

## PHYLOGENETIC ANALYSIS OF AVIAN PARENTAL CARE

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**ABSTRACT.**—Phylogenetic patterns can be used to generate detailed historical hypotheses about the evolution of character systems, including parental-care behavior. Phylogenetic analysis of 60 taxa using parental-care data (15 characters) in combination with anatomical data (69 characters) shows that biparental care is primitive for birds, and that biparental incubation arose from an ancestral condition in which neither parent incubated. Components of parental care may be decoupled, such that incubation and feeding of nestlings is biparental, but postfledging care is uniparental; the pattern of decoupling varies across taxa. Behavioral plasticity, environmentally induced variation, and quantitative variation in characters that are coded qualitatively are some of the problems inherent in such an analysis. Nevertheless, historical analysis offers a good vehicle for obtaining rigorous hypotheses about the coevolution of avian character systems. *Received 5 July 1991, accepted 29 October 1991.*

THE USE of phylogenetic pattern to elucidate questions about other evolutionary and ecological patterns or processes has become increasingly common in the last 15 years. Several rigorous attempts to incorporate behavioral data into phylogenetic analyses or to compare such data with existing phylogenies have been made in the last five years. Clutton-Brock and Harvey (1977) recognized the pitfalls of comparing closely related species to study the origin of ecological phenomena, and this has been further emphasized by Clutton-Brock and Harvey (1979), Ridley (1978, 1983), Harvey and Mace (1982), Felsenstein (1985), Dobson (1985), Pagel and Harvey (1988), Höglund (1989), and Björklund (1990). Coddington (1988) outlined a method for using cladistic hypotheses of relationship to test hypotheses of adaptation, and this kind of approach has been fruitfully applied in a number of recent studies (Prum 1990, B. N. Danforth unpubl. data, R. J. Smith unpubl. data).

A historical approach is a profitable one, as it attempts to find the correct hierarchical level at which hypotheses of adaptation are meaningful. It is not enough simply to dismiss "adaptations" as artifacts of phylogenetic propinquity; rather, one must dissect out the effects of phylogeny so that adaptive explanations may be viewed in the appropriate context. Clutton-Brock and Harvey's (1979) concern about biasing investigations of ecological phenomena by examining closely related species was appropriate. However, they may have been somewhat tyrannized by taxonomy in their view of the problem—that is, equating taxonomy with

phylogeny (one of the "top three heinous 'crimes against phylogenetics'"; Brooks and McLennan 1991). Looking at numerous species from the same taxonomic family actually may be quite valid, depending on phylogenetic relationships among those species. What matters above all is the number of times the trait in question arose, rather than how many genera or families show the trait; this can only be determined by a detailed phylogeny of the organisms and traits. The trait could well have arisen numerous times within the family, in which case it is not only meaningful but necessary to include members of the same family in the study. With such information, one can ask appropriate questions about the adaptive significance of that trait. It is not profitable to begin the investigation by determining whether one should count genera, families or orders in which the trait occurs. Rather, one should begin with a detailed phylogeny and determine whether the trait arose once or many times, and the pattern of origin and loss. Adaptive explanations can only be tested with convergent cases, not with homologous ones. In other words, two species showing the trait can only serve as two data points in support of an adaptive explanation of origin if they did not inherit the trait from a common ancestor.

McLennan et al. (1988) lamented what they perceived as a decline in the use of behavioral data to construct phylogenetic hypotheses in the last three decades, citing work by Lorenz (1941) in which this was done successfully for ducks (Anatidae) and work by later authors in which phylogeny was ignored. A noncladistic

attempt to extend Lorenz's work was made by Johnsgard (1961), for example. McLennan et al. (1988) were remarkably successful in generating phylogenies for gasterosteid fishes using data on reproductive behavior, and argued that behavioral data are extremely useful for constructing phylogenies.

The evolution of parental care was an early focus of the phylogenetic approach. Ridley (1978) reviewed the circumstances of paternal care in a broad array of taxa to consider the effects of fertilization mode, territoriality, female choice and other factors on the evolution of paternal care. He recognized the possibility of phylogenetic bias in formulating hypotheses about the evolution of the phenomenon. Gittleman (1981) used phylogeny to test predictions about probabilities of transition among types of parental care in bony fishes (i.e. among states of uniparental [male], uniparental [female], biparental, and no parental care). He found that the most common evolutionary transition was from no parental care to uniparental care by males, but pointed out possible statistical problems with the conclusion that this transition had the highest likelihood.

Van Rhijn (1984, 1985, 1990) proposed that pure male parental care is the primitive condition in birds. His hypothesis is based upon the premise that "monogamous paternal care systems can easily evolve towards all recent mating systems in birds" (van Rhijn 1984:103), whereas biparental care systems cannot. This is in contrast with the suggestion by Emlen and Oring (1977:220) that "complete male parental care is most likely to develop in groups with ... a phylogenetic history of shared incubation." If van Rhijn's hypothesis is correct, then complete male care would probably have evolved from a condition where incubation was lacking, as in crocodylians and possibly nonavian dinosaurs; van Rhijn, however, limited his discussion to birds.

Van Rhijn (1990) attempted to support his view primarily by using Cracraft's (1981) classification of birds and Strauch's (1978) phylogeny of the order Charadriiformes (shorebirds and allies). Testing van Rhijn's intriguing hypothesis was somewhat hampered at the time by the unavailability of cladistic analyses of avian character data, with which the behavioral data could be either compared or combined to generate a detailed hypothesis about the evolution of parental care in birds. Furthermore,

Cracraft's (1981) classification, which lacks character data and explicit hypotheses of phylogenetic relationships, is of limited utility for the purpose of understanding the evolution of character systems (e.g. behavior). Without a phylogeny, van Rhijn was limited to making hypotheses based on statistical probabilities rather than historical evidence.

In this study, I use character data from the hindlimb musculature (from McKittrick 1991) in combination with published behavioral data to test van Rhijn's hypothesis that male-only parental care is primitive in birds, and to generate, in effect, phylogenies of avian parental-care behavior. In doing so, I also was able to test some of the hypotheses of Silver et al. (1985) about the causal nature of associations among certain aspects of parental care. In considering the question of what aspects of parental care are primitive for birds, however, it should be borne in mind that there is nothing magical about statements regarding the primitive or derived nature of these character states. A character state that is derived for birds is primitive within birds. A state may be derived for birds, but show early transitions to a different state, such that the majority of birds show a different state from the one that arose at the base of the avian lineage. These terms are relative, and the hierarchical level to which they refer should always be considered.

Phylogenies are hypotheses about character evolution and, as such, they allow the refinement of ecological questions such as, why does species X exhibit biparental care? With a phylogeny, one can go beyond the proximate answer to this question, namely, "Because its ancestors exhibited biparental care," and seek ultimate answers by examining the ecological parameters that may have contributed to the origin of biparental care in the various lineages in which it arose. My study is not an attempt to pose and answer such questions, but rather to begin to construct a historical framework within which such questions may be explored.

The hindlimb musculature of birds has been used effectively to generate cladistic hypotheses for restricted lineages (e.g. Old World suboscines; Raikow 1987), and has recently been analyzed for a large and diverse group of birds (McKittrick 1991). The latter data set was chosen to complement the behavioral data summarized here because it is the most taxonomically comprehensive set of character data available for

birds. No assumptions are made here about the independence of the hindlimb musculature and parental-care behavior.

#### METHODS

I used published data on 66 characters from avian hindlimb musculature (for details, see McKittrick 1991), and combined these with 15 behavioral characters taken from the literature. The behaviors were chosen because they summarize parental care in birds and because they seemed amenable to relatively unambiguous interpretation and coding. All characters are described briefly in Appendix 1.

Complete or interpretable behavioral data were not always available for the same taxa used by McKittrick (1991). Therefore, in 13 cases a species classified in the same genus was substituted (see Appendix 2). Behavioral characters were obtained for 76 avian taxa.

An ancestor based on crocodylians was used as the outgroup. "Dummy" characters for paleognath (ratites and tinamous), neognath (all other birds), and avian monophyly were included as well. These helped to ensure that the outgroup would always remain outside of the ingroup (for justification, see McKittrick 1991). Furthermore, the analyses were constrained (using a "Topological Constraints" option in program used; see below) such that paleognaths were the sister group to neognaths. Thus, the paleognaths were designated as the sister group to neognaths, and the Ancestor was included as the sister group to all the birds. This structure is the basis for outgroup comparison (Raikow 1982, Maddison et al. 1984) and permits one to test hypotheses of synapomorphy; if a character state is synapomorphic for the ingroup, then the two outgroups (in this case the "sister group" and outgroup) should have the alternative character state.

The combined data set was analyzed using PAUP 3.0s (Phylogenetic Analysis Using Parsimony; Swoford 1990) on a Macintosh IIfx computer. The hindlimb characters also were analyzed separately to determine whether the behavioral characters actually were making a difference in the resulting tree topology. The Heuristic algorithm was used, as it finds the minimum length trees and is recommended for data sets with more than 20 taxa. The shortest trees were found using the Random Addition option because the order in which the taxa are read by the program can make a significant difference in whether the shortest tree is found. With this option, the taxa are read in random order 10 different times, and for each replication I allowed a maximum of 50 trees to be generated. I then took one of the resulting shortest trees and used this as a "seed" to complete the analysis (i.e. from this seed all possible minimum-length trees were sought). Initial analysis produced a number of groups that were considered by PAUP to be "the same"; in other words, these groups contained three or more taxa at the same node. In order to reduce the final

number of trees and thereby reduce the number of assumptions that were necessary for formulating hypotheses about character evolution, I examined each of these groups of "same" taxa and arbitrarily eliminated all but one of the taxa in each group. This resulted in elimination of 17 taxa, leaving a total of 60.

A 75% majority-rule consensus of the final trees was obtained (Fig. 1); such a tree shows all groupings that are present in 75% of all trees. It was chosen over the strict-consensus tree because the latter collapses all groupings that do not occur in 100% of the trees. I consider the majority-rule tree to be a more representative and informative summary of relationships.

Because the consensus tree is a summary, rather than an actual hypothesis of character transitions, I used one of the actual shortest-length trees (Fig. 2; designated Tree 1) to illustrate these transitions. Of 58 nodes in the consensus tree (Fig. 1), only four (6.9%) were unstable; this indicates that all of the fundamental (actual) trees were generally very similar. For this reason, using one tree to represent all of the trees is a useful way to illustrate possible character transitions. Three optimization routines were applied to Tree 1 (Acctran, Deltran, and MinF; see below). These optimizations are different methods of assigning character states to the interior nodes (hypothetical ancestors) of the trees generated by PAUP. For example, in Figure 2 the terminal taxa *Rhea* and *Crypturellus* are linked at node 61. For some characters, there is a transition of character states between node 62 and node 61, and between node 61 and *Rhea*. The three optimization routines always will yield trees with the same overall number of transitions (steps), but the transitions between nodes 62 and 61, and between node 61 and *Rhea* will not be the same for each optimization. The Acctran (Accelerated Transformation) algorithm is based on the assumption that reversals ( $0 \rightarrow 1 \rightarrow 0$ ) are more common than independent origins of a character state ( $1 \rightarrow 0 \rightarrow 1$ ), while Deltran (Delayed Transformation) assumes the opposite (i.e. independent origins are more common than reversals). The MinF routine maximizes the number of autapomorphies (derived states unique to that terminal taxon) wherever possible. Therefore, the algorithms make different assumptions about evolutionary processes.

Several of the characters used in this analysis are relatively unenlightening because little information is available about them in the literature. Nevertheless, I included such characters to call attention to the lack of information. One such example is mate guarding by males (character 72). In most cases, the information is simply unavailable (see Birkhead 1979); in others, the author may have observed mate guarding but did not mention it, or was not explicit about whether it occurs. For example, Mock (1979) noted that males are very strongly territorial during the egg-laying stage in *Ardea herodias*; however, he did not refer to

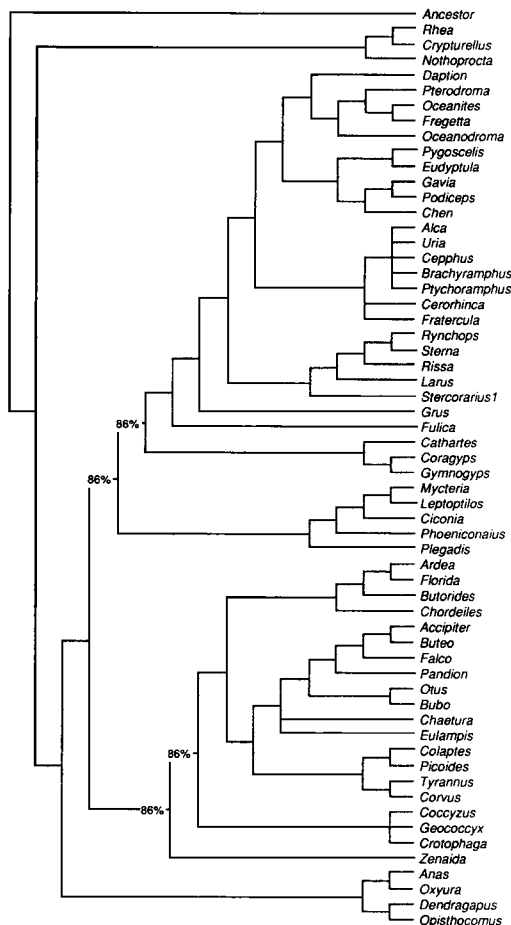


Fig. 1. A 75% majority-rule consensus of 63 trees based on hindlimb muscle and behavioral data; all groups occurred in 100% of these trees unless otherwise indicated.

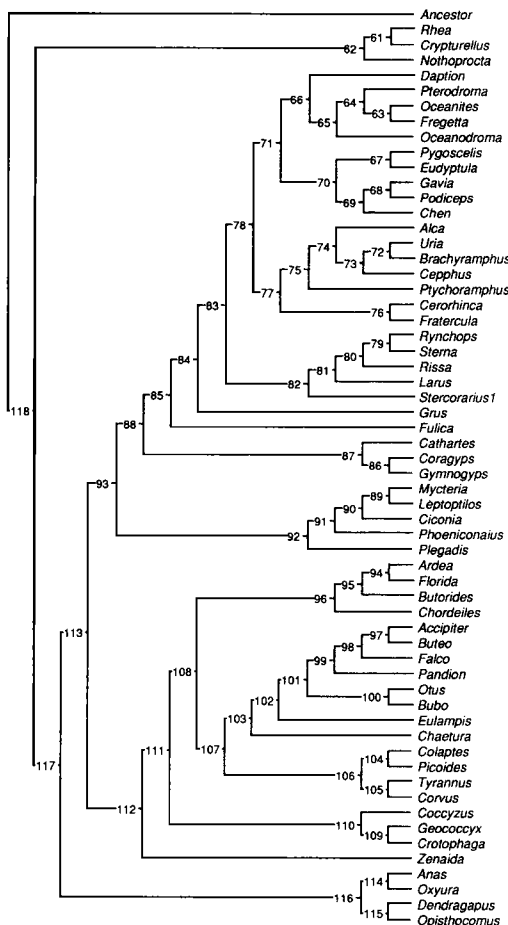


Fig. 2. Tree 1 of 63 based on hindlimb muscle and behavioral data. Internal nodes are numbered.

this behavior as mate guarding and, therefore, I coded that character with "?" (missing) for that species.

A growing number of apparently monogamous species have been shown to exhibit multiple parentage in their broods (for a review, see McKittrick 1990). Unfortunately, little information on actual parentage is available for most of the primarily nonpasserine species included in the present analysis. Extra-pair copulations have been reported in several of these species (see Gladstone 1979, Ford 1983). Because the species exhibiting the behavior appear to be primarily monogamous, I have coded species showing multiple parentage or extra-pair copulations as "0" (monogamous) for character 70.

Character 75 (defense of young/parental care) is in effect a summary of parental care in birds. Generally, if a species was biparental for other aspects of care it was biparental for character 75 as well. Occasionally,

however, a species had female-only care in most respects, but males contributed defense. In these cases, character 75 was coded as biparental, while the other care-related characters were coded as female-only.

Character 76 (distinguishable reversed sexual dimorphism) was coded in a nontraditional manner for owls. Although owls are considered to exhibit reversed sexual dimorphism (Mueller 1986), I did not so code the two owls included in this analysis. The ratio of male wing length to female wing length is 0.975 in *Otus asio* and 0.952 in *Bubo virginianus* (Mueller 1986:table 1); these numbers are so close to 1.000 that classifying these species as showing reversed sexual dimorphism seemed unwarranted.

Character 84 (posthatching development) was coded based on the classification system of Winkler and Walters (1983), but their three categories of precociality were lumped into one, as were their two categories of altriciality. Taxa whose classification was speculative were coded as having that speculative condition.

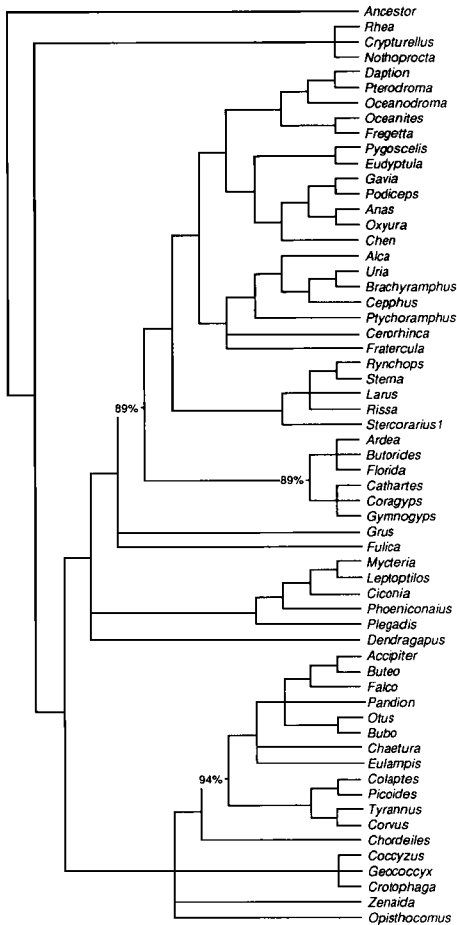


Fig. 3. A 75% majority-rule consensus tree of 161 trees based on hindlimb muscle data only; all groups occurred in 100% of these trees unless otherwise indicated.

See Appendix 1 for a complete list of characters used in the analysis. The character data are shown in Appendix 2.

## RESULTS

I found 63 shortest-length trees of 339 steps based on muscle and behavioral data; the consistency index (ci) excluding uninformative characters was 0.353. Uninformative characters are those that show only one transition at a terminal taxon (i.e. they are autapomorphies). A 75% majority-rule consensus tree, showing the percentage of the 63 trees in which each group appears, is depicted in Figure 1. Figure 2 shows the first of the 63 trees (Tree 1); the

hypothesized character transitions described in Appendix 3 are based on this tree.

For the analyses based on hindlimb data only, 161 trees of 247 steps were found (consistency index excluding uninformative characters was 0.357). A 75% majority-rule consensus of these trees is shown in Figure 3.

## DISCUSSION

The consistency indices are higher than expected for this number of taxa (consistency index of 0.30 expected for 60 taxa; the expected value decreases with increasing numbers of taxa based on empirical analysis by Sanderson and Donoghue 1989). The level of homoplasy, therefore, is not high for a data set of this size. However, many nontraditional groups appear in these analyses compared with the topology of the trees obtained by McKittrick (1991) using hindlimb muscle data for a larger number of taxa. For example, whereas auks are monophyletic and gulls and terns are as well, the two groups do not cluster together. Auks (Fig. 2, node 77) cluster with procellariiforms, penguins, loons and grebes (node 71). The results of the analysis of morphology plus behavior are very similar to those from the analysis of morphology alone, differing primarily in the placement of grouse, ducks, herons, and the hoatzin. This suggests that neither data set is biasing the results unduly, and that both data sets contain a comparable degree of historical information.

I suggest that the present results can be regarded as a starting point, an exercise illustrating how comparative phylogenetic data may be employed to understand the evolution of character suites (such as behaviors involved in parental care). As more data become available, the results of such analyses will be more representative of the true phylogeny and of character evolution as well.

The results of such analyses may be appraised from two perspectives. The trees may be considered as hypotheses about the phylogenetic relationships among the taxa under consideration. The trees also may be considered as hypotheses about the evolution of the characters themselves, although some authors would disagree (e.g. Brooks and McLennan 1991:63, 1991:141). These hypotheses are constrained by one's starting assumptions, namely, that ratites are the sister group to neognaths and crocodylians

are the sister group to birds. Appendix 3 shows the hypothesized changes in the behavioral characters using three optimization routines. The hypotheses are based on Tree 1 of 63. A few of these are described below.

For character 70 (mating system), monogamy (state 0) is primitive within birds (as has been generally assumed) when Acctran is used; Deltran and MinF show polygyny (state 1) at the base of the avian lineage with a transition to monogamy occurring near the basal node (at node 117, with only ratites excluded from this clade). Acctran shows three independent origins of polygyny, while MinF shows one. All optimizations show two independent origins of promiscuity (state 3).

Character 75 (defense of young/parental care) is of particular interest, as it summarizes the roles of the sexes in caring for the young. All three optimizations indicate that some form of biparental care (defense of young) is primitive for birds.

Character transitions for character 78 (incubation) are complex. According to Acctran, a transition from no incubation (state 3; crocodilians do not incubate) to female-only incubation (state 0) occurs at the base of the avian lineage (between nodes 117 and 113). Female-only incubation occurs in the lineage at node 116, the duck-galliform clade. Biparental incubation (state 1) is a synapomorphy (shared-derived character state) for the remainder of the neognaths (see Methods) and, therefore, primitive within this group. Male-only incubation (state 2) arises once, at the base of the ratite lineage (node 62). In all, female-only incubation arises four times. Deltran represents no-incubation as being the primitive condition for birds and, thus, female-only incubation is derived for the duck-galliform clade rather than primitive. Biparental incubation is a synapomorphy for the remainder of the neognaths, and male-only incubation is a synapomorphy for the ratites. Female-only care arises a total of six times. Finally, MinF represents biparental incubation as a synapomorphy for birds and, thus, it is primitive within that lineage. Again, female-only incubation is derived for the duck-galliform lineage, and for five other lineages as well. Male-only incubation is derived for ratites.

For character 80 (posthatching care), the three optimizations each lead to different hypotheses.

According to Acctran, female-only care (state 0) is primitive for birds, with biparental care (state 1) arising near the base of the avian lineage, at node 113 (neognaths minus the duck-grouse group). There is one transition to male-only care, in ratites, and one reversal to female-only care, in *Eulampis*. With Deltran, no-care is primitive for birds, with a transition to biparental care at node 113, one to male-only care in ratites, and two to female-only care, in the duck-grouse group and in *Eulampis*. With MinF, biparental care is primitive, and male-only care arises in ratites, while female-only care arises in the duck-grouse group and in *Eulampis*.

For character 81 (postfledging care), all optimizations yield identical hypotheses. Biparental care (state 1) is primitive within birds. In addition, there is one transition to female-only care (at the duck-grouse clade), two to male-only care (at nodes 62, 73 and in *Zenaidra*), and three to no-care (at node 78 and in *Florida* and *Chaetura*).

For character 82 (group breeding), state 1 of character 82 has arisen unambiguously three times (in *Chaetura*, *Corvus*, and *Crotophaga*).

For character 84 (posthatching development), all transitions are unambiguous. Precociality is primitive (state 0), and altriciality (state 1) arose in the large clade (node 113) that contains all birds except ducks, grouse, the hoatzin, and ratites. Altriciality was subsequently lost three times: at node 85, and in *Phoeniconaius* and *Chordeiles*.

Silver et al. (1985) used canonical-correlation analysis to determine which ecological and life-history parameters were the best predictors of various aspects of avian paternal care. Their results indicated that mode of posthatching development, mating system, some habitat characteristics, and relative clutch mass explain the most variance in paternal-care activities. I used the phylogenetic framework of the present analysis to test the hypothesis of Silver et al. (1985) that the evolution of paternal care is causally correlated with the occurrence of altriciality.

The more data that become available for phylogenetic analysis, the more ways we can invent for studying character evolution; unfortunately, the invention of algorithms for testing hypotheses about character evolution necessarily lags behind. At present, no algorithms are available for testing significance of association be-

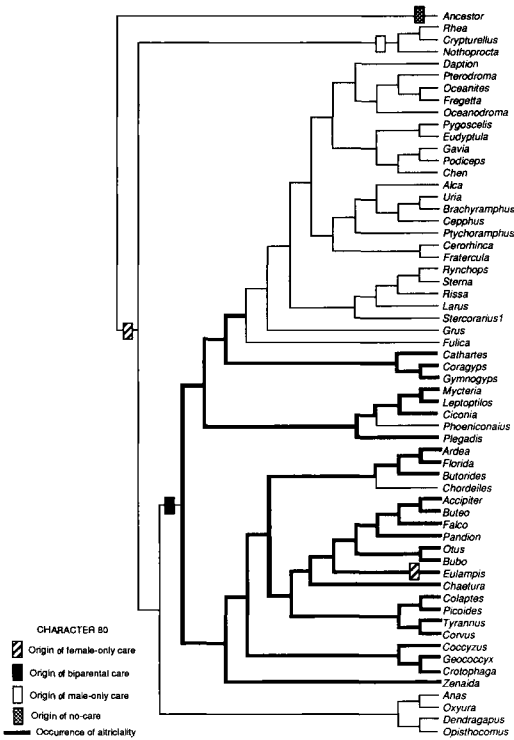


Fig. 4. Tree 1 showing occurrence of altriciality (heavy black lines) and state transitions for character 80 (posthatching care of young).

tween multistate characters. Maddison (1990) presented an algorithm to test association between binary characters; that is, to determine the likelihood of an observed number of gains and losses in a "dependent" variable occurring by chance with respect to the occurrence of an independent variable. This test is designed not to study correlation of change in one variable with change in another, as other methods have done (e.g. Felsenstein 1985), but rather to test the significance of the origin of the dependent variable anywhere subsequent to the origin(s) of the independent variable on the tree. In other words, it tests the null hypothesis that gains and losses of the dependent character are randomly distributed on the tree with respect to the state of the independent character. This makes the test ideal for studying evolutionary causality in correlations among character states.

Maddison (1990) suggested ways to recode multistate characters as binary characters for purposes of this test, and he further pointed out that the test is probably more conservative when the characters tested were used to build the trees.

I examined the distribution of state changes in character 80 (posthatching care) with respect to the occurrence of an independent character (see below), and recoded the character as presence or absence of paternal care. For example, "biparental care" became "paternal care present"; "female-only care" became "paternal care absent." The origin of female-only or no parental care subsequent to the origin of biparental or male-only care was interpreted as a loss of paternal care. Figure 4 shows the state changes for character 80 before recoding; Figure 5 shows the recoded transitions for this character.

Of the predictors studied by Silver et al. (1985), posthatching development and mating system were the only ones analyzed in the present study. Of these two, posthatching development was the only one for which hypothesized character transitions were identical for all three optimizations on Tree 1. I traced the occurrence of the derived state of this character, namely altriciality, onto that tree (Figs. 4 and 5). Its occurrence is referred to as the black area of the tree. To test the hypothesis of Silver et al. (1985), I wished to determine the probability of obtaining as many or more gains in the black and as many or fewer losses in the black simply by chance. In other words, does the black area attract gains and repel losses? Should the occurrence of altriciality lead to the origin of paternal care in character 80? The observed pattern of gains and losses in the black area was zero gains and one loss (Fig. 5), and the probability of obtaining this pattern by chance is 0.814. In other words, the pattern is not significant and altriciality does not appear to lead to the origin of paternal care. The implicit assumption of Silver et al. (1985) was that female-only care is primitive for birds, whereas in fact biparental care is primitive (and widespread; Fig. 4). Evidently, factors other than altriciality were the selective agent for the origin of paternal care in birds.

Emlen and Oring (1977) hypothesized that "complete male parental care" (which I interpret to mean male-only care) arose in taxa with a shared history of incubation. To examine this hypothesis, I mapped onto Tree 1 the occurrence of shared incubation (character 78), as indicated by Acctran optimization (Fig. 6), and the origin of male-only care for character 81 (postfledging care). The map shows an early origin of shared incubation within birds, with four out of five origins of male-only care arising

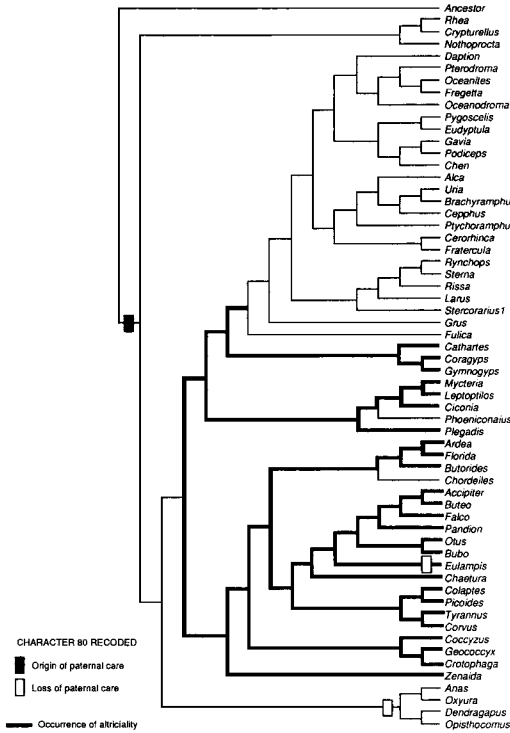


Fig. 5. Tree 1 showing character 80 recoded.

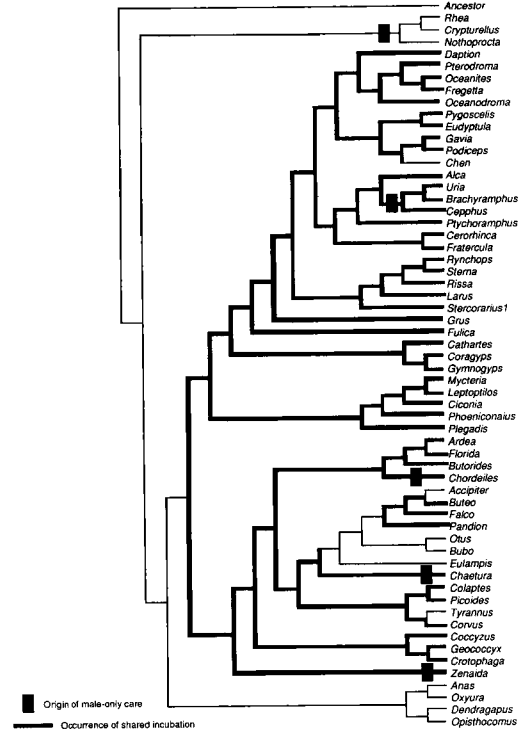


Fig. 6. Tree 1 showing origin and loss of shared incubation and origin and loss of male-only care for character 81 (postfledging care).

in taxa with a history of shared incubation. One origin of male-only care occurred in a group (ratites) with no history of parental incubation. Thus, Emlen and Oring's (1977) hypothesis appears to be largely supported. However, Maddison's (1990) test indicates that the probability of obtaining four or more gains in the black area is 0.757. This is partly due to the fact that shared incubation is so widely distributed on the tree. A higher representation of members of Passeriformes in the tree might well change this result, as many passerines do not have shared incubation.

Based on the data presented here, van Rhijn's (1990) hypothesis that male-only parental care is primitive within birds is incorrect. I believe that van Rhijn's approach has merit in that it attempts to place the study of behavioral evolution within a phylogenetic framework, where it belongs. However, his proposals regarding the direction of evolution are ad hoc in that they are ahistorical, are made outside the context of an explicit phylogenetic hypothesis, and are based on some notion of probability and the irreversibility of certain evolutionary pathways. It is more meaningful to formulate hy-

potheses based on phylogenetic analysis of character data and then examine the possible evolutionary pathways revealed by the data. Furthermore, separating parental-care behavior into component parts is more useful than examining parental care as a unit, as separation reveals the decoupling of some aspects of care. For example, care of nestlings may be biparental, while care of fledglings is uniparental, as in some auks.

*Drawbacks of the phylogenetic analysis.*—Several problems are inherent in a study of this kind. Immelman (1974) noted that certain kinds of behavioral characters are not "taxonomically" useful because of their plasticity in response to environmental variables. However, hypotheses of convergence can only be made within the context of a phylogenetic hypothesis; in other words, one cannot determine *a priori* whether a given character will be phylogenetically informative. The mean consistency index was not significantly different for the muscle characters (0.542) and the behavioral characters (0.420; Kruskal-Wallis,  $k = 1.095$ ,  $df = 1$ ,  $P =$



0.295), suggesting that the two kinds of characters have equal potential to be phylogenetically informative.

Through phylogenetic analysis one may learn more about the tendencies of certain characters to originate in many taxa. Even if a character exhibits homoplasy, however, it still may be informative at some lower taxonomic level. If, however, these environmental variables cause intraindividual variation in parental-care behavior, which they undoubtedly do (Emlen and Oring 1977), then the classification of behaviors used in the present study is probably somewhat inaccurate.

The classification of behavior may be complex (Shields 1984), and the classification of mating systems in particular can be cumbersome (Oring 1982, Mock 1983). Consequently, coding characters may fail to characterize the behaviors adequately, even though much attention was paid to this in the present analysis. Furthermore, even though both sexes may perform a certain care behavior, there may be quantitative or qualitative differences in the care provided by each (Winkler 1987); this is not reflected in the present qualitative coding system. There may be intraspecific geographic variation in parental care (e.g. *Agelaius phoeniceus*; Payne 1969, 1979) that is not accounted for in the present coding scheme.

For at least two reasons, I have attempted to be conservative in my interpretation of hypotheses yielded by the phylogenetic analyses in this study. One reason is that some of the phylogenetic relationships suggested by these analyses differ markedly from all others proposed in the literature, including those based on the same data but with more taxa included (McKittrick 1991). If the relationships as presented here are incorrect, as at least some undoubtedly are, then the hypotheses about character transformations are also incorrect. A second reason, related to the first, is that the addition or deletion of characters and taxa has an important effect on tree topology and, as more information becomes available for the taxa examined in this study or subsets of these taxa, more meaningful statements about character evolution will be possible.

A phylogenetic approach can yield hypotheses about the pattern of origin of behavioral characters, so that the appropriate kinds of questions can be asked about these patterns. Mock (1985) suggested several lines of inquiry

for future research on avian mating systems. One of these was to ask why males in monogamous systems contribute so much parental care. My analysis makes it possible to begin to try to answer such a question. For example, if we know how many times male-only postfledging care arose from biparental care, and how many times the absence of postfledging care arose, we can make comparisons of ecological variation across taxa and form useful hypotheses about the conditions leading to the evolution of such patterns of care.

Although my study is to date the most taxonomically comprehensive attempt to analyze phylogenetically avian parental-care data, it is nevertheless limited in its scope by the availability of information. Of great interest, for example, would be a cladistic analysis of the Charadriiformes, a group within which parental-care behavior varies widely. At present there are no comparable data on the limb musculature for the majority of this group, in particular the sandpipers (Scolopacidae), so very few representatives of the order are included here. Morphological work on that group is in progress (McKittrick unpubl. data, P. Chu unpubl. data) and, eventually, these data will be combined with behavioral data for a detailed phylogenetic analysis. Also, few passerine species were included in the current analysis, despite the interesting variation in their parental-care behavior, because their hindlimb musculature is relatively uninformative phylogenetically (e.g. Raikow 1978, McKittrick 1985). For the charadriiforms and passerines, the behavioral data base is richer than the morphological one. Collecting the original data is a painstaking process; collating the data from the published literature is fraught with difficulties, such as the danger of making errors in interpreting the work of many different researchers who have brought different methods, assumptions, and biases to their work. Furthermore, a morphologist is likely at times to misinterpret behavioral studies.

Brooks and McLennan (1991:342) noted that "We have discovered that there is a paucity of rigorous phylogenetic hypotheses from which we can begin historical ecological studies. . . ." This is an extreme understatement, and in expressing it the authors might well have mentioned also the paucity of comparative data sets for the same group of taxa. What I have presented here is an attempt to begin to remedy this for birds. I am optimistic that future work-

ers will continue to gather anatomical, behavioral and other "phenotypic" data (including molecular) for a wide variety of taxa. It is my hope that these workers will gather such data with the goal of using them for analyses like the present one, analyses that will be greater both in scope and in detail. Through such work we have an excellent chance of formulating rigorous hypotheses about phylogenetic relationships among birds and about the evolution of complex avian character systems.

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## APPENDIX 1. Characters used in the analysis.

1. M. ilirotibialis medialis: (1) present; (0) absent. 2. M. ilirotibialis lateralis, pars preacetabularis: (0) present; (1) absent; (2) vestigial. 3. M. ilirotibialis lateralis, pars acetabularis: (0) present; (1) absent; (2) aponeurotic; (A) 0 + 1. 4. M. ilirotibialis lateralis, pars postacetabularis: (0) present; (1) absent; (A) 0 + 1. 5. M. ilirotrochantericus caudalis: (1) reduced; (0) unreduced. 6. M. ilirotrochantericus cranialis, strongly fused with M. ilirotrochantericus caudalis: (1) fused; (0) unfused. 7. M. iliofemoralis externus: (0) present; (1) absent. 8. M. femorotibialis externus, distal head: (0) present; (1) absent. 9. M. femorotibialis internus, longitudinal division: (1) present; (0) absent. 10. M. iliofibularis, ansa iliofibularis forms a single ligament: (1) present; (0) absent. 11. M. iliofibularis, ansa iliofibularis arms elongated: (1) present; (0) absent; (2) moderately elongate. 12. M. flexor cruris lateralis, pars accessoria: (0) present; (1) absent; (A) 0 + 1. 13. M. flexor cruris lateralis, pars pelvica: (0) present; (1) absent. 14. M. flexor cruris lateralis, pars accessoria: (1) reduced; (0) not reduced; (?) absent. 15. M. caudofemoralis: (0) present; (1) absent; (2) poorly developed. 16. M. iliofemoralis: (0) present; (1) absent; (2) poorly developed; (A) 0 + 1. 17. M. flexor cruris medialis, two distinct parts: (1) present; (0) absent. 18. M. flexor cruris medialis and M. flexor cruris lateralis, tendons: (0) fused; (1) unfused. 19. M. pubo-ischio-femoralis, division into pars cranialis and pars caudalis: (1) divided; (0) not divided. 20. M. pubo-ischio-femoralis, muscular slip: (0) absent; (1) present. 21. M. pubo-ischio-femoralis, pars profundus divided into two parts: (0) undivided; (1) divided; (2) intermediate. 22.

## APPENDIX 1. Continued.

M. obturatorius lateralis, pars dorsalis: (0) present; (1) absent. 23. M. obturatorius medialis, two heads of origin: (0) absent; (1) present. 24. M. obturatorius medialis, number of tendons of insertion: (0) one tendon; (1) two tendons; (2) three tendons. 25. M. obturatorius medialis, enlarged in width: (0) no; (1) yes. 26. Mm. obturatorius medialis and obturatorius lateralis, distal fusion: (0) yes; (1) no. 27. M. iliofemoralis internus: (0) present; (1) absent. 28. M. iliofemoralis internus: (0) "typical"; (1) "unusually short and broad." 29. M. ambiens: (0) present; (1) absent. 30. M. ambiens, extent of origin: (0) limited to pectineal process; (1) extending from pectineal process to pubis; (2) one origin from pectineal process and one from pubis. 31. M. ambiens, longitudinal division: (0) absent; (1) present. 32. M. gastrocnemius pars lateralis: (0) single; (1) double; (A) 0 + 1. 33. M. gastrocnemius pars medialis, patellar band: (0) present; (1) absent; (A) 0 + 1. 34. M. gastrocnemius pars medialis, number of heads: (0) one head; (1) two heads; (A) 0 + 1. 35. M. gastrocnemius, fourth head: (0) absent; (1) present. 36. M. gastrocnemius, tendon of insertion contributes to ossification of the hypotarsus: (0) no; (1) yes. 37. M. tibialis cranialis, number of tendons of insertion: (0) bifurcated tendon; (1) one tendon. 38. M. extensor digitorum longus, number of heads of origin: (0) one head (from tibia); (1) two heads (from tibia and fibula); (2) two heads (from tibia and femur). 39. M. extensor digitorum longus, hallucal tendon: (0) absent; (1) present. 40. M. fibularis longus: (0) present; (1) poorly developed; (2) absent; (B) 0 + 2. 41. M. fibularis longus, tibial head: (0) present; (1) fibular head only; (2)

## APPENDIX 1. Continued.

arising from underlying muscles and from tibia. 42. *M. fibularis longus*, branch to FPD3: (0) present; (1) absent. 43. *M. fibularis brevis*: (0) present; (1) weak; (2) absent. 44. *M. flexor perforans et perforatus digiti III*, vinculum: (0) present; (1) absent. 45. *M. flexor perforans et perforatus digiti II*, relationship to *M. flexor perforans et perforatus digiti III*: (0) does not overlap and conceal FPPD3; (1) does overlap. 46. *M. flexor perforans et perforatus digiti II*, number of heads: (0) one head; (1) intermediate; (2) two; (3) three. 47. *M. flexor perforans et perforatus digiti II*, origin from *ansa iliofibularis*: (0) absent; (1) present. 48. *M. flexor perforatus digiti II*, position: (0) deeply situated; (1) superficial. 49. *M. plantaris*: (0) present; (1) absent; (A) 0 + 1. 50. *M. plantaris*: (0) "typical"; (1) very powerfully developed. 51. *M. flexor hallucis longus*, branch to hallux: (0) present; (1) lacking or weak. 52. *M. flexor hallucis longus* and *M. flexor digitorum longus*, type of flexor arrangement: see George and Berger (1966:447) for description of Types I-VIII, and Berman (1984) for description of Type X (coded 9 herein); modification found in hummingbirds is designated Type 0. 53. *M. flexor hallucis longus*, number of heads: (0) one head; (1) two heads; (2) three heads. 54. *M. flexor digitorum longus*, number of heads: (0) two heads; (1) three heads. 55. *M. flexor digitorum longus*, size: (0) "typical"; (1) very powerful; (2) intermediate. 56. *M. flexor digitorum longus*, location: (0) deeply situated; (1) superficially situated. 57. *M. popliteus*: (0) present; (1) absent. 58. *M. flexor hallucis brevis*: (0) present; (1) vestigial; (2) absent; (B) 0 + 2. 59. *M. flexor hallucis brevis*, number of tendons of insertion: (0) one; (1) two. 60. *M. extensor hallucis longus*: (0) present; (1) absent. 61. *M. extensor hallucis longus*, number of heads: (0) two heads; (1) one head; (A) 0 + 1. 62. *M. extensor hallucis longus*, accessory: (0) absent; (1) present. 63. *M. abductor digiti II*: (0) present; (1) absent; (2) vestigial. 64. *M. adductor digiti II*: (0) present; (1) weak; (2) absent. 65. *M. extensor*

## APPENDIX 1. Continued.

*brevis digiti IV*: (0) present; (1) vestigial; (2) absent; (C) 1 + 2. 66. *M. lumbricalis*: (0) absent; (1) present; (2) weak or vestigial. 67. Feathers: (1) present; (0) absent (to reflect monophyly of birds and thereby exclude Ancestor). 68. Neognath monophyly ("dummy variable"): (1) reflects monophyly of the ingroup (for actual synapomorphies, see Cracraft 1986, Cracraft and Mindell 1989); (0) all other taxa. 69. Paleognath monophyly ("dummy variable"): (1) reflects monophyly of the sister group of neognaths (for actual synapomorphies see Cracraft 1986, Cracraft and Mindell 1989); (0) all other taxa. 70. Mating system: (0) monogamy; (1) polygyny; (2) polyandry; (3) promiscuity; (A) 1 + 2; (B) 0 + 1; (C) 0 + 3. 71. Duration of pair bond: (0) seasonal; (1) brief; (2) longer than "brief" but less than one nesting effort; (3) longer than one season (ranging from across two seasons to life); (4) pair bond may be renewed annually but dissolves between seasons. 72. Mate guarding by males: (0) absent; (1) present. 73. Resource defense polygyny (harem): (0) absent; (1) present; (A) 0 + 1. 74. Lekking: (0) absent; (1) present. 75. Defense of young/parental care: (0) biparental; (1) uniparental (female); (2) uniparental (male); (3) double clutches; (4) no parental care; (A) 0 + 1. 76. Distinguishable reverse sexual dimorphism of any kind: (0) absent; (1) present. 77. Males feed females during nest care: (0) no; (1) yes. 78. Incubation: (0) by female; (1) by both parents; (2) by male only; (3) by neither parent. 79. Nest-building or nest-site selection: (0) by female only; (1) by both parents; (2) by male only. 80. Posthatching (prefledging) care (feeding, as distinct from defense, character 75): (0) female only; (1) both parents; (2) male only; (3) neither parent. 81. Postfledging care: (0) female only; (1) both parents; (2) male only; (3) neither. 82. Group breeding: (0) absent; (1) present. 83. Colonial nesting: (0) absent; (1) present. 84. Posthatching development: (0) precocial; (1) altricial.

APPENDIX 2. Matrix showing hindlimb muscle and behavioral character data for all taxa. Species originally used by McKittrick (1991) given in parentheses if different from that on which behavioral data are based. Missing data indicated by "?". Multistate characters are indicated by asterisk (\*).

		Character								Taxon		
1	2	3	4	5	6	7	8					
1234567890123456789012345678901234567890123456789012345678901234	*	*	*	*	*	*	*	*	*	*****	Ancestor	
00	0	0	0	0	0	0	0	0	0	0	0	Rhea americana
0000010100	0	0	0	0	0	0	0	0	0	0	0	Crypturellus boucardi
0000101000	0	0	0	0	0	0	0	0	0	0	0	Nothoprocta ornata
0001000010011?00	0	0	0	0	0	0	0	0	0	0	0	Diomedea immutabilis*
0001000010011?00	0	0	0	0	0	0	0	0	0	0	0	Phoebastria fusca (palpebrata)*
0001100010011?00	0	0	0	0	0	0	0	0	0	0	0	Daption capense
0001100010011?00	0	0	0	0	0	0	0	0	0	0	0	Fulmarus glacialis*
0001100010011?00	0	0	0	0	0	0	0	0	0	0	0	Procellaria parkinsoni (aequinoctialis)*
0001100010011?00	0	0	0	0	0	0	0	0	0	0	0	Puffinus puffinus (creatopus)*
0001100010011?00	0	0	0	0	0	0	0	0	0	0	0	Pterodroma inexpectata (heraldica)
0001000010011?0100	0	0	0	0	0	0	0	0	0	0	0	Oceanites oceanicus
0001000010011?0100	0	0	0	0	0	0	0	0	0	0	0	Fregata tropica (grallaria)
0001000010011?0100	0	0	0	0	0	0	0	0	0	0	0	Oceanodroma leucorhoa
0001000010011?0100	0	0	0	0	0	0	0	0	0	0	0	Pelecanoides urinatrix (garnoti)*
0001000010011?0100	0	0	0	0	0	0	0	0	0	0	0	Pygoscelis adeliae
00010000210?00	0	0	0	0	0	0	0	0	0	0	0	Eudypptes spp.*
00010000210?00	0	0	0	0	0	0	0	0	0	0	0	Eudypptula minor
00010000210?00	0	0	0	0	0	0	0	0	0	0	0	Spheniscus magellanicus*
00010000210?00	0	0	0	0	0	0	0	0	0	0	0	Gavia immer
00010000110?0100	0	0	0	0	0	0	0	0	0	0	0	Podiceps nigricollis
0101000011?21000	0	0	0	0	0	0	0	0	0	0	0	Fregata aquila (magnificens)*
0001000100010?0100	0	0	0	0	0	0	0	0	0	0	0	Phalacrocorax auritus*
0001000100010?0100	0	0	0	0	0	0	0	0	0	0	0	Anhinga anhinga*
0001000100010?0100	0	0	0	0	0	0	0	0	0	0	0	Sula bassanus (brewsteri)*
00000000000021000010001?0000010000000000000000000000000000000000	0	0	0	0	0	0	0	0	0	0	0	Ardea herodias
00000000000021000010001?0000010000000000000000000000000000000000	0	0	0	0	0	0	0	0	0	0	0	Butorides virescens
00000000000021000010001?0000010000000000000000000000000000000000	0	0	0	0	0	0	0	0	0	0	0	Florida caerulea
00000000000021000010001?0000010000000000000000000000000000000000	0	0	0	0	0	0	0	0	0	0	0	Mycteria americana
00000000000021000010001?0000010000000000000000000000000000000000	0	0	0	0	0	0	0	0	0	0	0	Ciconia ciconia
00000000000021000010001?0000010000000000000000000000000000000000	0	0	0	0	0	0	0	0	0	0	0	Leptoptilos crumeniferus
00000000000021000010001?0000010000000000000000000000000000000000	0	0	0	0	0	0	0	0	0	0	0	Plegadis autumnolis (guarauna)
10100000000010000200	0	0	0	0	0	0	0	0	0	0	0	Phoeniconaius minor (Phoenicopterus ruber)
0000001000	0	0	0	0	0	0	0	0	0	0	0	Cathartes aura
0000001000	0	0	0	0	0	0	0	0	0	0	0	Coragyps atratus



APPENDIX 2. Continued.

Character								Taxon
1	2	3	4	5	6	7	8	
1234567890123456789012345678901234567890123456789012345678901234								
**	*	*	*	*	*	*	*	
0000001000001100001000								<i>Gymnogyps californianus</i>
0001000100011?0100								<i>Accipiter gentilis (cooperii)</i>
0001000110011?0100								<i>Buteo jamaicensis</i>
0001000100011?0100								<i>Pandion haliaetus</i>
0001000100011?0100								<i>Falco sparverius</i>
000100010010?000								<i>Chen caerulescens</i>
000000100010?000								<i>Anas platyrhynchos</i>
000000100010?000								<i>Oxyura jamaicensis</i>
00								<i>Dendragapus obscurus</i>
00								<i>Lagopus mutus*</i>
00								<i>Canachites canadensis*</i>
00								<i>Bonasa umbellus*</i>
00								<i>Meleagris gallopavo*</i>
00								<i>Opisthocomus hoazin</i>
00								<i>Grus canadensis</i>
00								<i>Fulica americana</i>
000100000000101000								<i>Rynchops niger</i>
000100000000101000								<i>Stercorarius pomarinus</i>
000100000000101000								<i>Stercorarius parasiticus*</i>
000100000000101000								<i>Larus marinus (pipixcan)</i>
000100000000101000								<i>Rissa tridactyla</i>
000100000000101000								<i>Sterna hirundo (albifrons)</i>
000100000000101000								<i>Alca torda</i>
000100000000101000								<i>Uria aalge</i>
000100000000101000								<i>Cepphus columba</i>
000100000000101000								<i>Brachyramphus marmoratum</i>
000100000000101000								<i>Ptychoramphus aleuticus</i>
000100000000101000								<i>Cerorhinca monocerata</i>
000100000000101000								<i>Fratricula arctica</i>
0000001000								<i>Zenaidra macroura</i>
00200011000000101000								<i>Coccyx erythrophthalmus</i>
000000110000002201000012000000001100000000000000000000000000000000								<i>Geococcyx californianus</i>
000000110000000010000?20000000110000000000000000000000000000000000								<i>Crotophaga sulcirostris</i>
0001000000011?01010?0000000001?0100001102??01000001?01101000100000021100?								<i>Otus asio</i>
0001000000011?01010?0000000001?0100001102??0100001?011010001000000211003?00??11001								<i>Bubo virginianus</i>
0200001000000?010100000000011?0000000000000021000000050000001010000111000?0000?01012000								<i>Chordeiles minor</i>

APPENDIX 2. Continued.

Character								Taxon
1	2	3	4	5	6	7	8	
1234567890123456789012345678901234567890123456789012345678901234								
**	*	*	*	*	*	****		
0001001100010?010?0000000001?0110000002?0100001?050?010000100000A11000?00000?1113101								<i>Chaetura pelagica</i>
001100110001?010?00000011?1?010000202?010000100002010000010201103100?100000?001								<i>Eulampis jugularis</i>
0020001000000100000100000001?0100000001010000006000010001012201100?00000?111?001								<i>Colaptes auratus</i>
00200010000100010100010000001?010000000101000001016000010001012201100300000?1111001								<i>Picoides villosus</i>
00010010000001010010?000000001000100007212010001012201100010000?0011001								<i>Tyrannus tyrannus</i>
0000001?000000010010?00001001?01?0000000001000100007110010001012201100?000011?11101								<i>Corvus brachyrhynchos</i>

\* Eliminated from final analysis.

APPENDIX 3. Character-change lists for behavioral characters (70–84) based on Tree 1 (Fig. 2). The “ci” refers to consistency index. Each change is one step in length. Arrows with double lines indicate transitions that are the same for all optimizations (ALL). Arrows with single lines indicate transitions that are not the same for all optimizations (e.g. ACC-TRAN). The “wt” refers to “within-terminal taxon.” See Methods for explanation of optimization routines.

**Character 70** (ci = 0.667). ALL: node 102 0 ⇒ 3 *Eulampis* (a change from state 0 to state 3 between node 102 and *Eulampis*); node 115 0 ⇒ 3 *Dendragapus*. ACCTAN: node 118 0 ⇐ 1 Ancestor; node 62 0 → 1 node 61; *Rhea* 1 → 12 = A (wt); *Crypturellus* 1 → 12 = A (wt); node 114 0 → 1 *Anas*; *Oxyura* 0 → 03 = C (wt); *Opisthocomus* 0 → 01 = B (wt). DELTRAN: *Rhea* 1 → 12 = A (wt); *Crypturellus* 1 → 12 = A (wt); node 62 1 → 0 *Nothoprocta*; node 117 1 → 0 node 113; node 114 1 → 0 *Oxyura*; *Oxyura* 0 → 03 = C (wt); *Opisthocomus* 1 → 01 = B (wt). MINF: *Rhea* 1 → 12 = A (wt); *Crypturellus* 1 → 12 = A (wt); node 62 1 → 0 *Nothoprocta*; node 118 1 → 0 node 117; node 114 0 → 1 *Anas*; *Oxyura* 0 → 03 = C (wt); *Opisthocomus* 0 → 01 = B (wt).

**Character 71** (ci = 0.222). ALL: node 61 2 ⇒ 0 *Rhea*; node 64 4 ⇒ 3 *Pterodroma*; node 68 4 ⇒ 0 *Podiceps*; node 69 4 ⇒ 3 *Chen*; node 74 4 ⇒ 3 *Cephus*; node 84 0 ⇒ 3 *Grus*; node 115 2 ⇒ 1 *Dendragapus*. ACCTAN: node 117 2 → 0 node 113; node 83 0 → 4 node 78; node 88 0 → 4 node 87; node 90 0 → 4 *Ciconia*; node 103 0 → 1 node 102; node 102 1 → 3 node 101; node 106 0 → 3 node 104; node 111 0 → 3 node 110; node 109 3 → 4 *Crotophaga*; node 112 0 → 1 *Zenaida*; *Zenaida* 1 → 12 = A (wt). DELTRAN: node 113 2 → 0 node 93; node 83 0 → 4 node 78; node 88 0 → 4 node 87; node 90 0 → 4 *Ciconia*; node 111 2 → 0 node 108; node 102 0 → 3 node 101; node 102 0 → 1 *Eulampis*; node 104 0 → 3 *Picoides*; node 109 2 → 3 *Geococcyx*; node 109 2 → 4 *Crotophaga*; *Zenaida* 2 → 12 = A (wt). MINF: node 117 2 → 0 node 113; node 83 0 → 4 node 78; node 88 0 → 4 node 87; node 90 0 → 4 *Ciconia*; node 102 0 → 3 node 101; node 102 0 → 1 *Eulampis*; node 104 0 → 3 *Picoides*; node 109 0 → 3 *Geococcyx*; node 109 0 → 4 *Crotophaga*; node 112 0 → 1 *Zenaida*; *Zenaida* 1 → 12 = A (wt).

**Character 72** (ci = 0.143). ALL: node 102 1 ⇒ 0 *Eulampis*; node 106 1 ⇒ 0 node 104; node 114 0 ⇒ 1 *Anas*. ACCTAN: node 62 0 → 1 node 61; node 85 0 → 1 node 84; node 80 1 → 0 *Rissa*; node 113 0 → 1 node 112. DELTRAN and MINF: node 61 0 → 1 *Rhea*; node 83 0 → 1 node 78; node 79 0 → 1 *Rynchops*; node 112 0 → 1 node 111.

**Character 73** (ci = 1.000). ALL: node 62 0 ⇒ 1 node 61.

**Character 74** (uninformative).

**Character 75** (ci = 0.600). ALL: node 118 0 ⇒ 2 node 62; node 102 0 ⇒ 1 *Eulampis*. ACCTAN: node 117 0 → 1 node 116; node 114 1 → 0 *Oxyura*; *Opisthocomus* 1 → 12 = A (wt). DELTRAN and MINF: node 114 0 → 1 *Anas*; node 116 0 → 1 node 115; *Opisthocomus* 1 → 12 = A (wt).

**Character 76** (ci = 0.500). ALL: node 82 0 ⇒ 1 *Stercorarius* 1; node 101 0 ⇒ 1 node 99.

**Character 77** (ci = 0.250). ALL: node 81 0 ⇒ 1 node

## APPENDIX 3. Continued.

80. ACCTRAN: node 93 0 → 1 node 92; node 108 0 → 1 node 107; node 102 1 → 0 *Eulampis*. DELTRAN and MINF: node 89 0 → 1 *Leptoptilus*; node 102 0 → 1 node 101; node 105 0 → 1 *Corvus*.

**Character 78** (ci = 0.375). ALL: node 69 1 ⇒ 0 *Chen*; node 97 1 ⇒ 0 *Accipiter*; node 105 1 ⇒ 0 *Tyrannus*. ACCTRAN: node 118 0 → 3 Ancestor; node 118 0 → 2 node 62; node 117 0 → 1 node 113; node 103 1 → 0 node 102; node 101 0 → 1 node 99. DELTRAN: node 118 3 → 2 node 62; node 117 3 → 1 node 113; node 100 1 → 0 *Otus*; node 102 1 → 0 *Eulampis*; node 117 3 → 0 node 116. MINF: node 118 1 → 3 Ancestor; node 118 1 → 2 node 62; node 100 1 → 0 *Otus*; node 102 1 → 0 *Eulampis*; node 117 1 → 0 node 116.

**Character 79** (ci = 0.286). ALL: node 117 0 ⇒ 1 node 113; node 89 1 ⇒ 2 *Mycteria*; node 96 1 ⇒ 0 *Chordeiles*; node 102 1 ⇒ 0 *Eulampis*. ACCTRAN: node 118 0 → 2 node 62; node 71 1 → 2 node 66; node 106 1 → 0 node 105. DELTRAN: node 62 0 → 2 node 61; node 65 1 → 2 *Oceanodroma*; node 105 1 → 0 *Tyrannus*. MINF: node 62 0 → 2 node 61; node 66 1 → 2 node 65; node 105 1 → 0 *Tyrannus*.

**Character 80** (ci = 0.750). ALL: node 102 1 ⇒ 0 *Eulampis*. ACCTRAN: node 118 0 → 3 Ancestor; node 118 0 → 2 node 62; node 117 0 → 1 node 113. DELTRAN: node 118 3 → 2 node 62; node 117 3 → 1 node 113; node 117 3 → 0 node 116. MINF: node 118 1 → 3 Ancestor; node 118 1 → 2 node 62; node 117 1 → 0 node 116.

**Character 81** (ci = 0.333). ALL: node 118 1 ⇒ 2 node 62; node 83 1 ⇒ 3 node 78; node 70 3 ⇒ 1 node 69; node 74 3 ⇒ 2 node 73; node 94 1 ⇒ 3 *Florida*; node 96 1 ⇒ 2 *Chordeiles*; node 103 1 ⇒ 3 *Chaetura*; node 112 1 ⇒ 2 *Zenaidra*; node 117 1 ⇒ 0 node 116.

**Character 82** (ci = 0.250). ALL: node 103 0 ⇒ 1 *Chaetura*; node 105 0 ⇒ 1 *Corvus*; node 109 0 ⇒ 1 *Crotophaga*; node 115 ⇒ 0 *Opisthocomus*.

**Character 83** (ci = 0.200). ALL: node 85 0 ⇒ 1 node 84; node 69 1 ⇒ 0 node 68; node 93 0 ⇒ 1 node 92; node 95 0 ⇒ 1 node 94; node 109 0 ⇒ 1 *Crotophaga*.

**Character 84** (ci = 0.250). ALL: node 117 0 ⇒ 1 node 113; node 88 1 ⇒ 0 node 85; node 91 1 ⇒ 0 *Phoeniconaius*; node 96 1 ⇒ 0 *Chordeiles*.

## APPENDIX 4. References used for each taxon.

1. Ancestor, *Crocodylus* (Hunt 1975, Pooley 1977). 2. *Rhea americana* (Bruning 1974). 3. *Crypturellus boucardi* (Lancaster 1964). 4. *Nothoprocta ornata* (Pearson and Pearson 1955). 5. *Diomedea immutabilis* (Fisher 1971, Lefebvre 1977). 6. *Phoebetria fusca* (Weimerskirch et al. 1986). 7. *Daption capense* (Sagar 1979). 8. *Fulmarus glacialis* (Hatch 1987, 1990). 9. *Procellaria parkinsoni* (Imber 1987). 10. *Puffinus puffinus* (Palmer 1962, Harris 1966, Lack 1968). 11. *Pterodroma inexpectata* (Warham et al. 1977). 12. *Oceanites oceanites* (Palmer 1962). 13. *Fregetta tropica* (Beck and Brown 1971). 14. *Oceanodroma leucorhoa* (Palmer 1962). 15. *Pelecanoides urinatrix*

## APPENDIX 4. Continued.

(Thoreson 1969). 16. *Pygoscelis adeliae* (Ainley and Schlater 1972, Derkson 1977, Ainley et al. 1983). 17. *Eudypetes*, all spp. (Warham 1975). 18. *Eudypetula minor* (Reilly and Balmford 1975). 19. *Spheniscus magellanicus* (Boswall and MacIver 1975). 20. *Gavia immer* (McIntyre 1988). 21. *Podiceps nigricollis* (R. W. Storer, pers. comm.). 22. *Fregata aquila* (Stonehouse and Stonehouse 1963). 23. *Phalacrocorax auritus* (Palmer 1962). 24. *Anhinga anhinga* (Burger et al. 1978). 25. *Sula bassanus* (Nelson 1966). 26. *Ardea herodias* (Pratt 1970, Mock 1979). 27. *Butorides striatus* (Palmer 1962). 28. *Florida caerulea* (Rodgers 1980, Werschkul 1982a, b). 29. *Mycteria americana* (Palmer 1962, Kahl 1972). 30. *Ciconia ciconia* (Haverschmidt 1949, Noble-Rollin 1975). 31. *Leptoptilus crumeniferus* (Kahl 1966). 32. *Plegadis autumnolis* (Baynard 1913, Palmer 1962). 33. *Phoeniconaius minor* (Brown and Root 1971). 34. *Cathartes aura* (Coles 1944, Palmer 1988a). 35. *Coragyps atratus* (Stewart 1974). 36. *Gymnogyps californicus* (Palmer 1988a). 37. *Accipiter gentilis* (Møller 1987, Palmer 1988a). 38. *Buteo jamaicensis* (Fitch et al. 1946, Palmer 1988b). 39. *Pandion haliaetus* (Green 1976, Poole 1985, Birkhead and Lessells 1988). 40. *Falco sparverius* (Willoughby and Cade 1964, Palmer 1988b). 41. *Chen caerulescens* (Finney and Cooke 1978, Cooke et al. 1981, Lank et al. 1989). 42. *Anas platyrhynchos* (Lebret 1961, Goodburn 1984, McKinney 1986). 43. *Oxyura jamaicensis* (Siegfried 1976, Joyner 1977). 44. *Dendragapus obscurus* (Wiley 1974, Wittenberger 1978, Lewis 1985). 45. *Lagopus mutus* (McDonald 1970). 46. *Canachites canadensis* (Ellison 1973). 47. *Bonasa umbellus* (Gladfelter and McBurney 1971, Wittenberger 1978). 48. *Meleagris gallopavo* (Mosby and Handley 1942, Dalke et al. 1946). 49. *Opisthocomus hoazin* (Strahl 1988). 50. *Grus canadensis* (Walkinshaw 1965, Nesbitt 1989). 51. *Fulica americana* (Ryan and Dinsmore 1979). 52. *Rynchops niger* (Burger 1981, Quinn 1990). 53. *Stercorarius pomarinus* (Pitelka et al. 1955, Maher 1974). 54. *Stercorarius parasiticus* (Perdeck 1963, O'Donald 1983). 55. *Larus marinus* (Butler and Janes-Butler 1983). 56. *Rissa tridactyla* (Hodges 1969, Maunder and Threlfall 1972). 57. *Sterna hirundo* (Wiggins and Morris 1986, 1987). 58. *Alca torda* (Plumb 1965, Harris and Birkhead 1985). 59. *Uria aalge* (Johnson 1941, Birkhead et al. 1985, Hatchwell 1988). 60. *Cephus columba* (Drent 1965). 61. *Brachyramphus marmoratum* (Sealy 1974). 62. *Ptychoramphus aleuticus* (Thoreson 1964). 63. *Cerorhinca monocerata* (Wilson and Manuwal 1986). 64. *Fratrercula arctica* (Ashcroft 1979). 65. *Zenaidra macroura* (Westmoreland et al. 1986). 66. *Coccyzus erythrophthalmus* (Spencer, 1943). 67. *Geococcyx californianus* (Woods 1960, Ohmart 1973, Folse and Arnold 1978). 68. *Crotophaga sulcirostris* (Vehrencamp et al. 1986). 69. *Otus asio* (Sherman 1911, Allen 1924). 70. *Bubo virginianus* (Errington 1932, Keith 1977). 71. *Chordeiles minor* (Bent 1940, Weller 1984, Dexter 1961, Sutherland 1963). 72. *Chaetura pelagica* (Dexter 1952, Fischer 1958). 73. *Eulampis jugularis* (Wolf and Wolf 1971). 74. *Colaptes auratus* (Burns 1900). 75. *Picoides villosus* (Kilham 1966, 1968, 1969). 76. *Tyrannus tyrannus* (McKittrick 1990, pers. observ.). 77. *Corvus brachyrhynchos* (Good 1952).