birds become more specialized over time by using fewer host species and the second is that parasitic birds become more generalized over time.

The hypothesis of increasing specialization was proposed because hosts often evolve defenses against parasitism, such as rejection of foreign eggs, in response to reproductive losses

incurred by parasitism. Parasites in turn often evolve counter-defenses, such as mimicry of host eggs. These counterdefenses must be specific to a single host species or to a group of hosts with similar features, such as similar egg types. Because genetic constraints do not allow a single population to simultaneously maintain numerous alternative character states, such as many different mimetic egg types, parasitic birds should parasitize a smaller number of host species as time passes and as more and more potential host species evolve defenses. Thus, this body of coevolutionary theory (hereafter COEV) predicts that a parasitic bird will become more specialized the longer it is in contact with a particular avifauna (Davies and Brooke, 1989a; Lotem and Rothstein, 1995; Rothstein, 1990).

The alternative to COEV is derived from a phylogeny of parasitic cowbirds (*Molothrus* spp.) based on DNA sequence data (Johnson and Lanyon, 1999; Lanyon, 1992; Lanyon and Omland, 1999). The proposed order in which cowbird species branched off from the rest of their lineage is correlated with current numbers of known host species, ranging from one in the earliest branching species to > 200 for each of the two most recently derived ones (Lanyon, 1992). This correlation led to the conclusion (Alcock, 1993; Lanyon, 1992; Thompson, 1994), based on parsimony, that cowbirds show a phylogenetic trajectory toward generalization (hereafter PHYLO) and that this trend toward increased generalization conflicts with COEV.

While we accept the proposed cowbird phylogeny (it is consistent with DNA sequence data from two different genes), we argue that the relationship between this phylogeny and host number is not in conflict with COEV. First, we review COEV

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and trends in host use that might be seen in a clade of brood parasitic birds. Next, we show through use of an area cladogram and consideration of likely speciation processes that the correlation between branching order and current host numbers in cowbirds is compatible with both COEV and PHYLO, although the former provides a more cogent explanation. Although PHYLO is more parsimonious than COEV, we demonstrate that the difference is trivial, with the latter requiring only one more evolutionary change in the entire cowbird clade to produce the pattern that exists today. We also address the assumption according to PHYLO that current host numbers reflect historical character states and show that host numbers are instead labile features sometimes showing as much variation within species as between species. Nor are published host numbers reliable measures of parasite host selectivity, as they are due in part to researcher effort and range size. Finally, we present new molecular data on parasitic cuckoos (Cuculinae) that show that this group is older than the cowbird clade and is more specialized, a result consistent with COEV but in conflict with PHYLO. A point central to much of this article is the argument that present numbers of host species are not reliable guides to the numbers of hosts parasites had in the past (see also Davies and Brooke, 1998; Freeman and Zink, 1995) and cannot reveal whether specialization or generalization is the primitive condition. Our results agree with Schluter et al. (1997), who showed that determinations of ancestral character states via parsimony can have large degrees of uncertainty, especially for characters that are continuous, such as host numbers used by parasitic birds, rather than discrete, and that evolve rapidly (see also Frumhoff and Reeve, 1994).

### A review of parasite–host coevolution in birds

COEV predicts that a parasite's selectivity among hosts is a labile trait that varies inversely with the extent to which potential hosts have effective defenses against parasitism. The amount of time over which potential hosts have been exposed to parasitism will be a major determinant of their level of defenses. Thus, the longer a parasite interacts with a particular array of potential hosts, the more likely it is to be specialized; in other words, for any given interaction between a particular parasite and a particular avifauna, relative generalization is likely to be followed by specialization, regardless of a parasitic species' position in a phylogeny. The transition from generalist to specialist could be gradual, or it might occur in one or more major steps (Rothstein, 1976).

COEV allows for two exceptions to the trend toward increasing specialization. First, a specialized parasite should become more generalized if it colonizes a region where potential hosts are largely lacking in defenses. Second, if the first obligately interspecific parasite in a clade evolves from an intraspecific parasite (Hamilton and Orians, 1965; Payne, 1977; Rothstein, 1993), it might initially have a narrow host range but should become more generalized if there are unparasitized hosts without defenses. Nevertheless, in both of these cases, the transition from specialist to generalist is likely to be followed by increasing specialization as more hosts develop defenses.

In addition to time, the likelihood that hosts will have evolved defenses also depends on the abundance of parasites, which may include all parasitic species in a region. Parasite abundance is important because it in part determines rates of parasitism (Hoover and Brittingham, 1993) and rates parasitism are a major determinant of the selective value of host defenses (Davies et al., 1996; Rothstein, 1975a). Other species of parasites can be important because host defenses, such as egg recognition, are not necessarily specific to the parasite(s)

that a host experiences (Rothstein, 1982a,b). Thus, defenses evolved in response to one parasite can give hosts protection against other parasitic species.

Host defenses are not the only determinant of a brood parasite's degree of specialization. Even in the absence of host defenses, different sympatric parasitic species may specialize on different host species to minimize interspecific competition (i.e., two parasites using the same host nest) (Brooker and Brooker, 1989a; Friedmann, 1967). Intraspecific competition for hosts may also be a factor. A parasite that is relatively uncommon may specialize on a limited set of high-quality hosts because individual host nests will rarely be parasitized more than once. But if a parasite is abundant, selection may favor parasitizing a wider range of host species, even poor quality ones, to avoid competition in multiply parasitized nests. So regardless of its branching position in a phylogeny, COEV states that a parasitic species can be a generalist or a specialist depending on the number of potential hosts that have effective defenses and on the intensity of interspecific and intraspecific competition for hosts. Nevertheless, most generalist parasites should become more specialized the longer they are in contact with a particular avifauna.

A specialized parasite confronted with a community of potential host species, nearly all of which have well-developed defenses, may eventually reach a fairly constant level of specialization in which parasitism is concentrated on a handful of species. However, even this situation may be dynamic because the particular species parasitized may change over time (Brooke and Davies, 1987; Davies and Brooke, 1989a; Nakamura et al., 1998; Rothstein, 1990). A parasite may shift away from a host whose defenses become highly efficient and begin to use a past host that has lost all or some of its defenses in the absence of parasitism, although the period over which host defenses are retained in the absence of parasitism may be considerable (Bolen et al., 2000; Hosoi and Rothstein, 2000; Rothstein, 2001). Thus, over time, a specialized parasite may cycle through a large number of host species, even though only one or a few are used at any one time (Marchetti, 1992). In sum then, COEV assumes that the current number of hosts a parasite uses is related at least as much to the ecological circumstances it faces as to its phylogenetic history, whereas PHYLO gives priority to phylogenetic history.

In this article, we provide four major results: (1) an area cladogram that considers speciation mechanisms and shows that COEV predicts the present-day relation between branching order and cowbird host numbers; (2) an analysis that shows that COEV and PHYLO differ only slightly in terms of parsimony; (3) data showing that published lists of hosts are subject to biases that necessitate caution when used to assess evolutionary hypotheses; and (4) tests that use cowbird and cuckoo data to distinguish between COEV and PHYLO. These latter tests are based on the pattern that prompted formulation of PHYLO (i.e., host number increases with time and/or cladogenic events). Thus, species in older and/or more speciose clades of parasites should use more host species than parasites in younger, less speciose clades. Similarly, because PHYLO assumes that specialization is the primitive state, that host number retains a significant phylogenetic signature, and that host number increases with time and/or speciation events, it predicts that older clades of parasites show greater interspecific variation in host numbers than younger clades. COEV predicts that members of older parasitic clades use fewer host species, but makes no clear prediction regarding interspecific variation in host numbers because it assumes that many factors affect host number. We test these predictions using published DNA data on cowbirds and new DNA data on parasitic cuckoos to assess the relative ages and host numbers of these two clades. More specifically, we predicted that par-

asitic cowbirds are a younger clade than parasitic cuckoos because the cowbirds comprise 5 similar species in a single genus whereas the parasitic cuckoos include about 50 species and 12 genera with a remarkable range of colors, sizes, and forms (Johnsgard, 1997; Wyllie, 1981). Given our prediction about the ages of these clades, which was confirmed, cuckoos should have more host species and greater variance in host number than cowbirds if PHYLO is correct.

## METHODS

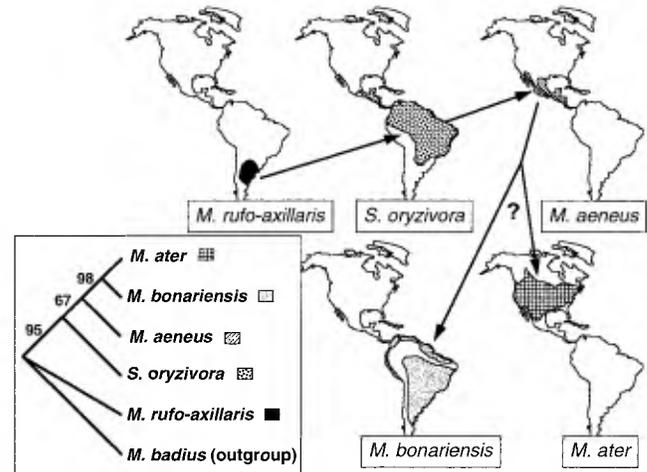
To assess the degree of genetic divergence among cowbird species, we used Lanyon's (1992) DNA data to compute Kimura two-parameter distances (Kimura, 1980), which correct for multiple basepair substitutions ("multiple hits"), for each pair of taxa within the parasitic cowbirds. Distances were used in MEGA (Kumar et al., 1994) to construct a neighbor-joining tree with a topology identical to that of Lanyon's maximum parsimony tree. To assess the extent of sequence divergence among parasitic cuckoos, we sequenced 484 basepairs of the cytochrome b gene from the common cuckoo (*Cuculus canorus*) and compared homologous sequences from GenBank for the oriental cuckoo (*C. saturatus*; Chikuni K et al., unpublished data; accession number 556489) and from Avise et al. (1994) for the pallid cuckoo (*C. pallidus*).

We determined the numbers of hosts used by parasitic cowbirds and cuckoos from the literature (especially Johnsgard, 1997), even though some species in host lists are rare hosts whose parasitism has little biological significance because they raise few or no parasites. Indeed, we discuss various problems with the use of such lists below, but we use this information nevertheless to make our analyses objective and compatible with analyses used to formulate PHYLO.

## RESULTS

### Speciation, cowbird branching order, and specialization: an alternative to PHYLO

Partly because speciation events often involve dispersal to new regions, especially in birds (Chesser and Zink, 1994; Mayr, 1963), it is likely that the amount of time each cowbird species has been in contact with its potential hosts is proportional to its branching position in the cowbird phylogeny. In other words, the earliest species to diverge have undergone the most prolonged coevolution with their particular array of potential hosts and accordingly have become more specialized even in the absence of cladogenesis. Therefore, greater specialization in the earliest branching species is predicted by COEV and not in conflict with it. To assess these hypothesized relationships among branching order, host numbers, and speciation via dispersal, we constructed an area cladogram (Figure 1) for parasitic cowbirds using historical range distributions from Friedmann (1929). The area cladogram indicates a shift to an allopatric region with each subsequent split or speciation event, most of which involved a northward expansion of the clade. The split from *M. rufoaxillaris* to *Scaphidura oryzivora*, for example, involved a range expansion from southern South America to northern South America and Central America (Figure 1). Likewise, any ordering of the splits from the *M. aeneus* to *M. ater* and *M. bonariensis* involves major changes in geographic ranges (from Central America to North and South America and the Caribbean). Our interpretation of this area cladogram is that speciation events in the cowbird radiation generally involved dispersal to a region where few or no cowbirds existed. Each cladogenic event was associated with a cowbird species becoming sympatric with a new suite of relatively naive host species, except that most of the area occupied



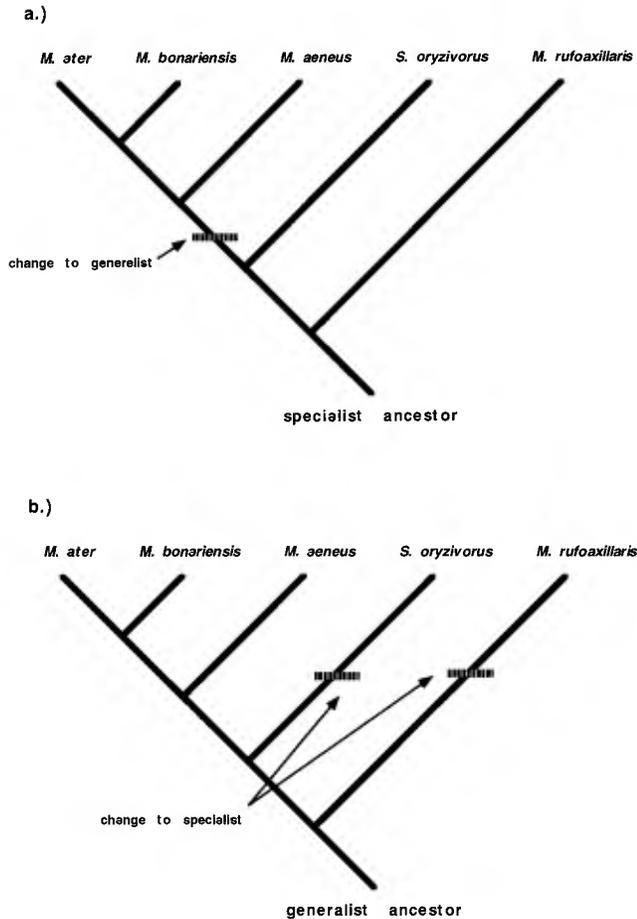
**Figure 1**

An area cladogram for the parasitic cowbirds. Shown is the single most parsimonious tree obtained using the exhaustive search on PAUP (Swofford et al. 1993) and the cytochrome b data set of Lanyon (1992). Numbers are the percentage of trees containing the adjacent node following a 250-replication bootstrap. The approximate ranges shown are from Friedmann (1929) and do not show the recent colonizations of Florida by *M. bonariensis* and *M. ater*. Note that three of four cowbird species that branched off after the first parasitic species (*M. rufoaxillaris*) branched off appear to have colonized geographic ranges previously unoccupied by the clade. The only exception, *M. bonariensis*, occupied a range that was mostly already occupied by *S. oryzivora* but might still have encountered a largely naive host community because the large size of the latter species limits it to a small number of hosts (see text).

by *M. bonariensis* was already occupied by *S. oryzivora* (Figure 1). However, this area was still largely devoid of a cowbird capable of parasitizing a large number of host species, because the huge size of *S. oryzivora* limits its number of hosts (assuming *S. oryzivora* has always been large).

### Parsimony and COEV versus PHYLO

PHYLO provides the most parsimonious explanation for the relation between host number and the branching order of cowbird species. But how much more parsimonious is PHYLO than COEV? Assume cowbirds have two levels of host specialization: specialized, as characterized by *M. rufoaxillaris* and *S. oryzivora*, each of which has 10 or fewer host species, and generalized as in *M. aeneus*, *M. ater*, and *M. bonariensis*, each of which has at least 80 hosts (Friedmann et al., 1977; Friedmann and Kiff, 1985; Lowther, 1995). Under PHYLO, the ancestral cowbird was a specialist, and the clade underwent one major evolutionary change with regard to host numbers, a change from specialized to generalized between the appearance of *S. oryzivora* and *M. aeneus* (Figure 2a). Under COEV (Figure 2b), the ancestral cowbird was a generalist that gave rise to *M. rufoaxillaris*, which then became specialized. A generalist then gave rise to *S. oryzivora*, which also became specialized after splitting off from the lineage. Thus COEV requires two evolutionary steps to produce the pattern seen today, whereas PHYLO requires one step. The difference in number of minimum steps between COEV and PHYLO would still be one if more levels of character states regarding host numbers were used in the analysis (e.g., specialized, intermediate, and generalized).



**Figure 2**  
 (a) The cowbird phylogeny showing the most parsimonious evolutionary history regarding specialist and generalist use of hosts according to the phylogenetic trajectory hypothesis (PHYLO). In keeping with parsimony, the switch from specialist (few hosts) to generalist (many hosts) is considered to be a single character state change. (b) The cowbird phylogeny showing the most parsimonious evolutionary history regarding specialist and generalist use of hosts according to the coevolutionary hypothesis (COEV). In keeping with parsimony, the switches from generalist (many hosts) to specialist (few hosts) are considered to be single character state changes.

### Biases inherent in published lists of hosts

The goal in assessing hypotheses such as COEV and PHYLO that deal with specialization is to determine the degree of selectivity a parasite expresses. Selectivity is more important than the number of known hosts because the latter can be influenced by extraneous factors such as the amount of research effort that has been applied to a parasite–host community and the number of potential host species that are sympatric with a parasite. An important determinant of sympatric host species is a parasite's range size. Published literature is much more extensive for the North American *M. ater* than for other cowbird species, all of which occur primarily or exclusively south of the United States. If research effort is a bias, new hosts should become known at a more rapid rate for these other cowbird species than for *M. ater*, for which there were numerous data more than a century ago (Bendire, 1893). Since Lanyon (1992) proposed PHYLO using published host lists, the known hosts of *M. rufoaxillaris* have increased threefold, from one to three (Mermoz and Rebores, 1996; Sick, 1993). Since Friedmann's (1929) classic host com-

pilation, the list of known hosts has increased by 39% for *M. ater*, from 158 in 1929 to 221 species at present (De Gues and Best, 1991; Lowther, 1993). In contrast, hosts of *M. bonariensis* increased 145%, from 82 to 201 species, and those of *M. aeneus* increased 413%, from 16 to 82 species, over the same period (Friedmann and Kiff, 1985; Lowther, 1995). The proportion of known hosts added since Friedmann (1929) is significantly smaller in *M. ater* than in *M. bonariensis* ( $\chi^2 = 41.2$ ,  $p < .001$ ) and *M. aeneus* ( $\chi^2 = 61.2$ ,  $p < .001$ ).

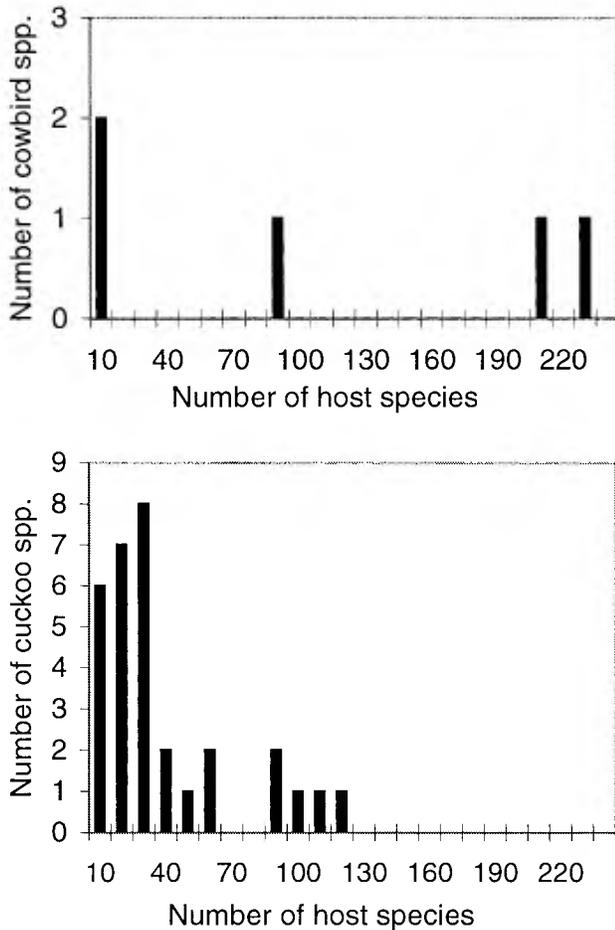
Parasitic cowbirds are arranged as follows according to range size, smallest to largest (Figure 1): *M. rufoaxillaris* (3 host species), *M. aeneus* (82), *S. oryzivora* (7), *M. ater* (221), and *M. bonariensis* (201). Thus, host number correlates well with range size among parasitic cowbirds, except for *S. oryzivora*, which has the third largest geographic range and the fourth largest host number. However, this species' relatively large body size, reflected in its common name (giant cowbird), restricts it to a limited subset of hosts. The volume of *S. oryzivora* eggs is three to five times that of the eggs of other parasitic cowbirds (based on measurements in Friedmann, 1929) and few passerine species are large enough to be suitable hosts.

### Differentiating between COEV and PHYLO: the relative ages and host numbers of the cowbird and cuckoo clades

The corrected DNA sequence divergence for cytochrome b of the entire radiation of parasitic cowbirds averages 4.0%, and the maximum divergence between the first species to branch off, the screaming cowbird (*M. rufoaxillaris*) and the other four taxa averages only 5.7%. Fleischer et al.'s (1998) calibration of the cytochrome b nucleotide substitution rate for passerine birds (see also Klicka and Zink, 1997) allows an estimate of the time each cowbird species has coexisted with its hosts. Applying the calibration of 1.5–2.0% divergence per million years to the radiation of parasitic cowbirds indicates that the most specialized species, *M. rufoaxillaris*, separated from the lineage leading to other parasitic cowbirds 2.8–3.8 mya. The most recent divergence, which is between the species that are the most generalized, the brown-headed and shiny cowbirds (*M. ater* and *M. bonariensis*), dates to about 0.8–1.2 mya.

The cytochrome b data for cuckoos (*Cuculus* spp.) support a close relationship between *C. canorus* and *C. saturatus*, which are sympatric in Eurasia and have a corrected divergence of only  $0.8 \pm 0.4\%$ . But *C. pallidus*, which occurs in Australia, has a corrected divergence of  $12.0 \pm 1.7\%$  with *C. saturatus* and  $12.6 \pm 1.8\%$  with *C. canorus*. The sequence differences between *C. pallidus* and its two congeners are more than twice as great as for the entire cowbird radiation and indicate that cuckoos have been parasites for at least 6.3–8.4 million years. Arbogast and Slowinski (1998) argued that a calibration of 1.5–2% substitutions per million years is 2.5 times too slow, but these arguments have been rebutted (Klicka and Zink, 1998). Regardless of which calibration is correct, cuckoos in the subfamily Cuculinae have likely been parasites at least twice as long as cowbirds have.

Given molecular data indicating that cuckoos have a longer history of parasitism than cowbirds, PHYLO predicts that they should be more generalized than cowbirds, whether it is based on time alone or on the number of speciation events. COEV predicts the reverse (i.e., cuckoos should be more specialized than cowbirds). Figure 3 shows frequency distributions of the numbers of known hosts for cowbirds and cuckoos using data from various sources for cowbirds (Friedmann and Kiff, 1985; Lowther, 1995) and cuckoos (Baker, 1942; Becking, 1981; Brooker and Brooker, 1989b; Fry et al., 1988; Johnsgard, 1997; Wyllie, 1981). The five cowbirds have a mean of 102.8 hosts



**Figure 3**  
Numbers of hosts known to be used by different species of parasitic cowbirds and cuckoos. See text for data sources.

and a median of 82, compared to 34.3 and 22.5 for the cuckoo species. The most generalized cuckoos are *Cuculus canorus* and *C. pallidus*, with about 111 and 110 known host species, respectively. In contrast, the two most generalized cowbirds, *M. ater* and *M. bonariensis*, each have more than 200 hosts and are therefore much more generalized than all 32 cuckoo species ( $p = .015$ , Fisher's Exact test on 2 of 5 versus 0 of 32.). Figure 3 includes all cuckoos traditionally placed in the *Cuculinae*. Four species in the genus *Clamator* may belong in another subfamily (Aragon et al., 1999), but they have little or no effect on overall results because host numbers for the *Clamator* species (9–52) have nearly the same median, 22, as the entire assemblage of 32 species, 22.5.

Total known host species (Figure 3) underestimate differences between cowbirds and cuckoos. Cuckoos known to parasitize many species over their entire ranges typically parasitize only one to six in any one region (Gibbs et al., 2000; Higuchi, 1998; Nakamura et al., 1998; Wyllie, 1981). In contrast, three of the five cowbirds (*M. ater*, *M. aeneus* and *M. bonariensis*) commonly parasitize seven or more species even at a single site (Carter, 1986; Mason, 1986a,b; Norris, 1947; Robinson, 1992). Furthermore, individual females typically parasitize multiple host species in generalist cowbirds (Alderson et al., 1999; Fleischer, 1985), but parasitize only a single species in cuckoos (Gibbs et al., 2000; Marchetti et al., 1998; Wyllie, 1981). Contrary to PHYLO, it is clear that cuckoos are more specialized than cowbirds at the levels of species, populations, and individuals. Reliable data on host numbers are not avail-

able for nearly 20 species of cuckoos, but the fragmentary data (Johnsgard, 1997) for these suggests that most or all specialize on a few host species, so their inclusion would strengthen the difference between cowbirds and cuckoos.

Even more striking than the greater generalist tendency of cowbirds is their greater variation in host number relative to that shown by cuckoo species. The variance in cowbird host numbers (Figure 3) is 10796.2, compared to 967.6 for cuckoos. Host numbers are significantly ( $p < .0001$ ) more variable among cowbirds than among cuckoos ( $F$  ratio = 11.16). This result, too, is contrary to PHYLO, which predicts that cuckoo species should be more variable in host number. Also in conflict with the assumption, under PHYLO, that host number has a strong phylogenetic signature is the fact that the two cuckoo species with the largest and smallest numbers of known hosts, *Cuculus canorus* with 111 species and *C. gularis* with 2, are sibling species that are barely distinguishable in the field except by voice (Fry et al., 1988). If two such similar congeners completely bracket the range of variation shown by the remaining 30 cuckoo species in 5 genera, it is clear that host numbers are too dynamic to elucidate ancestral states from present-day numbers.

Use of individual species as independent data points, as in the preceding Fisher's test, might seem to violate fundamental guidelines of the comparative approach because the characteristics of individual species within a clade may covary. However, this is unlikely to be a problem in the present case because host numbers in cowbirds are so labile that they bracket the range shown by all 32 cuckoo species (i.e., cowbird host numbers do not covary relative to the range of variation in the taxon to which they are being compared). Moreover, although it would be desirable to do this analysis on more than one old and one young clade of avian parasites, only these two clades, cuckoos and cowbirds, are suitable. DNA-based phylogenies are not available for other clades of parasites, some of which are too small (one to three species) to differentiate between COEV and PHYLO.

## DISCUSSION

### An alternative model for the relation between branching order and specialization

PHYLO deals with position in a phylogeny and therefore with cladogenesis, whereas COEV deals with anagenesis (i.e., change within a lineage with no branching). Although historical in nature, COEV does not necessarily relate a brood parasitic species' degree of specialization to its position in a phylogeny. But how, then, can COEV explain the cowbird data, which seem to support PHYLO (i.e., a trend in which newly arising species seem to be progressively more generalized)?

First, as argued above, the number of hosts a brood parasite uses today may be different from its past numbers. One informative guide to identifying the primitive character state within a clade, comparison with an outgroup, is not possible with host numbers of brood parasites because nonparasitic outgroup species have no hosts. However, once speciation mechanisms are considered (Figure 1), COEV provides an explanation for the relation between current host numbers and branching order in cowbirds.

Our hypothesis for range expansions accompanying cladogenesis was well supported by an area cladogram (Figure 1) and explains the phylogenetic pattern between host number and branching order in cowbirds because speciation events generally involved dispersal to a region where few or no cowbirds existed. The alternative of vicariance events in a single, continuously distributed taxon does not fit the tree or the geological history of the region. In contrast to our results,

Johnson and Lanyon (1999) suggested that parasitic cowbirds show a lack of phylogenetic conservatism of biogeographic distributions because two species have had recent range expansions and because the cowbirds are a mostly Neotropical group within a clade of blackbirds that is primarily found in North America and the Caribbean. However, the latter clade could have originated in the Neotropics given the distribution of basal blackbirds (Johnson and Lanyon, 1999), and other blackbird clades, such as the meadowlarks, also have representatives in North and South America (Lanyon and Omland, 1999). Furthermore, the range expansions are due largely to recent anthropogenic factors such as forest clearing and involve only the most generalized cowbird species (Cruz et al., 1989, 1998; Rothstein, 1994).

PHYLO might occur if a parasite responds to hosts that develop defenses by incrementally using additional host species (Lanyon, 1992: 78). Continued use of older, more well-defended host species would then result in an increased number of hosts. However, there is nothing in PHYLO that explains why, at each branching point, the lineage that gave rise to subsequent branching events (i.e., new cowbird species) was more likely to become more generalized than the lineage that showed no further branching. For example, if the primitive state is specialization and generalization is achieved by incremental additions of hosts, then the lineage that gave rise to the present-day *M. rufoaxillaris* should be as much of a generalist as the other four species because all have had the same amount of time to accrue the incremental steps putatively needed to become a generalist. The same problem exists with the other branching points. The failure of PHYLO to explain the pattern it is based on is a serious weakness. In contrast, our proposed model involving COEV and allopatric speciation provides the first causal explanation for the host-use pattern that exists among cowbirds in that anagenesis within lineages can produce a pattern among all taxa within the clade. Nevertheless, the relationship between branching order and host species number in cowbirds is in part fortuitous. Had *M. ater* colonized a continent with a number of parasitic cuckoo species, it likely would be much more specialized.

Unlike the case for cowbirds, COEV predicts a weak relationship, or none at all, between host number and the branching order of cuckoo species because cuckoos have been speciating for so long that many new species are likely to have appeared in regions that already contained other cuckoo species and other clades of brood parasites. Both of these complications are likely to have obscured relationships between branching sequence of cuckoo species and the level of defenses of potential hosts. In contrast, PHYLO predicts a correlation between branching order and host numbers of cuckoos. Although a complete phylogeny for cuckoos is lacking, the fact that sibling species (*Cuculus canorus* and *C. gularis*) bracket the range in host numbers shown by the entire cuckoo clade indicates that no clear phylogenetic pattern exists.

Instead of incremental host additions, a more likely basis for PHYLO might be a relationship between ecological success and parasite density. Each subsequent cowbird species may have speciated because it developed ecological innovations that allowed it to both colonize a new region and to develop a larger population. Large populations then may have provided pressures favoring increases in numbers of host species. However, we stress that with time these generalists are likely to become more specialized. This interpretation means that both PHYLO and COEV may occur within a clade of parasites, with the former preceding the latter. Low population size may explain the specialization of the three Neotropical parasitic cuckoo species (subfamily Neomorphinae) that

specialize on high-quality hosts with domed, predator-resistant nests (Johnsgard 1997).

### Parsimony and COEV versus PHYLO

In distinguishing between COEV and PHYLO, the former has the advantage of providing a cogent mechanistic explanation for the relation between phylogeny and host number. Although it provides no cogent mechanism, PHYLO is more parsimonious because it involves fewer evolutionary changes if one focuses only on numbers of hosts. However, we have shown above (Figure 2) that PHYLO is only slightly more parsimonious than COEV, as the former requires one change to produce the pattern seen today, whereas COEV requires two changes. Although strict adherence to parsimony would lead one to endorse PHYLO over COEV, such a tactic would inevitably lead to rejection of many cases of coevolution and of such established phenomena as parallel evolution.

Furthermore, the focus on host number obscures an important fact. Whether a parasite is a specialist or a generalist does not depend solely on genes influencing host number. All specialist brood parasites have adaptations specific to the particular host species they parasitize and therefore have important differences among themselves. For example, *M. rufoaxillaris* has a unique juvenile plumage that mimics that of its most common host and that is different from the plumage of all other cowbirds (Fraga, 1978, 1979, 1998). The next most specialized cowbird, *S. oryzivora*, also has unique features related to its hosts such as a light-colored juvenile bill, eggs maculated with scrawls, and preening of nest mates (Friedmann, 1929; Fraga, 1984; Smith, 1968; Orians, 1985; Fleischer and Smith, 1992; Robinson S, personal communication; Skutch, 1996). Thus, a new specialist branching off from an existing specialist will require evolutionary changes even if there is little or no change in its host number. In other words, sometime in its evolution, *S. oryzivora* had to undergo the many host-related changes by which it differs from *M. rufoaxillaris*. When all aspects of being a specialist are considered, the parsimony difference between PHYLO and COEV is much less than appears to be the case from a diagram (Lanyon, 1992: Figure 1) showing only branching position versus host number. Instead of a difference of one versus two changes (Figure 2), the difference is one less change for PHYLO out of the many changes both it and COEV require to explain today's pattern of host use in cowbirds.

### Intraspecific variation in host use by brood parasites

If the number of hosts a parasite uses is related more to the ecological circumstances it faces than to its phylogenetic history, as predicted by COEV, then brood parasites should show intraspecific variation in their use of hosts, especially on spatial scales. In contrast, because PHYLO (Lanyon, 1992) relates each cowbird species' branching order to its ranking determined by current host species number, it assumes that host use is stable over evolutionary time, except during speciation, or that it is stable enough so that a ranking of species based on current host numbers is the same as one based on host numbers at the time each parasite speciated. In accord with COEV, extensive geographic variation in host use occurs in both cowbirds and cuckoos.

Variation in host use occurs in even the most specialized cowbird, *M. rufoaxillaris*. Despite *M. rufoaxillaris*'s suite of adaptations that make it highly adapted to one particular host species, *M. badius*, there is frequent parasitism of the chopi blackbird (*Gnorimopsar chopi*) in areas where *M. badius* is absent (Fraga, 1996; Sick, 1993) and occasional parasitism of the brown and yellow marshbird (*Pseudoleistes virescens*) where *M.*

*badius* is present (Mermoz and Rebores, 1996). Both of these additional hosts are very different in appearance from *M. badius*, so parasitism of these species is not due to mistaken identity. *M. rufoaxillaris* parasitism of other species may have gone unnoticed in the past because field workers attributed its eggs to the sympatric generalist *M. bonariensis*, which parasitizes numerous host species and has similar eggs (Fraga, 1983; Friedmann, 1929). As more careful field work is done within the range of *M. rufoaxillaris*, more hosts will likely be found, and this cowbird's number of host species may come to surpass the seven known hosts of the next species to branch off, *S. oryzivora*. Indeed, Pereya (in Friedmann, 1963) listed six additional hosts beyond the three noted above, but these records were not accepted by Friedmann, who argued that the eggs cited by Pereya were *M. bonariensis* eggs because of the belief that *M. rufoaxillaris* parasitizes only one species, a belief now known to be incorrect.

It is clear that host use by *M. rufoaxillaris* is far more flexible than appeared to be the case only a decade ago. Another example of the flexible nature of host use is *M. ater* parasitism of the three species of phoebes (*Sayornis* spp.), all of which place their nests under a solid roof (rock overhangs or bridges), a habit shared by few other North American passerines (Harrison, 1978). *S. phoebe* of eastern North America is the fifth most parasitized of 221 known hosts, with more than 600 reported cases (Friedmann, 1963; Friedmann et al., 1977). In contrast, there is not a single reliable case of parasitism on a western congener, *S. nigricans*, even though both it and cowbirds reach their highest abundances in riparian habitats (Farmer, 1999). There are only 10 known cases of parasitism on the third species, *S. sayi*, which is also limited to the western half of North America (Friedmann, 1963; Friedmann and Kiff, 1985; Friedmann et al., 1977). All three phoebes accept cowbird eggs (Rothstein, 1986, unpublished data), so eastern *M. ater* include a highly unusual nest type (overhang nests) within their overall host niche, but western *M. ater* do not.

Despite having a large list of host species summed over its entire range, *M. bonariensis* shows different degrees of specialization in different regions. It concentrates on cavity-nesting house wrens (*Troglodytes aedon*) in northeastern South America and seems to parasitize few or no other species in parts of Guyana and Suriname, even though this wren is an uncommon host elsewhere (Friedmann, 1963). Elsewhere, this cowbird's main or exclusive host is a grackle (*Quiscalus lugubris*) in an area of Venezuela (Friedmann, 1963). In each of two areas in Puerto Rico (Wiley, 1985), this cowbird concentrates most of its parasitism (> 90 % of several hundred eggs) on only four host species. But in other regions, numerous host species are used at single sites (Fraga, 1978; Mason, 1986a,b).

Other parasites also show spatial shifts in host use. In Europe and parts of the Middle East, the great spotted cuckoo (*Clamator glandarius*) is nearly exclusively parasitic on the black-billed magpie (*Pica pica*), a species with an unusual domed nest (Soler, 1990). In Israel and Egypt, the great spotted cuckoo parasitizes a single species, the hooded crow (*Corvus corone*), which has a typical cup-shaped nest (Friedmann, 1964). At least 15 species of starlings (Sturnidae), which are cavity or tunnel nesters, and other species of crows, are parasitized in much of Africa (Arias-de-Reyna, 1998; Friedmann, 1964). So this cuckoo goes from one main host in the northern part of its range to 10 or more hosts farther south.

These various examples of geographic variation show that intraspecific variation in host use by some parasites approaches or exceeds the differences in host use among some species of brood parasites. This is further evidence that host use is too dynamic to allow present-day host numbers to reliably reflect historical host numbers. Similarly, the range in numbers

of hosts used by two sibling species of cuckoos, *Cuculus canorus* and *C. gularis*, exceeds the range shown by all other cuckoo species together. Sympatric "gentes" of *C. canorus* that parasitize different host species show only small mitochondrial DNA differences (Gibbs et al., 1996, 2000), indicating that changes in host use are frequent. Indeed, Nakamura et al. (1998) described a major host switch in the last several decades (see also Brooke and Davies, 1987).

#### Additional problems with the use of host number as a character in a cladogram

The use of published lists of known host species to assess specialization obscures important aspects of a parasite's biology. A more appropriate measure of specialization is selectivity, the extent to which a parasite uses potential hosts with which it is sympatric. As shown above, lists of known host species are strongly influenced by factors extraneous to degree of selectivity such as the amount of research effort devoted to a parasitic species and its range size. In addition, a parasite may not consider all sympatric passerines as potential hosts because of body size constraints, which is likely to be the case for *S. oryzivora*, as described above. A list of known hosts can also misrepresent selectivity solely because it is cumulative. If a specialized parasite switches from one host to another, as documented by Nakamura et al. (1998), both hosts will be in a cumulative host list when, in fact, only one of them is parasitized at any one time.

Thus it is not clear that a ranking of cowbird species based on host selectivity would be completely concordant with the divergence sequence (Figures 1 and 2) if it controlled for range and body size. For example, *S. oryzivora* might be as much of a generalist as the three later-branching cowbird species because it parasitizes most of the few passerines large enough to serve as hosts.

#### Clade age and host use in cowbirds and cuckoos

The demonstration that the Old World parasitic cuckoo clade (Cuculinae) is at least twice as old as the New World parasitic cowbird clade and that the cuckoos are more specialized in their host use clearly supports COEV over PHYLO. Similarly, the greater interspecific variation in cowbird than in cuckoo host numbers is inconsistent with PHYLO. Our comparison of cytochrome b sequence divergence within cuckoos and cowbirds is conservative because the cuckoo data come from three relatively undifferentiated congeners, whereas the cowbird data represent the entire clade. Thus, data from the 11 other cuckoo genera (Johnsgard, 1997) should show that the disparity between ages of the cowbird and parasitic cuckoo (Cuculinae) clades is greater than the twofold difference indicated by our data. Aragon et al. (1999) presented data on cytochrome b sequence divergence for eight species traditionally included in the Cuculinae. These divergences ranged as high as 31.6%, but the largest divergences involved two species in the genus *Clamator*, which Aragon et al. found to be a member of another clade. If sequence data are restricted to the Cuculinae, as restructured by Aragon et al.'s (1999) data, then the cuckoo with the most divergent cytochrome b sequence, *Cacomantis flabelliformis*, has 16.0–18.1% divergence with the other five species. This indicates that Old World cuckoos have been parasites for as much as three times as long as cowbirds. Furthermore, the entire Icterine radiation, of which parasitic cowbirds make up only 5 of 97 species, is apparently considerably younger than the group of these 5 cuckoos, as analyses of 59 species from all major subgroups within the Icterine showed a maximum cytochrome b divergence of only 11.0% among lineages (Lanyon and Ormland, 1999).

Even a threefold disparity in ages of the cowbird and Cuculinae clades is a likely underestimate because rates of sequence divergence slow down at higher levels of divergence due to rapid saturation of amino acid replacements. Furthermore, a much greater age for cuckoos than for cowbirds is in accord with the DNA-DNA hybridization data of Sibley and Ahlquist (1991). These authors identified Cuculiformes, the order to which parasitic cuckoos belong, as an ancient group (see also Johnson et al., 2000) that probably appeared in the Cretaceous.

In addition to their fewer hosts, there are further indications that cuckoo–host interactions are more highly coevolved than those of cowbirds in ways predicted by COEV. Nearly all species of cuckoos (Cuculinae) have eggs that mimic the eggs of one or more of their most common host species (Wyllie, 1981), as would be expected from COEV if cuckoos have been parasites for a relatively long time. In contrast, egg mimicry may occur in only one of the five cowbirds (Smith, 1968), but even this example is uncertain (Fleischer and Smith, 1992). Most species of cuckoos have eggs that are unusually small for their body size (Payne, 1974; Wyllie, 1981) because they parasitize small hosts that discriminate against large eggs (Davies and Brooke, 1988). In contrast, cowbirds lay eggs that are close to the size predicted by the body size–egg size relationships in related nonparasitic taxa (Rahn et al., 1988). The nestlings of nearly all species of parasitic cuckoos evict host eggs and young shortly after hatching and thereby monopolize all of the host's parental care (Wyllie, 1981). Despite its obvious adaptive value, cowbird nestlings do not kill off host young through direct action, and some host young often fledge from parasitized nests. [There is one report of a cowbird nestling ejecting a host nestling (Dearborn, 1996), but this may have been done passively.] These various comparisons of degrees of specialization between brood parasitic cowbirds and cuckoos clearly support COEV over PHYLO.

Examination of host numbers of three of the five other clades of parasitic birds (the cuckoo-finch, *Anomalospiza*; the black-headed duck, *Heteronetta*; the ground cuckoos, Neomorphinae) has little potential for distinguishing between COEV and PHYLO because each has only one to three species of obligate parasites. The two remaining clades, the viduine finches (Viduinae) and the honeyguides (Indicatoridae), are more speciose than the cowbirds, with at least 15 species each (Johnsgard, 1997). Most species in both clades are specialists with one to several hosts (Fry et al., 1988; Klein et al., 1993; Payne et al., 1993), with a maximum of 49 known host species in one honeyguide (Johnsgard, 1997). Given these high levels of specialization, COEV predicts that these clades are older than the cowbird clade, whereas PHYLO predicts the opposite

#### Macrogeographic variation in host use and host defenses

Besides the above support for COEV from comparisons among parasitic lineages, further support comes from comparisons between regions, especially for the hypothesis that there is a relation between number of parasitic species in a region and level of host defenses. The African avifauna is exposed to more than 30 species of parasitic birds in 3–5 lineages, depending on taxonomy (*Clamator* plus rest of Cuculinae, *Anomalospiza* plus Viduinae, and Indicatoridae), whereas there are only 3 in the Nearctic, only 1 of which (*M. ater*) is widespread, and 7 in the Neotropics, only 1 of which (*M. bonariensis*) is widespread and common (Johnsgard, 1997; Lack, 1968). As expected from COEV, rejection of nonmimetic eggs is much more prevalent among African passerines that are potential hosts than among Nearctic and Neotropical species (Rothstein, 1990, 1992). In fact, most New World passerines accept eggs strongly dissimilar from their own.

Similarly, the relatively small main island of Japan has four species of *Cuculus* cuckoos, each specialized on a different set of one to six host species (Higuchi, 1998; Higuchi and Sato, 1984; Lack, 1968; Nakamura et al., 1998). Three of these cuckoo species show weak to strong mimicry of host eggs in coloration. The fourth, *C. saturatus*, mainly parasitizes a single host whose domed nest may make discrimination via color difficult, although the cuckoo's eggs mimic its host's in size (Higuchi and Sato, 1984). The egg mimicry by these cuckoos indicates that egg rejection is widespread in Japanese passerines, an expectation borne out by experiments (Nakamura et al., 1998). Therefore, egg rejection is much more prevalent in Japanese birds than in New World ones, in accord with COEV. Variation in egg rejection holds even for potential hosts within a lineage. For example, egg rejection is uncommon or absent in New World emberizine sparrows or buntings (Mason, 1986a; Rohwer and Spaw, 1988; Rothstein, 1975b), although many are parasitized by cowbirds, but is highly developed in the smaller number of emberizine species that are potential cuckoo hosts in Japan (Nakamura et al., 1998) and Europe (Davies and Brooke, 1989a). Thus, COEV is consistent with both logical arguments and available data when considering both the duration of parasite–host interactions (previous subsection) and the numbers of parasites in different regions.

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