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Phylogenetic Analysis of the Evolution of Display Behavior in the Neotropical Manakins (Aves: Pipridae)

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Abstract

Phylogenetic systematic methods were applied in an investigation of the evolution of lek display behavior in the Neotropical manakins (Aves: Pipridae). Results of a previous investigation of the syringeal morphology of manakins were used as a behaviorally independent estimate of the phylogeny of the family. Three phylogenetic analyses of 44 display characters were performed: (1) display elements alone were used as systematic characters; (2) display elements and syringeal characters were combined into a single phylogenetic analysis; and (3) the behavioral characters were parsimoniously superimposed on the syringeal hypothesis of phylogeny. The results of the first two analyses were highly congruent with the independent syringeal hypothesis of phylogeny. Most detailed behavioral similarities among manakins are homologs. The three analyses support identical hypotheses of behavioral homology for 37 of the 44 behavioral characters. Manakin displays are phylogenetically highly informative. The least detailed displays are most likely to be convergent or lost independently (homoplasious). The last analysis yields the most behaviorally independent hypotheses of behavioral homology. Manakin display elements have evolved through a variety of ethological mechanisms, including elaboration of derived movements within a primitive posture, derivation of novel postures within primitive displays, and initial and terminal additions of novel elements to display sequences. Phylogenetic distributions of derived displays and correlated plumage traits indicate that differentiation of display behavior has driven some aspects of morphological evolution in manakins. These results confirm the applicability of phylogenetic methods to comparative ethological questions.

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Introduction

Since the mid-1960's, comparative systematic biology has undergone a revolution in methods of reconstructing phylogenetic hypotheses and making comparative evolutionary inferences (HENNIG 1966; ELDREDGE & CRACRAFT 1980;

WILEY 1981). Outside of taxonomy, phylogenetic systematics has been applied in investigations of biogeography (NELSON & PLATNICK 1981; CRACRAFT 1982), functional and evolutionary morphology (LAUDER 1981, 1982; SCHAEFER & LAUDER 1986), and adaptation (RIDLEY 1983; CODDINGTON 1988). Over the same period, however, interest in the comparative ethological approaches pioneered by LORENZ (1941, 1970, 1971), TINBERGEN (1951, 1952, 1959), and others has waned relative to adaptational, sociobiological, and neurobiological perspectives on behavioral evolution. In this investigation, I use phylogenetic, or cladistic, methods to analyze the evolution of display behavior in a family of lekking passerine birds, the manakins (Pipridae). I address two traditional, comparative ethological questions: 1) Are behavioral similarities homologs? 2) Through what ethological mechanisms have display elements evolved?

The manakins are a family of 40 species of Neotropical suboscine passerine birds (SNOW 1975, 1979; PRUM 1989, 1990, ms). Polygyny and lek/arena display are present in all manakin species that are behaviorally known (SICK 1959, 1967; SNOW 1963 c; PRUM 1989). Most species are highly sexually dimorphic in plumage, and many perform elaborate male courtship displays that may include acrobatic manoeuvres, mechanical display noises made with the wings, and coordinated display between males. Previous discussions of the evolution of manakin display behavior have been limited by the lack of any phylogeny for the group (SICK 1959, 1967; SNOW 1963 c). Traditional classifications of the manakins were based solely on overall similarity of plumage (SCLATER 1888; RIDGWAY 1907; HELLMAYR 1910, 1929). Recent hypotheses about the interrelationships of manakin genera have been based on presumed trends in male plumage and display behavior (SNOW 1975, 1979).

In a previous investigation, I used the morphology of the syrinx, the avian vocal organ, to produce a behaviorally independent hypothesis of phylogeny for the manakins (PRUM 1989, ms). I concentrated on syringeal morphology because of the extensive informative variation in this organ among manakins, and because syringeal morphology is likely to be more independent of the evolution of display behavior than some other morphological characters. For example, limb musculature could be correlated with acrobatic movements and mechanical production of wing noise that are part of many manakin displays. And male plumage may be correlated with the movements in which it is prominently displayed.

In this paper, I use manakin display behavior and syringeal morphology in three different phylogenetic analyses. In the first analysis, display characters alone are used to construct a hypothesis of phylogeny for the manakins. This hypothesis is compared to the independent phylogenetic tree based on syringeal morphology. In the second analysis, the behavioral and syringeal characters are combined into a single data set to produce a combined phylogenetic hypothesis. In the last analysis, the behavioral characters are superimposed on the syringeal consensus tree to identify the most parsimonious hypothesis of behavioral evolution within the context of the morphological hypothesis of phylogeny. These analyses employ increasingly less restrictive assumptions about behavioral evolution to assess phylogenetic patterns in behavioral homology and evolution.

The first analysis tests whether manakin display elements can be used to reconstruct the phylogeny of the group. It also provides an opportunity to investigate which kinds of display elements are most phylogenetically informative. The second analysis tests the assumption that the morphological characters alone yield an accurate estimate of manakin phylogeny. The last analysis requires the assumption that the morphological tree is an accurate estimate of phylogeny of the manakins, but it provides the most behaviorally independent assessment of behavioral homology and historical transition series in behavior. Together, the three analyses provide multiple perspectives on comparative ethology of manakin displays. Further, phylogenetic analyses of behavior provide an explicit historical context necessary for testing additional hypotheses about natural and sexual selection, and the process of character transformation (LAUDER 1981, 1982; RIDLEY 1983; DOBSON 1985; CODDINGTON 1988).

Introduction to the Manakins (Pipridae)

Phylogeny and Taxonomy

The manakins are suboscine passerine birds in the large and diverse superfamily Tyrannoidea, which also includes the cotingas (Cotingidae) and tyrant flycatchers (Tyrannidae). Traditionally, the manakin family (Pipridae) included over 50 species in 17 or more genera (SCLATER 1888; RIDGWAY 1907; HELLMAYR 1910, 1929; SNOW 1975, 1979). Recent phylogenetic analyses of the higher-level relationships of the tyrannoids using morphological characters indicate that the Pipridae, as traditionally defined, is polyphyletic (PRUM 1989, 1990; PRUM & LANYON 1989). Six genera — *Schiffornis*, *Sapayoa*, *Piprites*, *Neopipo*, *Tyrannetes*, and *Neopelma* — are more closely related to other nonpiprid tyrannoids than to the piprids. The remaining 40 species in ten genera — *Corapipo*, *Masius*, *Ilicura*, *Manacus*, *Machaeropterus*, *Chiroxiphia*, *Antilophia*, *Chloropipo*, *Xenopipo*, *Heterocercus*, and *Pipra* — all share a unique, derived syringeal novelty (PRUM 1989, 1990). These genera constitute the true manakins, which are the sole subject of this paper.

Investigations of the syringeal morphology of the manakins support an almost completely resolved hypothesis of phylogeny for the family (PRUM 1989, ms). This phylogeny indicates that 9 of the 11 above genera are monophyletic, natural groups, but that two genera are paraphyletic or polyphyletic. The four species of *Chloropipo* and *Xenopipo atronitens* are a monophyletic group, but *C. uniformis* is most closely related to *X. atronitens*. As a result, all five species were combined in the genus *Xenopipo*, the senior of the two generic names (PRUM 1989, ms). Also, the seven species of the *Pipra serena* species group are not most closely related to the rest of the genus *Pipra*. The syringeal characters, however, did not resolve the monophyly or relationships of the *serena* species group, so it was left provisionally in the polyphyletic genus *Pipra* (PRUM 1989, ms).

Throughout this paper, I follow the species-level taxonomy of SNOW (1979) with a few exceptions as follows. I recognize three species of *Manacus*: *manacus*, *vitellinus*, and *candei*. I also recognize the two diagnosable, allopatric geographic

forms of *Pipra serena* as separate species: *Pipra serena* and *Pipra suavissima* (PRUM 1988, 1989). For convenience, I refer to several monophyletic groups, or clades, of nonsympatric species ("species groups") in abbreviated form. The *Pipra erythrocephala* clade includes five species — *cornuta*, *mentalis*, *chloromeros*, *erythrocephala*, and *rubrocapilla*. The *Pipra aureola* clade includes *aureola*, *fasciicauda* and *filicauda*. The *Pipra serena* species group includes *serena*, *suavissima*, *coronata*, *isidorei*, *nattereri*, *vilasboasi*, and *iris*.

Display Behavior

The revised, monophyletic Pipridae (PRUM 1989, 1990) includes all of the strikingly sexually dimorphic species of traditional manakins. Typically, males are boldly patterned with patches of black, white, or bright colors, whereas females are olive or yellowish green. The genus *Xenopipo*, however, includes one species with reduced sexual dimorphism in plumage (*flavicapilla*) and two species with uniformly olive-green coloration in both sexes (*holochlora* and *uniformis*).

The courtship displays and breeding systems of 21 species of manakins are documented in some detail. Six other species are known from limited observations or from anecdotal accounts, and 13 species are completely unknown behaviorally. The display behavior of manakins has been previously reviewed and discussed by SICK (1959, 1967) and SNOW (1963 c), but the displays of a number of species have been studied since that time. A list of available references on manakin display behavior is presented in the Appendix.

The manakins are mainly frugivorous, specializing on melastome (Melastomataceae) and rubiaceous (Rubiaceae) fruits (SNOW 1962 a, b, 1976; SKUTCH 1967, 1981; WETMORE 1972; FOSTER 1977 a; WORTHINGTON 1982; PRUM & JOHNSON 1987). Frugivory has been hypothesized to have allowed the emancipation of males from parental care, initiating the subsequent evolution of lek breeding in the family (SNOW 1976).

The cotingas (Cotingidae) are the sister group to the manakins, and all or part of the tyrant flycatchers (Tyrannidae) are the sister group to the cotingas and manakins (a number of taxa may belong to either of these two major assemblages) (SIBLEY & AHLQUIST 1985; PRUM 1989, 1990; PRUM & LANYON 1989). Most tyrant flycatchers are monogamous, and the few polygynous, lekking species have simple displays that evolved independently of the displays of manakins (e.g., SNOW & SNOW 1979). The cotingas are a mixture of monogamous, cooperatively breeding, polygynous, and lekking species (SNOW 1982). All of the manakins whose behavior is known are polygynous and lek breeding. Although the behavior of a number of manakin species is poorly known, all of these species are most closely related to other manakins that are known to be lek breeders, including the sexually monomorphic species of *Xenopipo*. (*Xenopipo atronitens* is known to defend dispersed lek territories, but its display behavior has not been documented.)

Using outgroup comparison to the tyrannids (see Methods), the primitive breeding system in the manakin-cotinga clade is probably monogamy. The simplest, or most parsimonious, hypothesis is that lek breeding and display

behavior have evolved in the manakins a single time, independently of other polygynous tyrannoids. HÖGLUND (1989) has hypothesized that polygyny and lek breeding evolved in the manakins three independent times, but this result is confounded by the inclusion in the family of several traditional manakin genera and other tyrannoids (e.g. *Oxyruncus*) that are unrelated to the true manakins (PRUM 1990).

Manakin display behavior varies widely among species and genera. Manakins may perform displays on a variety of perches and surfaces including small horizontal branches, large horizontal tree limbs, mossy fallen logs, vertical perches or cleared courts on the ground. Spacing of male display territories varies among species from highly concentrated, classical leks of many males in small territories, to dispersed leks of a few males in larger territories.

The display repertoires of different species also vary in complexity. *Pipra serena* has a simple repertoire (PRUM 1985). It defends its display territory by calling incessantly; its displays are limited to the simple about-face display, to-and-fro flights between horizontal branches, and whirring or direct flights among vertical branches surrounding loosely organized display courts (Fig. 1A). Other manakins known to have simple display repertoires include *Pipra coronata*, *Pipra pipra*, and *Machaeropterus deliciosus*.

Species of *Corapipo*, *Masius*, *Ilicura*, *Chiroxiphia*, *Manacus*, and the *Pipra erythrocephala* and *aureola* clades have complex display repertoires including

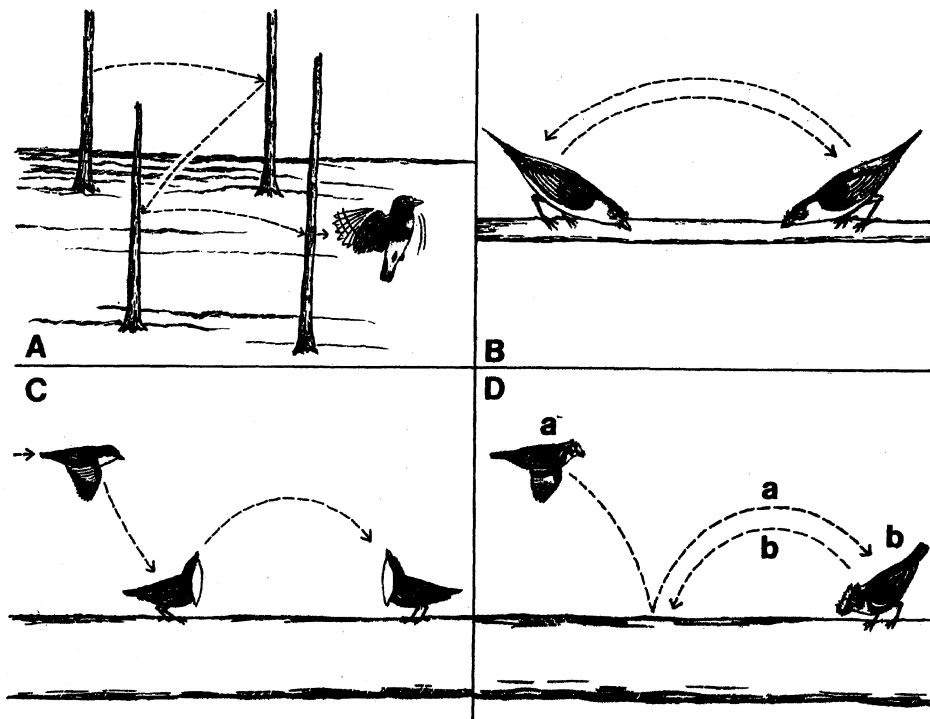


Fig. 1: Some manakin display elements. A: Whirring to-and-fro flight display of *Pipra serena* (PRUM 1985). B: Double-snap jump display in chin-down posture of *Ilicura militaris* (SNOW & SNOW 1985). C: Log-approach display in bill-pointing posture of *Corapipo gutturalis* (PRUM 1986). D: Coordinated log-approach display in chin-down posture of *Masius chrysopterus* (PRUM & JOHNSON 1987)

stereotyped postures, display movements, flight displays, or mechanical wing noises. PRUM & JOHNSON (1987) performed a preliminary cladistic analysis of display behavior in the four species of *Corapipo* (PRUM 1986), *Masius* (PRUM & JOHNSON 1987), and *Ilicura* (SNOW & SNOW 1985). The display repertoires of these species provide an excellent example of the complex patterns of behavioral similarity in the manakins.

Ilicura displays on large horizontal tree limbs, whereas *Corapipo* and *Masius* display on mossy fallen logs. The repertoires of all three species include the single perch jump with an about-face in flight, in which the male jumps off the display limb, turns around in flight, and lands 30 cm down the same perch facing back toward its original position. *Ilicura* performs this element in the double-snap jump display, in which the male jumps back and forth twice and produces a loud mechanical wing "snap" during each jump (Fig. 1B). Typically, *Ilicura* performs the double-snap jump display in chin-down posture with the tail pointed up and the plumage sleeked.

In both *Corapipo* and *Masius*, the single-perch jump with an about-face is incorporated into a log-approach flight display, in which a male flies to the log, rebounds up, turns around in flight, and lands back down on the log (Fig. 1C). *Masius* performs the log-approach display in the chin-down posture, but *Corapipo gutturalis* substitutes the distinct bill-pointing posture (Fig. 1C). The log-approach display of *Corapipo* and *Masius* lacks the mechanical "snap" of *Ilicura*. But *Corapipo* includes a different mechanical "pop" note before dropping to the log in the log-approach display. *Masius chrysopterus* performs a complex coordinated log-approach display involving two males that incorporates the log-approach display and the single-perch jump elements (Fig. 1D). (See display characters 1, 3, 31—32, 34—36.)

The display behavior of a number of species is too poorly known to analyze in detail here. The five species of *Xenopipo*, *Machaeropterus regulus*, *M. pyrocephalus*, the three species of *Heterocercus*, *Antilophia galeata*, and most species of the *Pipra serena* group are poorly known, though anecdotal accounts indicate that *Machaeropterus regulus*, *Xenopipo atronitens*, *Heterocercus linteatus* and *Antilophia galeata* defend male advertisement territories (SICK 1959, 1967).

Methods

Phylogenetic Methodology

Phylogenetic or cladistic systematics is a method of reconstructing the phylogeny or 'species genealogy' of a group based on shared, derived evolutionary novelties, called synapomorphies (HENNIG 1961; ELDREDGE & CRACRAFT 1980; WILEY 1981). Synapomorphies diagnose monophyletic groups, called clades, that include all of the descendants of the hypothetical common ancestor in which the derived character originally evolved. The phylogenetic method involves distinguishing synapomorphies from shared primitive similarities, called plesiomorphies, that are not phylogenetically informative.

Specific character states may be phylogenetically informative at one level and uninformative at another. For example, the presence of feathers is derived within tetrapods and indicates that all birds are more closely related to other birds than to any other animals. But feathers are primitive within birds, and presence of feathers does not indicate which birds are more closely related to one another. For this reason, phylogenetic analysis requires the formal recognition of specific level of investigation,

a monophyletic study group called the ingroup. Character variation within the ingroup can be polarized into primitive and derived character states by reference to the other most closely related monophyletic groups, called outgroups. By outgroup comparison, the ingroup character states that are also present in the outgroup are hypothesized to be primitive within the ingroup.

Each derived character is evidence supporting a clade including all the taxa that share that derived character. The combined set of derived characters supports a hierarchy of increasingly exclusive monophyletic groups that is a hypothesis of phylogeny for the ingroup. Convergent evolution, or the independent development of a derived character state in different lineages, can produce conflicts between the distributions of derived characters and errors in phylogenetic reconstruction, called homoplasies. Evolutionary reversals, or the secondary loss of a derived character in a lineage, can be another source of homoplasy.

Some conflicts among derived characters can be resolved by identifying the most parsimonious resolution of the phylogeny, or the tree that requires the fewest number of character changes including evolutionary developments and reversals. The most parsimonious phylogeny requires the fewest number of ad hoc hypotheses of character convergence or character loss. In the absence of a priori assumptions about how the characters have evolved, the most parsimonious phylogeny is the preferred scientific explanation of the data.

Frequently, it is impossible to distinguish convergent evolution from reversal as the cause of character conflict, or homoplasy, in a data set. For example, it is equally parsimonious to hypothesize two independent origins for a derived character as a single origin and a secondary loss in some lineage. Alternative equally parsimonious hypotheses of character evolution within a phylogeny are called character optimizations.

The parsimony or efficiency of explanation of a hypothesis of phylogeny can be expressed in terms of its length and its consistency index. The length of a phylogenetic hypothesis is the total number of character state changes, including both evolutionary developments and reversals, necessary to explain the distribution of the characters. The length of a phylogenetic hypothesis can be used to compare alternative resolutions based on the same data set. The consistency index (CI) is the minimum possible number of possible character state changes in the data set divided by the length of the phylogenetic hypothesis. A CI of 1 means that a phylogenetic hypothesis is completely consistent with the observed character data and requires only a single, unique origin for each derived character state, while a CI of 0.5 means that the phylogenetic hypothesis requires an average of two evolutionary character state changes, including developments and secondary losses, to explain the distribution of the characters. The CI is a useful index for comparing phylogenies that are based on different data sets.

Often many maximally parsimonious, equal-length trees are supported by a data set. Congruence among these phylogenetic hypotheses can be depicted in a strict consensus tree, a partially resolved tree that includes only the clades that appear in all of the equally parsimonious trees. As used here, a consensus tree is not an independent hypothesis of phylogeny, but a representation of the clades that are unambiguously supported by the characters.

Comparative biological investigations are based on the concept of homology, similarity among traits due to common ancestry. Ethologists have usually adopted the traditional morphological concept of homology that emphasized three criteria for recognizing homologs: (1) topographical similarity of relative position and shape, (2) special similarity in composition or development, and (3) existence of intermediate forms (MAYR 1958; ATZ 1970; LORENZ 1981). In phylogenetic systematics, homology of a character in any organisms is ultimately determined by the phylogenetic relationships of the organisms and the phylogenetic distribution of the character. Initially, hypothesized shared derived characters are putative homologs. Those derived characters that are congruent with other characters and diagnose clades are corroborated as homologs, whereas those characters that are incongruent with the others and are most parsimoniously hypothesized to be independently evolved in different lineages are inferred to be analogous, convergent similarities. The phylogenetic procedure of testing putative homologs based on congruence with other characters is known as the congruence test of homologs (PATTERSON 1982).

Phylogenetic Analyses of Manakin Displays

Manakin courtship displays described in the literature were reviewed. The available descriptions of the displays of manakins vary in quantity and documentation from species to species. I categorized

Table 1: The distributions of primitive (0), derived (1—4), and unknown (?) states of 44 phylogenetically informative display characters in the 21 behaviorally well known and partially documented species. Behavioral characters are described in Results. Sources of behavioral descriptions are listed in the Appendix. Presence of a display character is hypothesized as derived. All characters are primitive (absent) in other tyrannoids. Characters 1—43 have only a single derived state. Character 44 has four alternative derived states. *Chiroxiphia* includes all four species in the genus. *Chiroxiphia linearis* and *C. lanceolata* are unknown for character 18. Of the behaviorally poorly known taxa not listed in this table, *Heterocercus* is coded as derived for character 6, and *Machaeropterus regulus* and *M. pyrocephalus* are coded as derived for character 20

Species	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	3	3	3	3	3	3	3	3	3	3	3	3	4	4	4	4	
<i>Corapipo gutturalis</i>	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
<i>Corapipo leucorhoa</i>	0	0	1	0	?	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
<i>Masius chrysopterus</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	
<i>Ilicura militaris</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
<i>Manacus manacus</i>	0	0	0	1	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	
<i>Manacus vitellinus</i>	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	
<i>Chiroxiphia</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
<i>Machaeropterus deliciosus</i>	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
<i>Pipra serena</i>	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	
<i>Pipra coronata</i>	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	
<i>Pipra pipra</i>	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
<i>Pipra aureola</i>	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Pipra fasciicauda</i>	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
<i>Pipra filicauda</i>	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
<i>Pipra cornuta</i>	0	1	0	0	?	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
<i>Pipra mentalis</i>	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
<i>Pipra chloromeros</i>	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
<i>Pipra rubrocappilla</i>	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
<i>Pipra erythrocephala</i>	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	

the behavior of the 40 manakin species as well known ($n = 14$), partially documented ($n = 7$), poorly known ($n = 6$), or completely unknown ($n = 13$). The sources of behavioral descriptions for each manakin species and these behavioral categories are presented in the Appendix.

Descriptions of the displays were compared and putative homologs were identified based on detailed and consistent similarities in posture, movement, relative position to display perches, and other evidence of ritualized behavior (e.g., synchronization with a stereotyped vocalization). Only physical display elements that are hypothesized to be innate motor patterns were included in the analysis. The type of display perch or court is coded as a single, unordered multistate character, in which changes among any of the alternative character states are hypothesized to be equally likely. Physical displays that involve mechanical display noises were coded as behavioral characters, but the mechanical display noises themselves were not analyzed as separate characters. The social context or function of the displays were not considered in the analysis (e.g., no distinction was made between advertisement displays and precopulatory displays), so as not to confound homologous and analogous displays because of a transference or convergence in their social function.

Vocal portions of displays are mentioned in a few behavioral character descriptions as additional evidence of ritualization. But vocalizations themselves were not coded as characters because insufficient information is available, and because of the potential correlation between vocalizations and syringeal morphology used to reconstruct manakin phylogeny.

The variations in the display behavior were polarized into primitive and derived states by outgroup comparison (ELDRIDGE & CRACRAFT 1980; WILEY 1981; MADDISON et al. 1984). The closest outgroups to the manakins are the other tyrannoids, in which polygyny and courtship displays were independently evolved. The display behavior of the manakins was apparently uniquely derived within the family (see Introduction to Manakins). This conclusion is supported by the absence of any similarities between the displays of the cotingas and the manakins (SNOW 1982). As a result, the presence of a ritualized display behavior is hypothesized as derived. Two displays are here hypothesized to form a transition series when one display includes all of the details of another more broadly distributed behavior but also includes additional stereotyped movements or postures.

The known displays of manakins were coded as 43 binary characters, and the display perch/court character was coded as an unordered, multistate character. Transition series were coded as a series of binary characters. Unknown behavioral character states were coded as missing (?). Character distributions for the behaviorally well known and partially documented species are summarized in Table 1. I used the PAUP computer program, version 3 (SWOFFORD 1989), on a Macintosh computer to identify the most parsimonious phylogenetic hypotheses. Missing character states were hypothesized to be primitive or derived based on the simplest hypothesis for the evolution of that character given the resolution of the phylogeny based on all the other characters. This procedure makes the fewest ad hoc assumptions about the states of missing character data. All display characters were weighted equally.

Although different displays probably vary in their mutability and in their potential phylogenetic information, differential character weighting requires a priori assumptions about differences in the likelihood of character change that may have little objective support. Such assumptions also introduce direct biases and complications into subsequent inferences about character evolution. I have preferred to make the assumption of equal weighting, and to use incongruence among the characters and the independent phylogenetic hypotheses in multiple analyses to identify phylogenetically less informative displays (see Discussion). Strict consensus trees of the maximally parsimonious, equal-length phylogenetic hypotheses were identified using PAUP's consensus option.

In the first analysis, the behavioral data alone were used to construct a phylogenetic hypothesis for the manakins. The behaviorally poorly known and unknown species (*Machaeropterus regulus*, *M. pyrocephalus*, *Antilophia*, *Xenopipo*, *Heterocercus*, and the *Pipra serena* species-group, except *serena* and *coronata*) were not included in this analysis. The behavioral-consensus phylogeny was then compared to the consensus tree based on a previous analysis of syringeal morphology of the manakins (PRUM 1989, ms).

In the second analysis, the 44 behavioral characters were combined with 57 derived syringeal morphology characters from PRUM (1989, ms) to produce a single hypothesis of phylogeny. Behaviorally poorly known taxa were coded as unknown (?) for most behavioral characters. The PAUP program with mulpars, global-swapping options was used on the combined, equally weighted character set.

In the last analysis, the behavioral characters were superimposed on the syringeal consensus tree from PRUM (1989, ms) to identify the simplest hypothesis for the evolution of each display behavior within the independent morphological hypothesis of phylogeny (RIDLEY 1983). To do this with the PAUP program, the behavioral characters were excluded from the combined data set, and the most parsimonious syringeal phylogenies were used as input trees. The character-change lists for the behavioral characters yield a description of the most parsimonious hypothesis for their evolution.

Each of these analyses is a variation of the congruence test of homology (PATTERSON 1982) in which putative behavioral homologs are tested by congruence with a different set of the behavioral and morphological data. Each subset of the data used has a different degree of independence from the behavioral characters. Subsequently, the inferences about behavioral evolution drawn from each analysis also vary in their independence from the behavioral data.

In the first phylogenetic analysis of the behavioral characters alone, behavioral homologs are tested by congruence with other behavioral characters, assuming the independence of each of the behavioral characters from one another. This method also tests the phylogenetic content of the behavioral characters through comparison with the independent syringeal phylogeny. However, conclusions about the evolution of behavior that are based solely on this analysis are not independent of the behavioral evidence used to produce that phylogeny.

In the second analysis of the combined behavioral and syringeal data sets, behavioral homologs are tested by congruence with both behavioral and syringeal characters. This analysis tests whether the syringeal data are more reliable indicators of phylogeny than the behavioral characters, or, conversely, whether the morphological characters provide as accurate an estimate of phylogeny as all the data combined.

In the last analysis superimposing the behavioral characters on the morphological tree, the syringeal tree is assumed to be an accurate representation of evolutionary history. The behavioral homologs are tested individually based on congruence with this phylogenetic hypothesis. Inferences about behavioral evolution from this analysis are independent of the potentially confounding effect of behavioral information on reconstructing the hypothesis of phylogeny.

Results

Display-Behavior Characters (Table 1)

Each character includes a brief description of the derived display element and its distribution in the manakins. Presence of the display is hypothesized to be derived and absence is hypothesized to be the primitive state (see Methods). All these display characters are absent from other tyrannoids.

(1) Bill-pointing posture: body horizontal with bill pointing vertically, exposing throat (Fig. 1C). Present in *Corapipo gutturalis* (apparently not in *Corapipo leucorrhoea*).

(2) Upright posture: body and bill held erect with bill pointing upward and plumage sleeked. Present in the *Pipra erythrocephala* clade. In the 'upright posture' of *Manacus* (SNOW 1962 a) males raise the head but keep it horizontal; this display is unrelated to this derived character.

(3) Chin-down posture: foreparts and bill held low to the surface of the perch and tail held erect with plumage sleeked (Fig. 1B, D). Present in *Masius* and *Illicura* as an immobile display posture, and present in *Corapipo* in the wing-shiver log display (16).

(4) Horizontal posture: head lowered, body and tail held horizontal to the perch in a crouch, wings sometimes slightly open or flicked. Present in several displays of the *Pipra aureola* and *Pipra erythrocephala* clades (9—15).

(5) Hunched posture: entire body held low and horizontal to the fallen-log display site with tarsal joints raised. Present in *Corapipo gutturalis*, unknown in *C. leucorrhoa*.

(6) Throat feathers erect: throat feathers erected to form a ruff on the throat in display. Present in *Corapipo leucorrhoa*, *Manacus*, and *Heterocercus*. (The structures of the specialized throat feathers of these three taxa differ substantially from one another.)

(7) About-face display: a rapid 180° turn-around or about-face in place on a single perch, sometimes accompanied by a rapid flick of the wings. Present in *Corapipo gutturalis*, *Machaeropterus deliciosus*, the *Pipra erythrocephala* clade, the *Pipra aureola* clade, *Pipra serena*, and *Pipra coronata*.

(8) Slide-down display: moving down a vertical perch with head facing down in a series of rapid steps that give the appearance of sliding. Present in *Manacus*.

(9) Backward-slide display: in horizontal posture (4) oriented parallel to the perch, male makes many rapid steps backward along the perch, giving the appearance of sliding quickly. Wings often flicked during slide. Present in *Pipra erythrocephala* clade.

(10) Backward-slide display with forward rebound: a mechanical wing-buzz noise given at the end of a backward slide (9) and followed by a rebound flight forward to the original position on the perch. Present in *Pipra cornuta*.

(11) Side-to-side slide display: in horizontal position (4) oriented perpendicular to the perch, male makes a series of rapid side steps along the perch that give the impression of sliding. Present in *Pipra cornuta*.

(12) Side-to-side jump display: in horizontal position (4) oriented perpendicular to the perch, male hops down the perch in a single or a few large, rapid jumps, and quickly hops back to the original position. Present in *Pipra aureola* clade.

(13) Stationary display: in horizontal posture (4), with back feathers fluffed, wings are slightly opened and vibrated, but rest of bird remains perfectly still. Present in *Pipra aureola* clade.

(14) Wing-shiver display: with head held down, tail held up [exaggerated horizontal posture (4)], the wings are slightly opened and shivered rapidly. Present in *Pipra aureola* clade.

(15) Wing-shiver twist display: wing-shiver display (14) with a rapid 180° about-face in place. Tail feathers prominently raised above perch during the "twist." Present in *Pipra filicauda*.

(16) Wing-shiver log display: foreparts and bill held low, body held horizontal, wings rapidly opened and closed as the male walks backward along the surface of the display log. Present in *Corapipo*.

(17) Side-to-side bow display: with foreparts held low, body plumage fluffed, and tail cocked at an angle, male performs a series of rhythmic bows from one side to the other, lowering the bill to the log and raising the cocked tail. In between each bow, the male makes one or several side steps across the surface of the display log in the direction of that bow. Present in *Masius chrysopterus*.

(18) Bow display: stiff jerky bows on perch, sometimes with crown feathers ruffled. Present in *Chiroxiphia pareola* and *C. caudata* (unknown in other *Chiroxiphia*).

(19) Fanning display: with head held low, male leans from side to side with wings slowly beating. Present in *Manacus manacus* but not in *Manacus vitellinus*.

(20) Hanging/swinging display: single or pair of males hanging upside down by their feet from thin horizontal perch or swinging around the perch, with wings open, producing an insect-like mechanical noise. Anecdotally reported from *Machaeropterus regulus* and *M. pyrocephalus*.

(21) Rolling-snap display: persistent mechanical noise produced while perched by rapidly ruffling the wings. Present in *Manacus*.

(22) Mechanical Advertisement Call: a three-syllable mechanical noise ("tip-tip-waaaah") produced while perched by opening the wings briefly twice and then opening the wings and raising them above the back. Present in *Machaeropterus deliciosus*.

(23) Grunt-jump display: a rapid jump from a vertical perch to the display court on the forest floor and back to a vertical perch with a mechanical wing noise. Present in *Manacus*.

(24) Frenzied-flutter display: a brief rapid fluttering flight hovering above the display perch, sometimes in a small circular path back to perch. Present in the *Pipra aureola* and *Pipra erythrocephala* clades.

(25) Cart-wheel display: coordinated display involving two or three males perched next to each other on a branch. Each male, in turn, flutters up from the branch and lands beyond the other male(s) which simultaneously hop(s) up the perch. Present in *Chiroxiphia*.

(26) Butterfly-flight display: hovering from perch to perch in slow flight with deep, exaggerated wing beats. Present in *Corapipo*, *Chiroxiphia*, *Pipra pipra*, and the *Pipra aureola* clade.

(27) Butterfly-chase display: two males chase one another in butterfly flight (26). Present in *Pipra fasciicauda*, and possibly in *Pipra aureola* and *Pipra filicauda*.

(28) Whirring-to-and-fro flight display: hovering, arc-shaped flights among vertical perches near the ground, with whirring, rapid wing beats and body held vertical (Fig. 1A). Present in *Pipra serena* and *Pipra coronata*.

(29) To-and-fro flight display: forward and back flights between horizontal perches, usually with an about-face in flight immediately before landing on perch. Present in *Corapipo gutturalis* (about-face after landing), *Machaeropterus deliciosus*, *Pipra pipra*, the *Pipra erythrocephala* clade, the *Pipra aureola* clade, *Pipra serena*, and *Pipra coronata*.

(30) Mechanical wing noise with to-and-fro flight display: a sharp mechanical wing "snap" produced while leaving the perch. Present in *Ilicura*, *Pipra cornuta*, and *Pipra mentalis* (possibly in *Pipra chloromeros*).

(31) Single-perch jump with about-face in flight: a short, arc-shaped flight or jump up from the perch or log, with an about-face in flight, landing on the same perch or log, facing back toward the starting point. Present in *Corapipo*, *Masius*, and *Ilicura*. In *Masius*, this display element is performed exclusively as part of the

log-approach display (34) and the coordinated log-approach display (36). In *Corapipo*, it is performed as an independent log-display element, often in bill-pointing posture (1), and in the log-approach display (34). In *Ilicura*, it is performed as an independent display, often with the chin-down posture (3) and in the form of the double-snap jump (32).

(32) Double-snap jump display: a jump parallel to a single thick perch with an about-face in flight (31) combined with mechanical wing "snaps" at the initial take-off and on the return take-off (Fig. 1B). Present in *Ilicura*.

(33) Snap-jump display: a jump between two vertical perches with a sharp mechanical wing-"pop" note in flight between perches. Present in *Manacus*.

(34) Log-approach display: a direct flight to a fallen-log display site, first landing on the log, then rebounding down the log and turning around in flight before landing down the log, facing back toward the original direction of approach (Fig. 1C). Performed with a complex, synchronized display call. Present in *Corapipo* and *Masius*.

(35) Log-approach with mechanical wing "pop": identical to (34) but with an additional mechanical wing-"pop" note produced by a stall in flight immediately before dropping initially to the display log (Fig. 1C). Present in *Corapipo*.

(36) Coordinated log-approach display: a coordinated display involving two males. One male waits on the log while the other approaches and performs a typical log-approach display (34). As the approaching male rebounds down the log from his initial landing point toward the waiting male, the waiting male hops up in the direction of the approaching male, about-faces in mid-flight, and lands. Both males perch momentarily facing one another in chin-down posture (3). The waiting male then flies off and the display is repeated with the roles reversed (Fig. 1D). Present in *Masius*.

(37) Butterfly log-approach display: a fluttering, undulating flight with slow, deep wing beats to land softly on the display log. Present in *Corapipo*.

(38) Above-the-canopy flight display: a buzzy, rapid flight straight up, to 20–30 m above the canopy, and then rapidly plummeting back down to the forest. May be performed independently or as a prelude to a log-approach display (34). Present in *Corapipo*.

(39) S-curve or Swoop-in flight display: a rapid flight, to the display perch from another perch 10–30 m away, that first drops below the level of the perch and then rises to land on the display perch from above, tracing a horizontal S-pattern in flight. A synchronized display call is given during landing. Present in the *Pipra aureola* and *Pipra erythrocephala* clades. The S-curve flights reported for *Pipra pipra* (SNOW 1961) and *Pipra serena* (PRUM 1985) are much less stylized, not accompanied by synchronized vocalizations, and are not performed in flight to a specific, main display perch. These less ritualized displays are hypothesized to be to-and-fro displays (29) that are independent of this derived behavioral character.

(40) Mechanical wing noise in S-curve flight display: a brief mechanical "kloop" note produced at the nadir of the S-curve flight display (39). Present in the *Pipra aureola* clade.

(41) Coordinated S-curve flight display. A coordinated display involving two males. One waits on the display perch while a second arrives in a typical S-curve flight display (39). The waiting male drops from the perch the moment the approaching male arrives, and gives a coordinated vocalization. The waiting male then flies off and the display is repeated with the roles reversed. Present in the *Pipra aureola* clade.

(42) S-curve fly-by display: similar to the typical coordinated S-curve flight display except that the male flies rapidly by the display perch and lands on another perch just beyond it. Present in *Pipra filicauda*.

(43) Mechanical-noise flight: controlled, whirring mechanical wing noise given in stereotyped flight around display area. Present in *Ilicura*, *Pipra chloromeros*, and *Pipra mentalis* (possibly in *Pipra cornuta*). The whirring flight noises in male *Manacus* and *Machaeropterus deliciosus* are automatic in flight and are not used in a controlled display behavior.

(44) Type of display perch/court: an unordered, multistate character for the type of perch or substrate on which most displays are performed and copulation takes place. 1: One or more horizontal perches; present in *Ilicura* (a thick horizontal limb), *Machaeropterus deliciosus*, *Chiroxiphia*, *Pipra pipra*, the *Pipra aureola* clade, and the *Pipra erythrocephala* clade. 2: A fallen log or exposed buttress root; present in *Corapipo* and *Masius*. 3: Loosely organized court near the ground composed of a few vertical and horizontal perches but without cleared ground; present in *Pipra serena* and *Pipra coronata* (possibly also in *Machaeropterus regulus* and *M. pyrocephalus*). 4: A true court composed of a patch of ground cleared of vegetation bordered by a few vertical or horizontal perches; present in *Manacus*. The derived states of character 44 are referred to as 44-1 through 44-4 below and in Fig. 4.

Phylogenetic Analyses

The first phylogenetic analysis of the 44 behavioral characters resulted in 126 maximally parsimonious trees for the 19 behaviorally known and distinct taxa. (The four species of *Chiroxiphia* were included as a single taxon, and the 19 behaviorally least known species were excluded from the analysis.) Each of the 126 trees had a length of 54 and a consistency index of 0.85. The strict-consensus tree includes four basal clades with unresolved interrelationships (Fig. 2).

A clade including *Ilicura*, *Masius*, and *Corapipo* was supported by two behavioral synapomorphies (3, 31). *Masius* was the sister group to the two behaviorally distinct species of *Corapipo*.

The genera *Manacus* and *Chiroxiphia* were each supported as monophyletic. Their relationships to other manakins, however, were not resolved.

The largest clade including *Machaeropterus deliciosus*, *Pipra pipra*, *Pipra serena*, *Pipra coronata*, the *Pipra aureola* clade, and *Pipra erythrocephala* clade was supported by two derived displays (7, 29). Within this group, *Pipra serena* and *Pipra coronata* were united by two derived behavioral characters (28, 44-3), and *Pipra aureola* and *Pipra erythrocephala* clades were supported as sister groups.

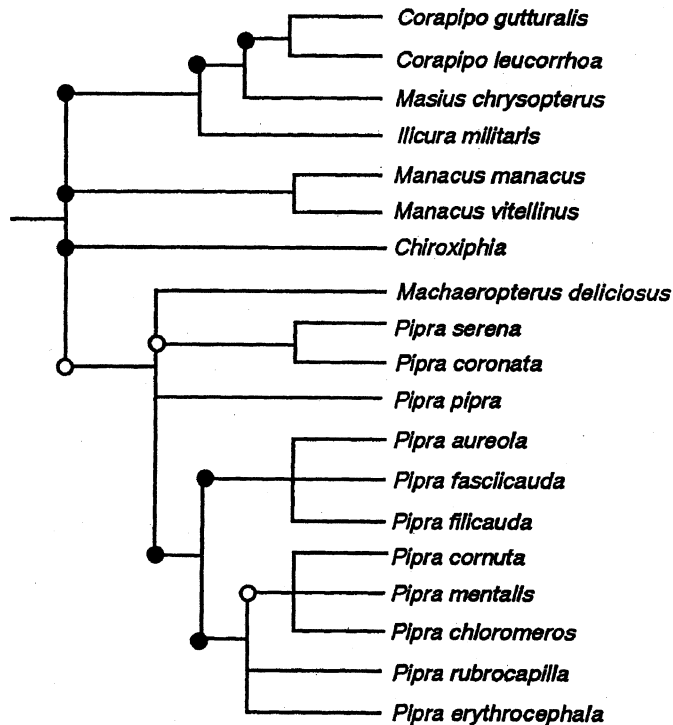


Fig. 2: Strict-consensus tree of 126 maximally parsimonious phylogenetic hypotheses based on 44 display behavior characters for the 21 behaviorally best known species (Table 1). The 8 clades marked with a closed circle are present in the syringeal-consensus tree (Fig. 3). The three clades marked with an open circle are incongruent with the syringeal characters and are not present on the syringeal-consensus tree. *Chiroxiphia* includes all four species in the genus

The *Pipra aureola* clade was diagnosed by five derived behavioral characters (12, 13, 14, 40, 41), but relationships among the three species in the clade were not resolved. The only behavioral variations within the clade were two unique displays present in *Pipra filicauda* (15, 42), and a single derived behavioral character (27) known in *Pipra fasciicauda* but not known to be absent from either *aureola* or *filicauda*.

The monophyly of the *Pipra erythrocephala* clade was supported by two behavioral characters (2, 9), and there is some behavioral variation within the group. *Pipra cornuta* has two unique, derived behavioral characters (10, 11). *Pipra mentalis* and *P. cornuta* share a derived display (30) that is not known to be present in or absent from *P. chloromeros* (coded as unknown). *Pipra chloromeros* and *P. mentalis* share a derived behavioral trait (43) that is not known to be present in or absent from *P. cornuta*, but both characters are absent from *P. erythrocephala* and *rubrocapilla*. The simplest resolution of these behavioral characters is to assume that each derived character evolved only a single time and that the derived states are present where unknown. Under these simplifying assumptions, the available behavioral data support a *cornuta-mentalis-chloromeros* clade.

Additional, unique, derived behavioral characters (autapomorphies) diagnosed eight of the 19 behaviorally distinct manakin taxa included in the analysis: *Corapipo gutturalis*, *Masius chrysopterus*, *Illicura militaris*, *Manacus manacus*, the genus *Chiroxiphia*, *Machaeropterus deliciosus*, *Pipra filicauda*, and *Pipra cornuta*.

8 of the 11 clades in the behavioral-consensus trees are also supported by derived syringeal characters and appear in the syringeal-consensus tree (Fig. 2). None of the poorly known taxa that are excluded from this analysis are members

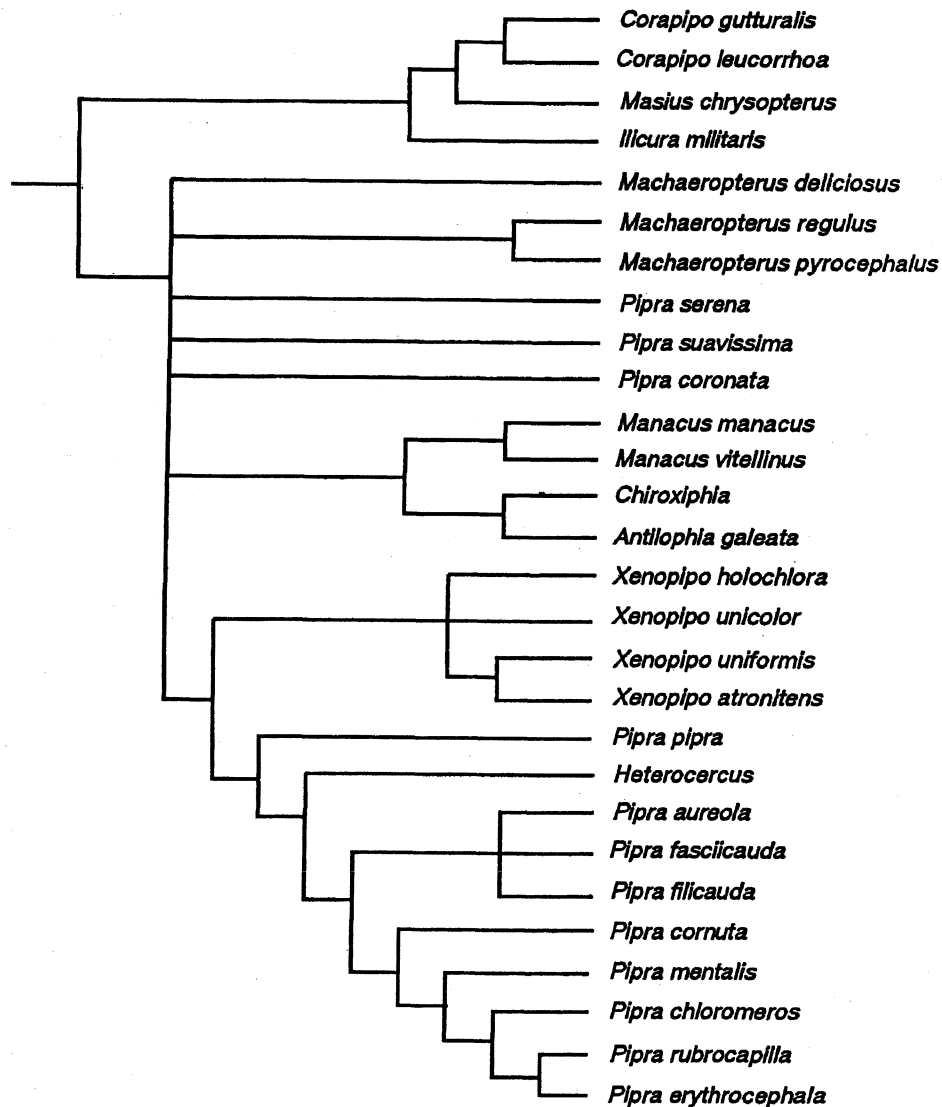


Fig. 3: Strict-consensus tree for the manakins from 14 maximally parsimonious phylogenetic hypotheses based on 44 behavioral and 57 syringeal characters combined

of these 8 clades in the syringeal-consensus tree including all manakins. This congruence does not require assuming that any derived behavioral characters are present in any of the behaviorally little known species. The relationships among the four species in *Corapipo*, *Masius*, and *Ilicura* are completely congruent with the syringeal phylogeny of these genera. The monophyly of both *Manacus* and *Chiroxiphia* is also supported by syringeal synapomorphies. Lastly, the *Pipra aureola* clade, the *Pipra erythrocephala* clade, and the clade including both these groups, are all supported by syringeal synapomorphies.

Three of the 11 clades in the behavioral-consensus tree were not supported by syringeal synapomorphies, including the largest clade that contains all species of *Pipra* and *Machaeropterus deliciosus* (Fig. 2). This major group is supported by two derived behavioral characters: (7) the about-face display, and (29) the to-and-fro flight display. In the syringeal-consensus tree, the genus *Pipra* is polyphyletic;

Pipra pipra is the sister group to a clade including the behaviorally little known genus *Heterocercus* and the *Pipra aureola* and *erythrocephala* clades (Fig. 3) (PRUM 1989, ms). Also, *Pipra serena*, *Pipra coronata*, and *Machaeropterus deliciosus* have unresolved relationships within the large clade that includes all manakins except *Corapipo*, *Masius*, and *Ilicura*, but neither is most closely related to the clade including *Heterocercus* and the rest of *Pipra* in any of the most parsimonious resolutions of the syringeal characters (Fig. 3).

The *Pipra serena* group includes 7 species (SNOW 1975, 1979; PRUM ms), and the two behaviorally known species in the group, *Pipra serena* and *P. coronata*, share a derived display (28) and form of display court (44-3; this form of display court may be present in *Machaeropterus regulus*, and *M. pyrocephalus*). The species of the *Pipra serena* group have characteristic syringeal morphology, but their syringeal similarities are not arguably derived (PRUM 1989, ms). The behavioral clade including *Pipra cornuta*, *P. mentalis*, and *P. chloromeros* is not supported by syringeal characters either. This hypothesis is the result of the simplifying assumption that the unknown character states (30 in *chloromeros*, 43 in *cornuta*) are present in these taxa.

In the second analysis, the 44 behavioral characters (Table 1) were combined with the 57 characters from the syringeal-morphology data set (PRUM 1989, ms) in a single phylogenetic analysis. The result was 14 maximally parsimonious trees, each with a length of 132 and consistency index of 0.80. The consensus tree based on these 14 phylogenetic trees included 20 corroborated clades, and is exactly congruent with the consensus tree based on the most parsimonious syringeal trees (Fig. 3). The syringeal-consensus tree (PRUM 1989, ms) and the consensus tree from this combined analysis include all the same resolved monophyletic groups. However, the exact phylogenetic hypotheses supported by the combined data were not the same as those supported by the syringeal data. Both data sets led to the same areas of ambiguity, but each implied different sets of resolutions of these areas of ambiguity.

These minor differences between the results of the combined data set and the syringeal characters alone come from the unresolved relationships of the species of *Machaeropterus* and the *Pipra serena* species group. The syringeal characters alone were insufficient to support unambiguously the monophyly of *Machaeropterus* or the *Pipra serena* group (PRUM 1989, ms). This ambiguity is compounded by the fact that only three species in these two groups are behaviorally known — *Machaeropterus deliciosus*, *Pipra serena*, and *Pipra coronata*. In the combined analysis, these species share two derived behavioral characters (7, 29) with some or all other *Pipra* species. That places them in a large clade including *Xenopipo*, *Heterocercus*, and the rest of *Pipra* (assuming that the two former genera have these displays).

Machaeropterus regulus and *M. pyrocephalus* are behaviorally little known and were coded as unknown for the critical behavioral characters 7 and 29. As a result, these two species can be placed equally parsimoniously with the *Pipra serena* group or with *Machaeropterus deliciosus*, assuming they have these displays, or as the sister group to *Manacus*, *Chiroxiphia*, and *Antilophia*, assuming that they lack these displays. However, the monophyly of both *Machaeropterus*

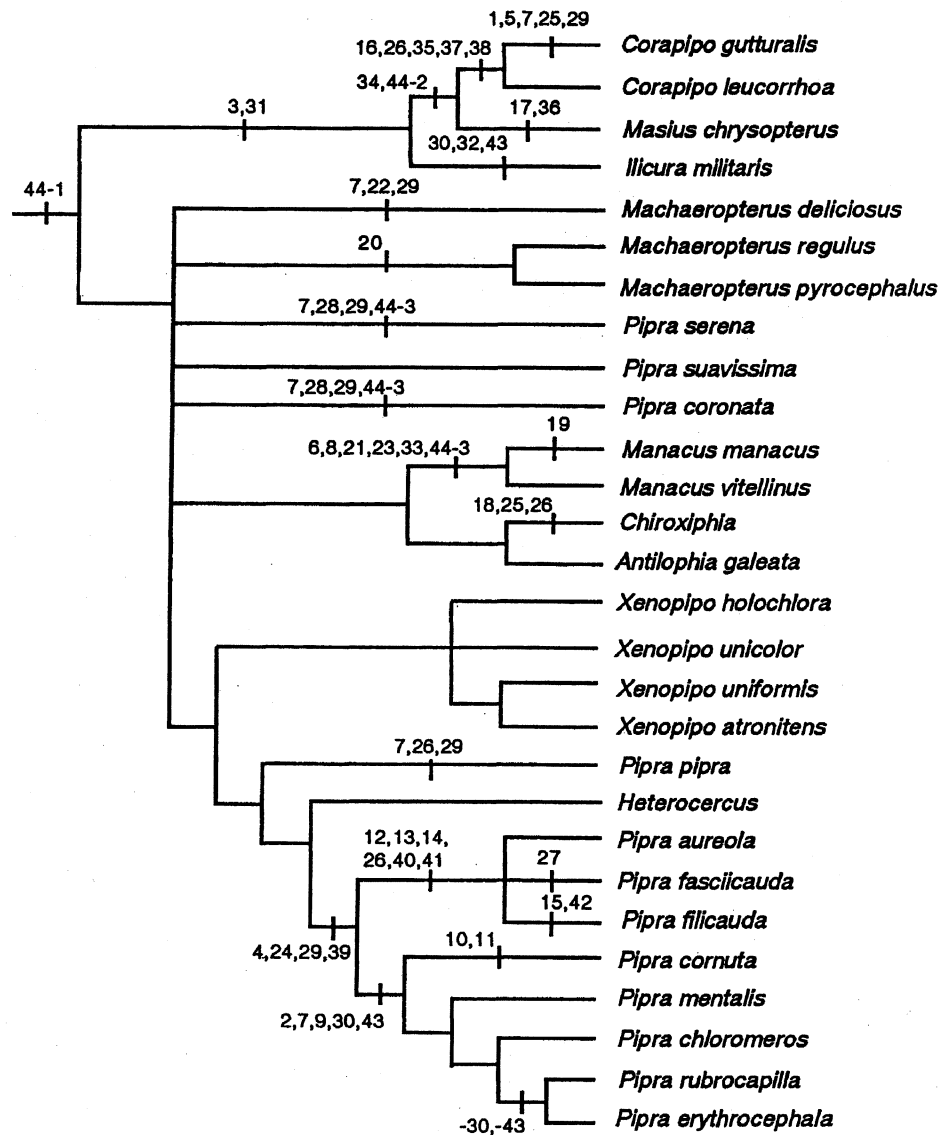


Fig. 4: 44 behavioral characters parsimoniously superimposed on the strict syringeal-consensus tree of the manakins from PRUM (1989, ms)

and the *Pipra serena* species group is supported by derived plumage traits (PRUM 1988, 1989, ms). In all the most parsimonious resolutions of the combined data set in which *Machaeropterus* and the *Pipra serena* group are each monophyletic, *Machaeropterus* and the *Pipra serena* group are the sister groups to the large clade including *Xenopipo*, *Heterocercus*, and the rest of the genus *Pipra*.

In the last analysis, the behavioral characters were parsimoniously superimposed on the syringeal-consensus tree. 38 of the 44 behavioral characters mapped unambiguously onto the syringeal-consensus tree, requiring a total of 46 steps (Fig. 4). The other six characters are present in taxa with unresolved relationships in the syringeal-consensus tree; the number of changes hypothesized for these characters varies among the resolutions of the phylogeny and with the assumed character states of the behaviorally unknown taxa.

The ambiguous characters include those that support the major clade in the first behavioral analysis that contains all *Pipra* species and *Machaeropterus deliciosus*. The simplest hypothesis for the evolution of the to-and-fro flight (29) in *Corapipo*, *Pipra serena*, *P. coronata*, *Machaeropterus deliciosus*, *Pipra pipra*, and the *Pipra aureola-erythrocephala* clade is that the display arose twice independently and was lost once, assuming that the poorly known *Xenopipo* and *Heterocercus* have the display. Alternatively, if the display were absent where unknown, it would be necessary to hypothesize five independent origins. Similarly, the about-face display (7) may be hypothesized as having evolved two to five times depending on the assumed states of the poorly known taxa and which resolution of the consensus tree is chosen. The butterfly-flight display (26) is most parsimoniously hypothesized to have evolved four times independently: once each in *Corapipo*, *Chiroxiphia*, *Pipra pipra*, and the *Pipra aureola* clade.

The unresolved portions of the syringeal phylogeny limit the resolution of this third superimposition analysis. The lack of syringeal support for the monophyly of the *Pipra serena* species group makes it difficult to interpret the evolution of the two derived behavioral elements found in these species (28, 44-3). These displays can be interpreted either as convergences or reversals. The two behavioral variations in the *Pipra erythrocephala* clade (30, 43) that are each unknown in one species are most parsimoniously hypothesized in the third analysis to be either absent where unknown and convergent in the species pairs where they are present, or present where unknown, derived in the common ancestor of the *Pipra erythrocephala* clade, and subsequently lost in the *erythrocephala-rubrocapilla* lineage.

Discussion

Comparison of the Three Phylogenetic Analyses

The results of all three phylogenetic analyses indicate that the diversity of manakin display behavior contains considerable phylogenetic information. Independent phylogenies based on behavior and syringeal morphology are highly congruent. The vast majority of the detailed behavioral similarities shared by manakin species are homologs. The three different phylogenetic analyses performed support identical hypotheses of behavioral homology for 37 of the 44 behavioral characters, and they differ in the historical interpretation of only 7 behavioral characters.

In the first analysis, the majority of derived behavioral characters were completely congruent with the independent syringeal hypothesis of phylogeny (PRUM 1989, ms). This degree of congruence supports the criteria used to recognize behavioral homologs in the initial character analysis, and indicates that the process of behavioral diversification has resulted in a phylogenetically coherent radiation of behavioral traits.

The majority of behavioral characters diagnose clades of allopatric or parapatric species that are supported by syringeal synapomorphies (PRUM 1989, ms). These include the *Pipra aureola* clade, the *Pipra erythrocephala* clade,

Chiroxiphia, and *Manacus*. The behavioral characters also diagnose and resolve the relationships of the four species of the *Corapipo-Masius-Ilicura* clade. A much smaller portion of the derived behavioral characters is uniquely derived in single species (7 to 9 characters), and none is found in all of the behaviorally known manakin species.

Only three derived behavioral characters (7, 29, 44-1) are broadly distributed. Two of these support a single large clade including a little over half of the behaviorally known species of manakins. These characters — (7) the about-face display and (29) the to-and-fro flight display — are among the least detailed of the behavioral characters in the data set. Each requires a simple action that is apparently stereotyped and ritualized but that lacks any of the striking or special details that categorize many of the other derived behavioral characters.

Displaying on a horizontal perch (44-1) is the only display behavior that is found in most piprids. This character state is apparently primitive to the other derived display site types in the family. It is the only extant piprid display behavior that can be confidently hypothesized to have characterized the lek displaying common ancestor of the family.

In the absence of a priori assumptions about the quality of the behavioral and morphological characters as phylogenetic evidence, the second analysis tests the congruence of all the characters. Although it is difficult to equate the 'weights' of such different types of character systems, the congruence between the combined-consensus tree and the syringeal-consensus tree confirms that the syringeal characters alone are sufficient indicators of phylogenetic history to be used to test independently the homology of manakin displays. This assumption is critical to the third superimposition analysis and it is supported strongly by this result. The combined-consensus tree, however, cannot be considered as independent from the syringeal tree, since both hypotheses are based largely on syringeal data. The large amount of missing behavioral character states also means that the topology of the combined-data consensus tree is overwhelmingly determined by the phylogenetic structure of the completely known syringeal characters.

The patterns of distribution of the two behavioral characters (7, 29) that produced the main incongruence between the behavioral-consensus tree, and the morphological hypothesis of phylogeny, may be interpreted in two ways in the second analysis. Either these undetailed, broadly distributed behavioral traits were more likely to be mistakenly identified as homologs in the initial character analysis, or they are among the oldest, primitive displays within the group, and have been retained in some manakin lineages and lost repeatedly in others.

The three analyses differ in the degree of independence of the hypotheses of behavioral homology from the assumptions about behavioral evolution because, in each analysis, behavioral homologs are tested based on congruence with different subsets of the data. The third, superimposition analysis assumes the most about the morphological characters but constitutes the least behaviorally confounded method of testing the homology of behavior. Congruence between the combined-consensus tree from the second analysis and the syringeal-consensus tree confirms this assumption. The combined analysis of both data sets adds

no resolution to the consensus tree for the group, but provides additional, though ambiguous, evidence for the monophyly of the *Pipra serena* species group.

This minimal phylogenetic contribution of the combined analysis comes at a significant cost to the independence of any inferences about behavioral evolution from the methods used in this analysis. For subsequent comparative analyses of the evolution of manakin display behavior, the superimposition analysis provides the most robust and behaviorally independent assessments of behavioral homology. The first two analyses, however, provide necessary checks to test the assumptions of the third analysis.

Because each method of analysis requires a different set of assumptions about morphological and behavioral evolution, future investigators interested in specific questions can choose a method using appropriate evolutionary assumptions. Investigators interested in behavioral systematics may feel that combining morphological and behavioral data assumes too much about the similarity of these distinct sets of characters, and they may prefer the first method. Others may be unwilling to assume that one character system is a better indicator of phylogeny than another, and may prefer phylogenetic analyses based on all the data combined. Ethologists with primary interests in evolutionary process may feel that the assumptions necessary for phylogenetic reconstruction using behavior (e.g. character definition, weighting, and polarity) are too restrictive or unrealistic, and may prefer comparative analysis based on superimposing behavior on a phylogeny.

Phylogenetic Reconstruction Using Display Behavior

LORENZ (1941, 1970) performed a ground-breaking comparative study of the behavioral diversification of the ducks (Anatinae). The main goal of the investigation was not elucidation of the process of behavioral evolution but confirmation that behavioral homologies are as phylogenetically informative as morphological homologies. HENNIG (1966) criticized the behavioral technique of LORENZ (1941) because LORENZ did not distinguish primitive and derived behavior, but HENNIG concluded that behavioral characters were potentially useful for phylogenetic reconstruction. HENNIG was correct that LORENZ did not explicitly polarize the behavioral characters in his duck study. LORENZ assumed that ritualization of a display implies that behavior is evolutionarily derived. To the extent that this assumption is valid, LORENZ's analysis is essentially a phylogenetic treatment of the data. LORENZ (1941, 1970: 111) also included a few morphological characters in his analysis "to show how similar their distribution is in many cases to that of the innate behavior patterns."

The results of these analyses of manakin displays strongly confirm LORENZ's conclusion that avian displays can be used in accurately reconstructing phylogeny. Furthermore, the incongruencies between analyses of behavior and morphology indicate which putative behavioral homologs are less informative. Displays that are composed of detailed and complex postures and movements yield the most reliable hypotheses of homology. As a whole, behavioral diversification in the manakins has been neither too fast to recover phylogenetic informa-

tion nor too slow to provide informative variation. As other character systems used in systematics, manakin displays have phylogenetically informative variation at a number of taxonomic levels but do not resolve historical relationships at all levels or in all clades of the family.

A major limitation of reconstructing phylogenies with behavior is that subsequent inferences about behavioral evolution are confounded by the dependence of the phylogenetic hypothesis on the behavioral evidence used to construct it. Furthermore, comparative understanding of many types of behavior may be limited by the strict assumptions of phylogenetic analysis. Some classes of behavior may be inappropriate for use in phylogenetic reconstruction (e.g. cooperation), but their phylogenetic distributions may be critical to understanding their evolution. The superimposition method employed in the third analysis can be used to avoid some of these problems.

Phylogenetic Tests of Behavioral Transition Series

In traditional ethological analyses, scenarios for the evolution of displays and other behavior are typically hypothesized by aligning behavioral elements present in members of the study group or ingroup into a logical transition series (e.g., DAANJE 1951; TINBERGEN 1951, 1952, 1959; HINDE 1955—1956; MOYNIHAN 1959; CROOK 1963, 1964). (See LAUDER 1981 for discussion of morphological transition series.) The criterion for judging the hypothesized transition series is its ethological plausibility — the similarity or continuity in motivation, motor pattern, or context of the behavior in the transition series.

This procedure is confounded by two major sources of error. If the phylogenetic interrelationships of the species in the study group are not considered, then the historical or phylogenetic plausibility of the behavioral transition series is unassessable. The hypothesized 'phylogeny of behavior' may be incongruent with the phylogeny of the organisms, such that intermediate or derived displays are present in distantly related members of the ingroup. The traditional method may also confound the criteria for initial recognition of homologs with a priori assumptions about the process of behavioral evolution. The hypothesized transition series may be constructed by imposing a specific model of ethological change on the behavioral variation, rather than discovering a transition series in the hierarchical distribution of behavior in a phylogeny and inferring which processes were important in its evolution.

To control for these confounding factors, comparative ethological analyses should test behavioral transition series through superimposition on an explicit phylogeny. Phylogenies are necessary for testing hypotheses of morphological evolution and functional adaptation (LAUDER 1981, 1982; RIDLEY 1983; CODDINGTON 1988). They are also essential to testing hypotheses about the evolution and ritualization of behavior. The phylogenetic plausibility of a hypothesized behavioral transition series is an essential test of the hypothesis.

Details of the history of the evolution of specific manakin displays can be inferred from their patterns of phylogenetic distribution in the second and third analyses (Figs. 3, 4). Manakin display behavior has evolved through a number of

different ethological mechanisms, including elaboration and exaggerations of movements within primitive display postures, derivation of novel postures within a primitive display movement, and initial or terminal additions of novel movements or postures to a display sequence.

For example, the horizontal posture (4) is primitively present in the *Pipra aureola* and *P. erythrocephala* clades, but it has been elaborated in a number of derived display movements independently in these sister groups. The backward-slide display (9), the side-to-side slide display (11), and the side-to-side jump display (12) elements involve movements along the perch in horizontal posture. The stationary display (13), the wing-shiver display (14), and wing-shiver with twist display (15) involve the horizontal posture with increasingly exaggerated movements from a single position on a perch. Alternatively, the backward-slide with a forward rebound (10) in *Pipra cornuta* has apparently evolved through the terminal addition of a forward jump to the backward-slide display sequence (9), which is primitively present in the *Pipra erythrocephala* clade.

The four species of the *Corapipo-Masius-Ilicura* clade incorporate a conserved movement into a number of complex displays that include a variety of postures (Fig. 1B—D). The movement is the single-perch jump with an about-face in flight (31). It is used in the double snap-jump display (32) of *Ilicura*, with chin-down posture (3), in the log-approach display (34) of *Corapipo* and *Masius*, the coordinated log-approach display (36) of *Masius*, with the chin-down posture (3), and as a simple log display element in *Corapipo gutturalis*, with the derived bill-pointing posture (1). This stereotyped movement, primitive within this clade, has been elaborated in a number of derived displays through the addition of derived postures (1, 3) and initial or terminal addition of derived movements (32, 34), and derived coordination among males of primitive-display movements (36). Further, the remarkable above-the-canopy flight display (38) of *Corapipo* is sometimes performed as an initial addition to the primitively present log-approach display (34).

The phylogenetic distribution of manakin displays can also be used to examine the evolution of correlated plumage traits and displays. Functional associations between novel plumages and specific displays in which they are prominently featured are commonly asserted, but they are often untestable because the plumage and behavior are unique or completely correlated. Although comparative methods cannot address the proximate issue of how plumage and displays are perceived, they can be used to test hypotheses about the sequence of transformation of behavioral and morphological traits and assess indirectly some aspects of the evolution of behavioral and morphological correlations. If a derived display behavior is more generally distributed than the plumage novelty, then the behavior evolved prior to the plumage, and the hypothesis that plumage has evolved as a consequence of the display is corroborated. If the plumage is more generally distributed, then the opposite hypothesis is corroborated.

In manakins, several independent cases indicate that displays have evolved first, followed by derived plumage traits in which the plumage is featured. For example, males of the *Pipra aureola* clade perform a wing-shiver display in which the head is lowered, and the wings are opened slightly and rapidly quivered (14).

In *Pipra fasciicauda*, males occasionally about-face during this display (ROBBINS 1983). In *Pipra filicauda*, the central shafts or rachises of the tail feathers are lengthened, barbless, and curved. Male *P. filicauda* combine the wing-shiver display and the about-face into a single, ritualized display — the wing-shiver twist (15). In this display, the male steps backward along the perch toward a visiting bird while wing-shivering and about-facing and swishes his tail feathers back and forth across the 'face' of the visiting bird (SCHWARTZ & SNOW 1978). The wing-shiver and about-face displays are primitively present in the *Pipra aureola* clade. The specialized plumage and the derived association of these two display elements have evolved subsequently within the *Pipra aureola* clade in *P. filicauda*.

All three species of the *Pipra aureola* clade have derived white wing-patches that are concealed when the wings are closed and strikingly visible during the wing-shiver display (14). The complete correlation of these two traits does not permit a test of the sequence of this transformation. Elsewhere in the family, however, the two species of *Corapipo* perform a convergent wing-shiver log display. *Corapipo gutturalis* has similar, derived white wing-patches that are concealed when the wing is closed but prominently flashed during the wing-shiver display, but *C. leucorrhoa* lacks these wing-patches. In *Corapipo*, the transformation in behavior also preceded the change in morphology.

Another example comes from the derived, lengthened tail feathers in *Ilicura* and in *Chiroxiphia*. In *Ilicura*, the two lengthened and pointed central tail feathers extend the sharp profile of the body in the chin-down display posture (3). This posture is primitively present in the *Corapipo-Masius-Ilicura* clade, and preceded the evolution of this morphological novelty.

In *Chiroxiphia*, the lengthened tail feathers are independently evolved from *Ilicura* and *Pipra filicauda*. Male *C. pareola* lack any tail-feather specializations, whereas *linearis* and *caudata* have slightly lengthened central tail feathers, and *linearis* has very long, narrow central tail plumes. All members of the genus perform a coordinated cart-wheel display (25) involving two or more jumping males. The tail plumes of *linearis* bounce prominently in the cart-wheel display, but the much shorter tail feathers of the other species are not especially visible during this display. Although the evolution of the tail feathers in *Chiroxiphia* is not completely resolved (the lack of specialized tail feathers in *pareola* may be primitive or a reversal), the extreme tail feathers of *linearis* are certainly derived in that species and have evolved subsequent to the development of the cart-wheel display in the genus.

In each of these informative cases, derived male plumage traits in manakins have evolved subsequent to the behavioral novelties in which they are prominently featured. This consistent order of transformation implies that behavioral diversification is driving some aspects of morphological diversification within the family. The opposing hypothesis that novel plumage results in the evolution of derived displays can be rejected in manakins.

Limitations of Phylogenetic Analysis of Behavior

Phylogenetic analyses of behavior include a number of potential sources of error. Perhaps the greatest flaw in this investigation is the lack of information

about the displays of a number of manakin species. These gaps in knowledge of the distribution of display elements directly affect hypotheses of behavioral homology or convergence. I have outlined how the presence or absence of certain display elements in the behaviorally unknown manakins will influence hypotheses of their homology and evolution. Secondly, this investigation is based on behavioral descriptions from the literature that are written by many different observers, often based on limited observations of a few individuals, and almost always at a single locality. Such summaries are subject to many potential sources of error.

Unassayed individual, temporal or geographic variation in display behavior could also alter the currently defined display characters and inferred behavioral homologies. Furthermore, the character definitions necessarily require compartmentalizing behavior typologically, possibly distorting the degree of individual and interspecific variation. The present knowledge of the phylogeny of manakins is dependent on available character data, which does not completely resolve the phylogeny of the group and may be subject to unknown sources of homoplasy.

Despite these and other limitations, enough information is available about manakin displays and morphology to attempt this initial phylogenetic analysis of behavioral evolution in the family. Some sources of error can be eliminated by additional observations of poorly known species and detailed investigations of intraspecific and geographic variation in behavior of other well known groups. Additional morphological or molecular characters may also help to resolve the phylogeny of the family.

At present, there is no published direct evidence that manakin displays are innate and not learned. If manakin displays are learned, then these results indicate extensive congruence between genetically evolved and culturally evolved character systems. This striking result would require a much lower rate of learning errors and behavioral novelties than has been observed in investigation of culturally inherited, avian song types (e.g. PAYNE et al. 1981; PAYNE 1985). LORENZ (1981) argued that congruence between behavioral and morphological homologies demonstrates their common genetic basis. Although this reasoning is convincing, experimental observations of behavioral ontogeny in manakins are necessary to determine whether phylogenetic patterns in manakin behavior are the result of genetic or cultural evolution.

Resumen

Métodos sistemáticos filogenéticos fueron empleados para investigar la evolución de los despliegues de los saltarines (Aves: Pipridae). Los resultados de una investigación previa acerca la morfología de las siringes de los saltarines fueron empleados como una filogenia de la familia estimada independientemente de la conducta. Tres análisis filogenéticos fueron efectuados con 44 caracteres de despliegues: (1) solamente empleando elementos de despliegue como caracteres sistemáticos, (2) combinando caracteres de despliegue y de morfología de la siringe en un análisis filogenético, y (3) los caracteres de despliegue se sobrepusie-

ron parsimónicamente en la hipótesis filogenética de morfología siringeal. Los resultados de los dos primeros análisis fueron altamente congruentes con la hipótesis filogenética de morfología siringeal. La mayoría de las semejanzas de los despliegues son homólogas. Los tres análisis sostienen hipótesis de homología idénticas para 37 de los 44 caracteres de despliegue. Los despliegues de los saltarines son muy informativos filogenéticamente. Los despliegues más sencillos son los más probables de ser convergentes o pérdidas secundarias (homoplasias). El tercer análisis sostiene hipótesis de homología de comportamientos deducidas lo más independientemente de los despliegues mismos. Los elementos de despliegue de los saltarines han evolucionado por una variedad de métodos etológicos que incluyen la elaboración de los movimientos derivados dentro de las posturas primitivas, la evolución de las posturas derivadas dentro de los movimientos primitivos, y las adiciones iniciales y finales a las series de despliegues primitivos. Las distribuciones filogenéticas de los caracteres derivados de despliegue y de plumaje indican que en los saltarines la diferenciación de despliegues ha conducido unos aspectos de la diferenciación en la morfología. Estos resultados confirman que los métodos filogenéticos son aplicables a preguntas de etología comparativa.

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Appendix

List of the available sources of information about display behavior of manakins (Pipridae). Following each species, an indication is given as to whether its display behavior is well known (W), partially documented (Pa), poorly known (Po), or completely undescribed (U). The 21 well known and partially known species were included in the first analysis as 19 taxa, and the 19 poorly known and unknown species were not included in the first analysis.

- Corapipo gutturalis* — W — DAVIS 1949; DAVIS 1982; PRUM 1986.
Corapipo leucorrhoea — Pa — ALDRICH & BOLE 1937; SKUTCH 1967; SLUD 1967; WETMORE 1972.
Masius chrysopterus — W — PRUM & JOHNSON 1987; SNOW & SNOW, pers. comm.
Ilicura militaris — W — SICK 1959, 1967; SNOW & SNOW 1985.
Manacus manacus — W — SNOW 1962 a; LILL 1974 a, b; OLSON & McDOWELL 1983.
Manacus vitellinus — W — CHAPMAN 1935; WETMORE 1972.
Manacus candei — U — no information available.
Chiroxiphia linearis — W — ALDRICH & BOLE 1937; WAGNER 1946; SLUD 1957; WETMORE 1972; FOSTER 1977 a.
Chiroxiphia lanceolata — Po — FRIEDMANN & FOSTER 1955; WETMORE 1972.
Chiroxiphia pareola — W — GILLIARD 1959; SNOW 1963 b, 1971.
Chiroxiphia caudata — W — SICK 1942; LAMM 1948; SNOW 1976, FOSTER 1977 b, 1981.
Antilophia galeata — Po — SICK 1959, 1967.
Machaeropterus deliciosus — W — WILLIS 1966; OREJUELA et al. 1982; PRUM, unpubl. obs.
Machaeropterus regulus — Po — SICK 1959, 1967; SKUTCH 1969; PRUM, unpubl. obs.
Machaeropterus pyrocephalus — Po — SICK 1959, 1967.
Xenopipo (Chloropipo) unicolor — U — no information available.
Xenopipo (Chloropipo) flavicapilla — U — no information available.
Xenopipo (Chloropipo) holochlora — U — no information available.
Xenopipo (Chloropipo) uniformis — U — no information available.
Xenopipo atronitens — Po — SICK 1959, 1967.
Heterocercus linteatus — Po — SICK 1959, 1967.
Heterocercus flavivertex — U — no information available.
Heterocercus aurantiavertex — U — no information available.
Pipra pipra — Pa — SNOW 1961; PRUM, unpubl. obs.
Pipra aureola — Pa — SNOW 1963 a.
Pipra fasciicauda — W — ROBBINS 1983, 1985.
Pipra filicauda — W — SCHWARTZ & SNOW 1978.
Pipra cornuta — Pa — SNOW 1977.
Pipra chloromeros — Pa — NIETHAMMER 1956; KINKEL, pers. comm.
Pipra mentalis — W — SKUTCH 1949, 1969.
Pipra erythrocephala — W — SNOW 1962 b; LILL 1976.
Pipra rubrocapilla — Pa — SICK 1959, 1967.
Pipra serena — W — PRUM 1985.
Pipra suavissima — U — no information available.
Pipra isidorei — U — no information available.
Pipra coeruleocapilla — U — no information available.
Pipra coronata — Pa — SKUTCH 1969; PRUM, unpubl. obs.
Pipra nattereri — U — no information available.
Pipra vilasboasi — U — no information available.
Pipra iris — U — no information available.