PHYLOGENETIC TESTS OF ALTERNATIVE INTERSEXUAL SELECTION MECHANISMS: TRAIT MACROEVOLUTION IN A POLYGYNOUS CLADE (AVES: PIPRIDAE)

RICHARD O. PRUM*

Natural History Museum and Department of Systematics and Ecology, University of Kansas, Lawrence, Kansas 66045-2454

Abstract.—Alternative mechanisms of intersexual selection yield distinct macroevolutionary predictions about the magnitude and patterns of trait and repertoire diversity in clades exposed to persistent intersexual selection. Phylogenetic analyses of the evolution of lek display elements and secondary sexual plumages in manakins (Aves: Pipridae) were conducted to test these predictions and determine which sexual selection mechanisms may have had a predominant role in the evolution of traits within a clade of lekking species. The diverse trait repertoires of manakins are composed of independent, hierarchically distributed (historically nested), behavioral, and morphological novelties. In comparison with the closely related, predominantly monogamous tyrant flycatchers (Tyrannidae), the diversity of manakin traits and trait repertoires is explosive, indicating that manakin traits have evolved by an unconstrained evolutionary mechanism. The macroevolutionary patterns in manakin traits are consistent with the predictions of the Fisherian and broad sensory bias mechanisms, but they are not consistent with the predictions of the indicator, direct selection, species isolation, or sensory drive mechanisms. The diverse repertoires and hierarchically distributed traits in the lekking manakin clade indicate that Fisherian selection may have played an important role in diversification of secondary sexual traits in other groups of polygynous animals.

Recent research on intersexual selection has contributed both theoretical and empirical insights into the evolution of secondary sexual traits and preferences in populations (reviewed in Kirkpatrick and Ryan 1991; Maynard Smith 1991; Andersson 1994). However, the microevolutionary emphasis of most current research on sexual selection has diverted attention from critical macroevolutionary questions: How do mate preferences lead to the diversification of secondary sexual traits among species? How do diverse repertoires of traits evolve? Which sexual selection mechanisms contribute to phylogenetic patterns in secondary sexual traits within a clade?

Proximate tests of alternative intersexual selection mechanisms have proven difficult in populations of many organisms (e.g., Kirkpatrick and Ryan 1991). Alternative mechanisms of intersexual selection yield testable predictions about macroevolutionary patterns in traits and preferences that can evolve within and

among lineages as a consequence of sexual selection. Explicit methods of phylogenetic reconstruction and macroevolutionary character analysis are now available to document patterns in diversity and test alternative mechanisms of evolutionary process (Hennig 1966; Wiley 1981; Coddington 1988; Prum 1990a; Brooks and McLennan 1991; Harvey and Pagel 1991; Maddison and Maddison 1992). Comparative investigations have already been employed to examine whether specific preferences evolved prior to traits (Ryan et al. 1990; Basolo 1991; Ryan 1991; Hill 1993) and to analyze the historical relationship between sexual selection and the origin of sexual size dimorphism (Emerson 1994).

Here, I apply phylogenetic methods to examine macroevolutionary patterns in male secondary sexual traits in a polygynous group of birds—the manakins (Pipridae). First, I present macroevolutionary predictions about secondary sexual trait evolution within clades based on the major, alternative intersexual selection mechanisms. Following Kirkpatrick and Ryan (1991), I categorize current models of intersexual selection and trait evolution into six classes: Fisherian, quality indicator, direct selection on mate choice efficiency, species isolation, sensory bias, and sensory drive mechanisms. The macroevolutionary predictions focus on the magnitude of differentiation, the diversity of trait repertoires, and the phylogenetic patterns in traits that can evolve as a consequence of these sexual selection mechanisms.

In the second portion of the article, I test these predictions by examining phylogenetic patterns of trait diversity in the manakins (Aves: Pipridae). Rather than focus on the microevolutionary origin of traits and preferences within populations, these tests examine the historical consequences of persistent, intense sexual selection on trait evolution subsequent to the initial origin of traits and preferences within the ancestor of a clade. The manakins include 42 species of frugivorous, Neotropical perching birds that are well known for their lek breeding systems, elaborate display behavior, and striking, colorful sexually dimorphic plumage (Snow 1963; Prum 1990a, 1990b, 1992, 1994). In previous research, I have established a well-resolved phylogeny for the manakins, based on syringeal morphology (Prum 1992), that was largely congruent with a phylogenetic analysis of manakin display behavior elements (Prum 1990a). Lekking is primitive to the manakin clade (Prum 1994), which may be 40 million yr old (Sibley and Ahlquist 1990), and a significant pair bond has evolved secondarily in only a single species in the family (Marini and Cavalcanti 1993).

MACROEVOLUTIONARY PREDICTIONS OF ALTERNATIVE INTERSEXUAL
SELECTION MECHANISMS

Fisherian Mechanisms

In Fisherian models, traits and preferences evolve through a genetic correlation between genes for extreme traits and preferences (Fisher 1958; Lande 1980, 1981; Kirkpatrick 1982; Pomiankowski and Iwasa 1993). This correlation results in the evolution of arbitrary traits that are highly variable in direction of elaboration and that lack any correlation with male viability or condition. Because of the lack

of deterministic processes, Fisherian selection should produce limited convergence in secondary sexual traits.

The most rapid mechanism for the elaboration of a Fisherian trait is a "runaway," which may occur with extreme correlation between trait and preference (Fisher 1958; Lande 1980, 1981; Kirkpatrick 1982). At the macroevolutionary level, runaways should result in rapid differentiation in secondary sexual traits among lineages in a clade with little convergence among lineages.

In the absence of direct selection on female preferences, the Fisherian mechanism creates a stable polymorphism in trait and preference in populations at equilibrium (Lande 1980, 1981; Kirkpatrick 1982). Perturbations from equilibrium through drift, isolation, or dispersal will result in the rapid evolution of traits and preferences in arbitrary directions determined by the displacement from equilibrium and the strength of the trait/preference correlation (Lande 1980, 1981; Kirkpatrick 1982). Direct selection on female preferences will collapse the stable equilibria to a single point and constrain subsequent trait evolution (e.g., Pomiankowski et al. 1991).

The Fisherian mechanism can result in the evolution of multiple secondary sexual traits and complex trait repertoires even when there are high, combined preference costs to females (Møller and Pomiankowski 1993; Pomiankowski and Iwasa 1993). At intermediate rates of differentiation, a Fisherian process should yield a hierarchical, or historically nested, distribution of characters that are shared among various lineages within a clade (fig. 1A). In complex hierarchical distributions, trait repertoires are composed of independent traits that have evolved at various nodes in the history of a lineage. If diversification among lineages is extremely rapid, each lineage will be characterized by a diverse repertoire of unique traits (autapomorphies) in a nonhierarchical distribution that is skewed toward the tips of the phylogeny (fig. 1D).

Quality Indicator Mechanisms

The quality indicator mechanisms function through selection on preferences for those traits that indicate high-quality mates (Zahavi 1975, 1977; Andersson 1982, 1986; Hamilton and Zuk 1982; Kodric-Brown and Brown 1984; Kirkpatrick 1986; Pomiankowski 1987; Heywood 1989; Grafen 1990a, 1990b; Iwasa et al. 1991; Price et al. 1993; Schluter and Price 1993; Andersson 1994; Iwasa and Pomiankowski 1994). Quality indicators can evolve through direct selection on preferences that confer viability and fecundity advantages to females or through indirect selection on heritable fitness advantages to the offspring.

Variation in quality-indicating traits are the sum of a component of variation that is correlated with quality, a genetic component, and a random environmental component (e.g., Nur and Hasson 1984; Price et al. 1993). Indicator traits should be costly to produce or incorporate limited resources from the diet, to prevent counterfeiting of the trait by low-quality individuals (Zahavi 1977; Andersson 1982; Nur and Hasson 1984; Grafen 1990a, 1990b; Hill 1991, 1992, 1994; Price et al. 1993). An indicator trait can also communicate quality by conferring a direct survival cost to males, but such viability-based indicators require unrealistic fitness variation among males to evolve and are considered unlikely (Iwasa et al.
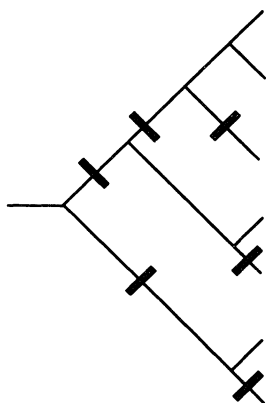
A. Hierarchical Distribution
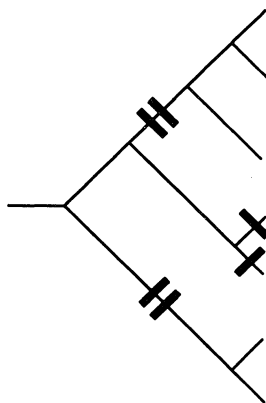
B. Non-hierarchical Distribution
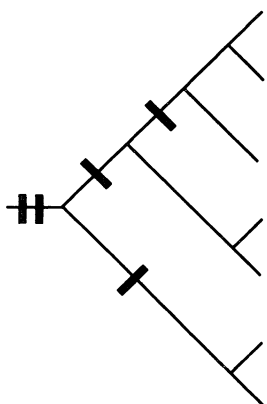
C. Trait Distribution Skewed
toward Basal Branches
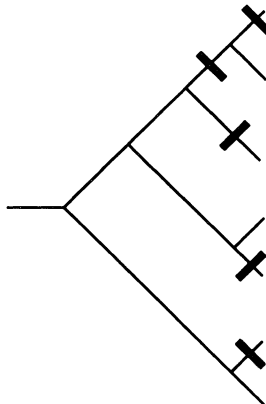
D. Trait Distribution Skewed
toward Tips

Fig. 1.—Hypothetical distributions of character changes on a phylogenetic hypothesis. *A*, A hierarchical distribution of traits is composed of historically nested character states that have evolved independently along different nodes in the history of lineages within a clade. *B*, A nonhierarchical distribution of traits is composed of nonnested character state changes that have evolved along only a single node in the history of any lineage. *C*, A distribution of trait character state changes that is skewed toward the basal branches, or trunks, of a clade, as may result from a constrained evolutionary mechanism. *D*, A distribution of trait character state changes that is skewed toward the terminal branches, or tips, of a clade as may result from an unconstrained evolutionary mechanism.

1991; Andersson 1994). Indicator traits must either start with a high or significant initial component of variation that is correlated with quality (Price et al. 1993). Because the number of such traits is limited, indicator selection should result in frequent convergence in traits among lineages in a clade.

A trait under indicator selection should evolve low genetic variation for the trait itself (Andersson 1982; Nur and Hasson 1984; Grafen 1990; Price et al. 1993; Hill 1994). The efficiency of an indicator trait is negatively related to genetic variation for the trait and thus to its potential to evolve (Fisher 1958; Zahavi 1975, 1977; Hamilton and Zuk 1982; Kodric-Brown and Brown 1984; Kirkpatrick 1986; Pomiankowski 1987; Hill 1994). Although indicator mechanisms may yield rapid microevolution of male traits, the inevitable fixation of a trait/preference combination at equilibrium will constrain subsequent diversification in that trait (fig. 1C). Females can evolve preferences for novel indicator traits that provide more efficient quality information at no additional cost (Schluter and Price 1993). Trait switching could result in unconstrained diversification among lineages and lead to the evolution of unique traits in each lineage (fig. 1B). But trait switching should not result in the accumulation of traits into diverse repertoires because costly, former indicator traits should be eliminated. Trait switching should be further constrained by the chance evolution of particularly robust, high-fidelity indicators (e.g., indicators of parasite resistance; Hamilton and Zuk 1982).

Indicator mechanisms can also result in the evolution of a multiple-trait equilibrium in a population if the combined costs of preferences to females are low (Iwasa and Pomiankowski 1994). But, in contrast to Fisherian traits, any additive cost of multiple preferences to females will result in the fixation of a single trait/ preference combination and the elimination of other indicator traits (Iwasa and Pomiankowski 1994). Once preference for a single, high-preference-cost indicator has been fixed, this trait is resistant to invasion by additional indicator traits and is evolutionarily stable, even if novel traits are better indicators of quality (Iwasa and Pomiankowski 1994). The fixation of a single high-preference-cost indicator trait at any time in the history of a lineage should eliminate all indicator trait diversity from that lineage and constrain evolution of subsequent indicator traits (Iwasa and Pomiankowski 1994).

For a repertoire of indicator traits to evolve, each novel trait must provide an additional, independent, and accurate assessment of male quality without producing any additional cost to females (Iwasa and Pomiankowski 1994). The macroevolutionary consequence of such a process would be the progressive evolution of increasingly informative repertoires within the lineages of a clade. Constraints on the evolution of each additional indicator should also increase since the likelihood of evolving an additional, independent quality-correlated trait should decrease with repertoire size.

The low, combined preference cost conditions that could foster the evolution of multiple indicator traits should also favor the evolution of multiple Fisherian traits (Pomiankowski and Iwasa 1993; Iwasa and Pomiankowski 1994). However, indicator traits require an initial correlation with quality that Fisherian traits lack. Under these less stringent conditions, novel Fisherian traits are not constrained by limited initial conditions and should arise by mutation more frequently than

novel indicator traits, which require a substantial and independent initial correlation with quality. At high combined preference costs, only the Fisherian mechanism can contribute to the evolution of multiple novel traits within a repertoire. Under low combined preference costs, both Fisherian and indicator mechanisms can produce the evolution of new traits, but the Fisherian mechanism should contribute more substantially to diversification.

Direct Selection on Mate Choice Efficiency

Direct intersexual selection can act on variation in female viability associated with searching for a mate (Parker 1983; Kirkpatrick and Ryan 1991). This mode of selection should result in the evolution of traits that maximize efficiency and minimize risks of mate choice to females, and it should produce fixation of an optimum trait/preference combination through stabilizing selection on preferences. Direct selection on preferences should produce divergence in traits with variation in selection and convergences among lineages that secondarily share similar ecologies and environments. The magnitude, diversity, and phylogenetic patterns of secondary sexual traits should be similar to those of other traits under stabilizing natural selection and should vary with environment. Complex trait repertoires should evolve if additional, novel traits contribute successively to mate choice efficiency and female survival.

Direct Selection on Species Isolation

Natural selection can act directly on preferences to avoid hybridization and can result in differentiation of secondary sexual traits (e.g., Andersson 1984). Natural selection for species isolation should be ephemeral because selection should cease once traits and preference have diverged sufficiently to eliminate hybridization. The force of natural selection against heterospecific matings is unlikely to be strong if females can accurately differentiate among and prefer appropriate conspecific males. Once elaborate traits and preferences have evolved within a lineage, the strength of sexual selection should preclude natural selection against hybrids. Thus, selection for species isolation should be weak or nonexistent in species or lineages with an extensive history of intersexual selection, unless there have been striking convergences among lineages. On a macro-evolutionary scale, direct selection for species isolation should yield limited differentiation among sympatric and parapatric lineages of a polygynous clade. Selection for species isolation should also select against shared, homologous traits among lineages, eliminating repertoire diversity and hierarchical complexity in a clade, because homologous traits should contribute to confusion in mate recognition.

Sensory Bias

The sensory bias mechanism predicts that novel traits that exploit previous, neurologically based preferences will evolve (Basolo 1990; Ryan et al. 1990; Kirkpatrick and Ryan 1991; Ryan 1991). Sensory biases are hypothesized to evolve as a consequence of natural selection on other aspects of the neural system that have pleiotropic effects on mate choice (see *Sensory Drive*). Sensory biases pre-

dict the evolution of traits that are arbitrary in their direction of evolution and lack of correlation with quality, because natural selection on unrelated aspects of the neural system should result in unpredictable effects on mate choice.

Macroevolutionary predictions about the diversity and phylogenetic patterns of trait evolution by the sensory bias process depends on several factors: the specificity or breadth of the sensory bias, essentially the shape of the bias function; the frequency of origin of novel sensory biases within lineages; and the frequency of origin of novel male traits that exploit an existing sensory bias. Narrow sensory biases should produce limited macroevolutionary elaboration. The origin of male traits that match a narrow bias function should be rare, and opportunities for further elaboration of these traits should be highly constrained. If sensory bias functions are broad preferences for a wide variety of stimulating novelties, they could result in an elaborate radiation of arbitrary traits among lineages. Broad sensory biases could produce multiple traits and complex repertoires within lineages if traits that exploit sensory biases originate frequently. Sensory biases could lead to convergent evolution in traits if similar biases and traits originate frequently in different lineages.

Sensory Drive

Sensory drive refers to biased or correlated evolution in sensory biology and signal systems through natural selection for efficient communication within an environment (Endler 1989, 1992; Endler and McClennan 1989). Sensory drive includes the sensory bias mechanism and some aspects of direct selection on mate choice described earlier (Endler 1992). Here, sensory drive will be used to refer specifically to natural selection on sensory biology and signal structure.

In a macroevolutionary context, sensory drive predicts the differentiation of traits and preferences among species and lineages that live in environments that differ psychophysically and convergences among lineages that share psychophysically similar microhabitats. Trait variation in a clade should be correlated with variations in the habitat and their effects on sensory biology. Sensory drive has not been used to make explicit predictions about signal repertoire size, since the evolutionary origin of signals is considered a tactical rather than structural aspect of communication that is under other natural and social selection pressures (Endler 1992). However, sensory drive could be hypothesized to favor the evolution of multiple signal repertoires as an adaptation to psychophysically variable environments.

METHODS

Phylogenetic Hypothesis for the Manakins

In previous research, I have established the monophyly of a manakin clade (Pipridae; Prum 1990b) and presented a hypothesis of phylogeny for the group based on syringeal morphology (Prum 1992). (The taxonomy used here follows Prum 1992, with the additional recognition of *Corapipo altera* and *Corapipo heteroleuca* as distinct species.) This phylogenetic hypothesis was well resolved at many levels for most genera, but it did not support resolved phylogenetic relation-

ships for many closely related species'or the monophyly of the genus *Lepidothrix* (formerly the *Pipra serena* species group). To further resolve the phylogenetic relationships of the manakins at all levels, I scored variations in plumage among male manakin species as 44 binary and multistate phylogenetic characters (plumage characters are described in the appendix; table 1). I identified the most parsimonious phylogenetic trees based on a combined data set of 59 syringeal and 44 plumage characters using PAUP (Swofford 1989) and assuming the monophyly of *Lepidothrix*. The data set was too large to perform an exact search, so the data were analyzed using the heuristic algorithm. Behavioral data were not included in the analysis because they are completely missing for many taxa; it is difficult to estimate a parsimonious phylogenetic tree with many missing character states for a large number of taxa.

More than 1,000 equally parsimonious trees were identified with a consistency indices (CIs) of 0.756 (CI excluding autapomorphies = 0.672). The strict consensus tree of these hypotheses was almost entirely resolved except for a few intrageneric relationships and relationship of the genera *Lepidothrix* and *Machaeropterus* to two other major clades. The analyses performed here require a completely resolved phylogenetic hypothesis, so one of the resolved output trees was arbitrarily chosen. This phylogenetic hypothesis is intended only for this analysis of patterns of character evolution and is not proposed as a resolved hypothesis of phylogeny for the family. The results of these analyses of the distribution of character state changes should not vary substantially with various phylogenetic resolutions, since each tree was the same length and maximally parsimonious. The alternate hypotheses are phylogenetically indistinguishable because they require the same number of character state changes in nearly identical alternative distributions.

Plumage trait repertoires were estimated by considering each contiguous patch of distinctly colored, sexually dimorphic plumage as a separate trait. The 44 behavioral characters analyzed come from earlier work (Prum 1990*a*) with additional observations of a unique display in *Heterocercus flavivertex* (Prum et al. 1996). Each behavioral character is a hypothesized behavioral homolog. Based on the original behavioral descriptions, behavioral trait repertoire sizes were estimated for each species (table 1). Not all behavioral characters are independent traits, since some current traits are recently modified versions of earlier behavioral homologs.

In these analyses, male plumage and behavioral traits are assumed to have evolved by intersexual rather than intrasexual selection. This assumption is supported by the observation that manakins either are sexually monomorphic in size or have significant reverse (female-biased) sexual size dimorphism (Payne 1984; R. O. Prum, unpublished data). Intramale competition should result in male-biased sexual size dimorphism (e.g., Payne 1984). Small male size has likely evolved by female choice for correlated acrobatic display elements.

Between-Clade Comparisons of Phylogenetic Patterns in Traits

In the first test, I compare phylogenetic patterns in a set of dependent variables in two closely related clades that differ in an independent variable (e.g., Mitter et al. 1988). Here, the magnitude and phylogenetic patterns of the display behav-

TABLE 1

MANAKIN TRAIT REPERTOIRE SIZES AND THE DISTRIBUTION OF MANAKIN PLUMAGE TRAITS

SPECIES	DISPLAY REPERTOIRE SIZE	PLUMAGE REPERTOIRE SIZE	PLUMAGE CHARACTERS													
			1	2	3	4	5	6	7	8	9	10	11	12	13	14
Corapipo gutturalis	9	3	1	1	0	0	1	0	0	0	0	0	0	0	0	0
Corapipo leucorrhoa	7	3	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Corapipo heteroleuca	?	3	1	0	1	1	0	0	0	0	0	0	0	0	0	0
Corapipo altera	?	3	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Masius chrysopterus	4	5	0	0	0	0	0	1	1	1	1	0	0	0	0	0
Ilicura militaris	4	4	0	0	0	0	0	0	0	2	0	1	1	0	0	0
Machaeropterus deliciosus	3	3	0	0	0	0	0	0	0	0	0	0	0	2	1	0
Machaeropterus regulus	?	4	0	0	0	0	0	0	0	0	0	0	0	1	1	1
Machaeropterus pyrocephalus	?	4	0	0	0	0	0	0	0	0	0	0	0	1	1	0
Manacus manacus	7	5	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Manacus vitellinus	6	5	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Manacus candei	6	6	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Chiroxiphia pareola	3	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chiroxiphia caudata	3	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chiroxiphia linearis	3	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chiroxiphia lanceolata	?	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Antilophia galeata	?	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lepidothrix serena	3	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lepidothrix suavissima	?	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lepidothrix coronata	3	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lepidothix nattereri	?	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lepidothrix vilasboasi	?	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lepidothrix iris	?	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lepidothrix coeruleocapilla	?	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lepidothrix isidorei	?	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Xenopipo holochlora	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Xenopipo unicolor	?	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Xenopipo flavicapilla	?	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Xenopipo uniformis	?	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Xenopipo atronitens	?	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Heterocercus flavivertex	2	5	1	0	0	0	0	0	0	0	0	0	0	0	1	0
Heterocercus linteatus	?	5	1	0	0	0	0	0	0	0	0	0	0	0	1	0
Heterocercus aurantiavertex	?	5	1	0	0	0	0	0	0	0	0	0	0	0	1	0
Dixiphia pipra	3	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pipra aureola	9	5	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Pipra fasciicauda	11	5	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Pipra filicauda	10	6	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Pipra cornuta	7	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pipra mentalis	7	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pipra chlromeros	?	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pipra rubrocapilla	5	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pipra erythrocephala	5	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ancestor/Outgroup	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0

NOTE.—Estimates of display repertoire size come from an earlier work (Prum 1990*a*). For plumage charac-
ter 27, subspecies of *Lepidothrix coronata* vary in male body plumage from almost entirely black (2) to
green (0). This state was coded as variable (0&2) in the PAUP analysis.

TABLE 1 (*Extended*)

PLUMAGE CHARACTERS

15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44
0	0	0	0	0	0	0	0	0	2	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	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	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	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	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	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	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
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	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	1	1	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	1	1	1	1	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	1	1	2	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1	0	1	0	0	0	1	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1	0	1	0	0	0	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1	0	1	0	0	0	1	2	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1	0	1	0	0	0	1	3	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1	0	?	0	0	0	0	1	2	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	0	0	0	2	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	1	0	0	0	2	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	2	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	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	1	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	1	0	1	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	2	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	2	0	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	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	2	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	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	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	1	2	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	1	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	1	3	1	0	0	0	0
0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0
0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0
0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0
0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0
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0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	2	0
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0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	2	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

ior and plumage of manakins are compared to those of the largely monogamous tyrant flycatchers (Tyrannidae). The test examines differences in trait macroevolution between a lekking clade and a clade with extensive male investment in reproduction.

The tyrant flycatchers are a closely related family of suboscine passerine birds that include over 350 species, most of which have extensive pair bonds and biparental care (Bent 1943; Skutch 1960, 1967, 1969, 1972, 1981; Smith 1966, 1967, 1969, 1971a, 1971b, 1977; Willis et al. 1978; Snow and Snow 1979; Traylor 1979; Sick 1993; Ridgely and Tudor 1994; Wescott and Smith 1994). There is no completely resolved hypothesis of phylogeny for the tyrant flycatchers, but a number of studies by W. E. Lanyon (1984a, 1984b, 1985, 1986, 1988a, 1988b, 1988c; Lanyon and Lanyon 1988; see also Mobley and Prum 1995) provide resolved phylogenetic hypotheses for five diverse subfamilial groups that include almost all the genera and species of the family. Patterns of evolution in secondary sexual displays and plumages of tyrant flycatchers are simple enough to be largely resolved by current phylogenetic hypotheses.

The cotingas (Cotingidae) are actually the sister group to the manakins; the tyrant flycatchers are the sister group to the cotinga-manakin clade (Sibley and Ahlquist 1985, 1990; Prum 1990b). Although the cotingas are more closely related to the manakins, the cotingas vary extensively in breeding and social system (Snow 1982) and would not be an appropriate group for this comparison.

Within-Clade Analysis of the Phylogenetic Skew in Distribution of Traits

To test alternative predictions about the processes of trait and repertoire diversification, I developed a new statistical method for analyzing patterns of character change within a clade. Given an observed amount of character evolution within a clade (i.e., a parsimonious number of character state changes within a matrix), alternative evolutionary mechanisms may yield different predictions about how those character changes should be distributed on the branches of a phylogenetic tree. Character systems that evolve by an unconstrained macroevolutionary process can be expected to diversify continuously and more rapidly than the origin of new lineages, and they may be skewed in distribution toward the terminal branches, or "twigs," of a phylogenetic tree. Unconstrained traits will essentially erase their own history as they evolve and reduce the possibility of identifying broadly distributed homologues that would be distributed toward the basal branches of the phylogeny (fig. 1D). Conversely, characters that evolve by a constrained macroevolutionary process, in which the initial evolution of a derived state constrains the magnitude of subsequent trait novelty, should be skewed in distribution toward the basal branches, or "trunks," of a phylogenetic tree (fig. 1C). Since lekking and consequent sexual selection are primitive to the manakin clade (Prum 1994), trait evolution diversification throughout the history of the group should be influenced by the nature of the predominant mechanism of sexual selection in the family.

It is difficult to examine the skew in the phylogenetic distribution of character state changes away from a null distribution toward the "twigs" or "trunks" of a phylogeny with traditional statistical tests. Phylogenetic trees do not provide balanced samples of twigs or trunks for statistical analysis. Trees are also fre-

quently highly asymmetrical; branches that are the same age do not necessarily include the same amount of diversity.

To address this problem, I compared the distribution of manakin display and plumage traits with a simulated, null distribution of characters evolved on the same phylogeny. First, I created an index for each clade in the morphological phylogeny—a branch rank—with a value equal to the number of species descended from that lineage. Branch rank values range from 42 to 1. I then identified the branch rank for each behavioral and plumage character change using the delayed transition optimization in MacClade (Maddison and Maddison 1992). (In contrast to accelerated transition optimization, delayed transition optimization emphasizes convergence over reversals and skews character distribution toward branch tips. Only four of 44 plumage characters had ambiguous optimizations, so alternate optimization assumptions would not effect the plumage results. However, 15 of 44 behavioral characters had ambiguous optimizations because of the large number of species lacking behavioral data. I used delayed transition optimization for the behavioral data because accelerated transition optimization would require hypothesizing that numerous behavioral traits were present in many behaviorally unknown species.) I then compiled the distributions and calculated the means and standard deviations for the branch ranks for behavioral and plumage data sets.

To compare the branch rank distributions of the display and plumage characters to a null hypothesis of character distribution on the same tree, I produced a simulated data set of 100 variable, binary characters using the Evolve Characters option of MacClade 3.0 (Maddison and Maddison 1992). Characters were simulated to evolve along the branches of the same resolved hypothesis of phylogeny with a constant per-node probability of transition or reversal of 0.01 (the default settings). The simulated data set included a total of 667 character changes. I scored the branch rank of each character change in the simulated data set under delayed transition optimization. To establish a probability distribution for the mean branch rank, I created 500 bootstrap replicates of 50 character changes each and plotted the distribution of the mean branch rank for the bootstrap samples. The mean branch ranks of the observed behavioral and plumage data sets were then compared with the probability distribution of the mean branch rank based on simulated character changes.

The simulated data were generated under equiprobable conditions to simulate the effect of tree asymmetry on the distribution of branch ranks. An equivalent distribution of character changes would result from any simulation using any constant per-node probability of character change. The method, however, could be used to test other hypotheses by simulating evolution with differential probabilities of character change along lineages.

RESULTS

Display Behavior

Manakin display elements are extremely varied, encompassing a broad diversity of movements, postures, and elaborate sequences of elements assembled in

complex behavioral repertoires. Manakin display repertoires are also diverse. The mean display repertoire size for behaviorally known manakin species is 5.5 display elements ($n = 22$, SD $= 2.6$; table 1).

Manakin display elements demonstrate little convergence among lineages (fig. 2). The vast majority of behavioral similarities among species are behavioral homologs (figs. 2, 3). The consistency index (CI = the minimum possible number of character changes/the observed number) of the behavioral characters is 0.81. The CI measures homoplasy—character convergence and reversal combined. The observed value is very high for a data matrix including this number of taxa ($n = 19$) and characters ($n = 44$) (Sanderson and Donoghue 1988; de Queiroz and Wimberger 1993), indicating a low level convergence. This estimate of convergence is inflated by homoplasious traits that exhibit reversals. For example, the most homoplasious display element is a broadly distributed, simple movement that is parsimoniously interpreted as one convergent origin and several losses (the about-face display; Prum 1990a, character 7).

The phylogenetic distribution of manakin display elements is hierarchically complex (figs. 2, 3). The display repertoires of manakin species are composed of multiple traits that have evolved independently at different times in the evolutionary history of manakin lineages (figs. 2, 3). Although some behavioral traits are unique to single species (autapomorphies), most display elements are historical homologs that evolved in the common ancestor of more than one manakin species. All behaviorally known manakin species share at least one display trait with another closely related species (Prum 1990a).

In comparison with the pattern in the closely related family of tyrant flycatchers (Tyrannidae), the phylogenetic pattern in display behavior in manakins is explosive. Pair bonds in monogamous tyrant flycatchers are typically established by passive association rather than intersexual display; copulation often proceeds without any stylized or stereotyped display behavior (Smith 1977). The vast majority of known displays in tyrant flycatchers are associated with aggression, territoriality, the probability of flight, and indecision. Furthermore, tyrannids do not have complex vocal repertoires, so the limited diversity in display traits is not complimented by some other complex behavioral repertoire.

According to phylogenetic hypotheses of Lanyon (1986, 1988c), elaborate secondary sexual display behavior has evolved in four or five independent instances within the tyrant flycatchers—in *Gubernetes, Alectrurus, Mionectes, Knipolegus* and *Hymenops,* and *Pyrocephalus.* These tyrant flycatchers exhibit almost as many display elements as origins of intersexual display, indicating a simple and nonhierarchical pattern of trait evolution.

The mean branch rank for the 57 display character changes in the manakins was 3.19 (SD $= 8.5$). This value is essentially identical to the mean of the probability distribution of the branch ranks of the simulated data samples ($P > .5$). Based on this test, the null hypothesis cannot be rejected in favor of either a significantly constrained or unconstrained process hypothesis.

Plumage Traits

Manakin plumage traits and repertoires are diverse (fig. 4). If we count each distinctively colored, contiguous patch of sexually dimorphic plumage as a sepa-
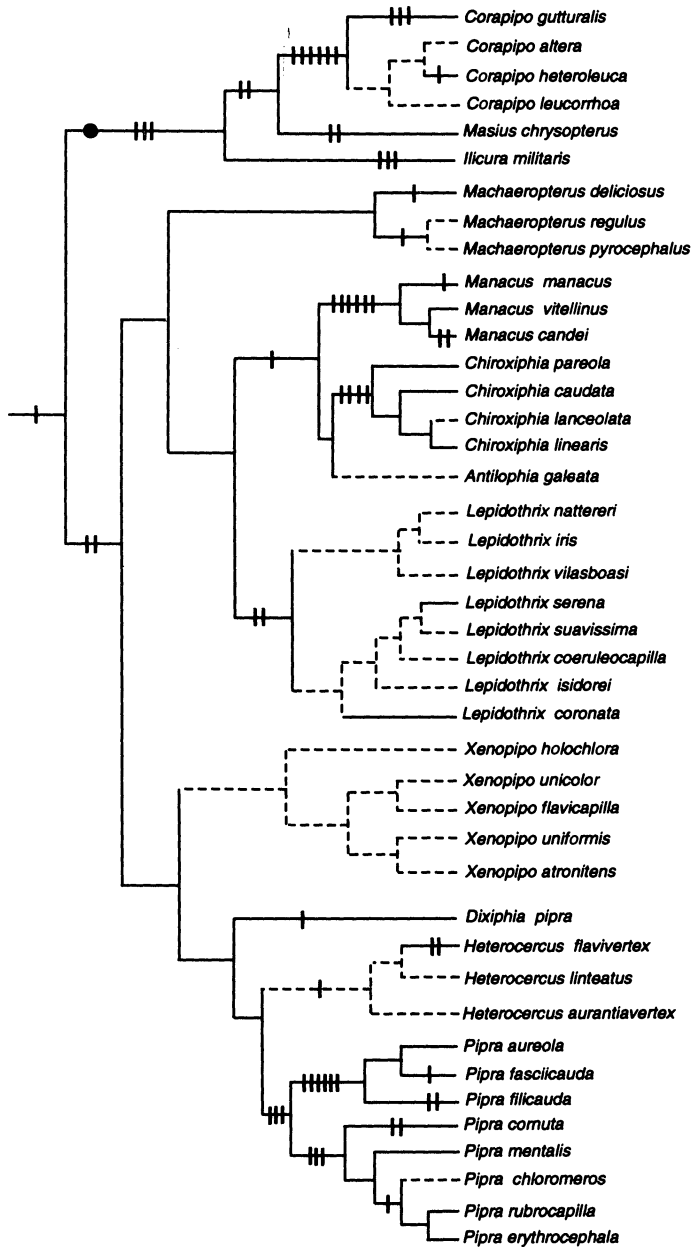
FIG. 2.—The phylogenetic distribution of character changes for lek display elements on a hypothesis of phylogeny for the Neotropical manakins (Pipridae). Hatch marks across a branch indicate a hypothesized display element character state change (either developments or losses). Dashed lines indicate lineages for which little behavioral information is available. Behavioral characters are from an earlier work (Prum 1990a), with the additional observation of a unique display in *Heterocercus flavivertex* (Prum et al. 1996). The evolution of display element repertoires in the clade marked with a dark circle at the top is detailed in figure 3.
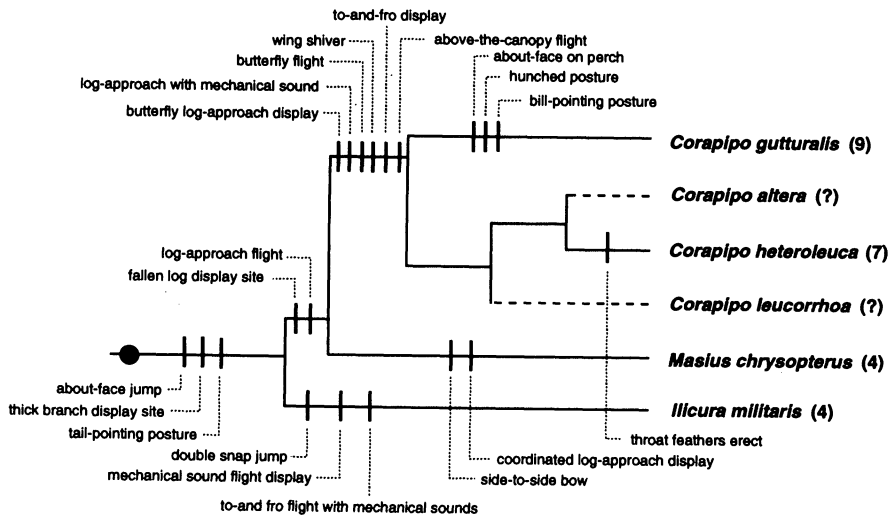
FIG. 3.—Detail of the complex, nested, hierarchical pattern of display trait evolution in a clade of three genera of manakins (highlighted with a dark circle in fig. 2). The historical origin of each derived display element is indicated on the phylogenetic hypothesis. Estimates of known display element repertoires are indicated in parentheses after species names (*Corapipo altera* and *Corapipo leucorrhoa* are too poorly known to characterize). The display repertoires of each species are composed of historically nested traits that evolved in that species alone, in the common ancestor of that species and its most recent sister taxa, and in the original common ancestor of the entire group. Display traits that have evolved on different nodes in the history of these lineages are historically independent.

rate trait, manakin species have an average of 3.76 plumage traits in each repertoire ($n = 42$; SD $= 1.38$; table 1). Manakin plumage traits demonstrate little convergence. Plumage traits have a consistency index of 0.71, a level of homoplasy that is quite low for a data set with this number of taxa and characters (Sanderson and Donoghue 1988; de Queiroz and Wimberger 1993). Most of the homoplasy in the entire data set comes from a single binary character (black male plumage, character 24) that requires 11 evolutionary changes, including numerous losses, to explain its evolution.

The phylogenetic distribution of manakin plumage traits is also hierarchically complex (fig. 4). Almost all manakin species share plumage traits with other closely related lineages. All species repertoires are composed of traits that have evolved independently on multiple nodes within the history of each lineage.

In comparison with that of manakins, diversification in secondary sexual plumage of the tyrant flycatchers has been highly constrained. Most tyrant flycatchers show no sexual dimorphism in plumage. Among the more than 375 species of tyrant flycatchers, only 17 species have elaborate sexual dimorphism in plumage in the genera *Pyrocephalus, Lessonia, Hymenops, Knipolegus, Arundinicola,* and *Alectrurus*. According to current phylogenetic hypotheses for tyrant flycatchers (Lanyon 1986), strongly sexually dimorphic plumage has evolved two to four times independently within the family. These few instances have led to little
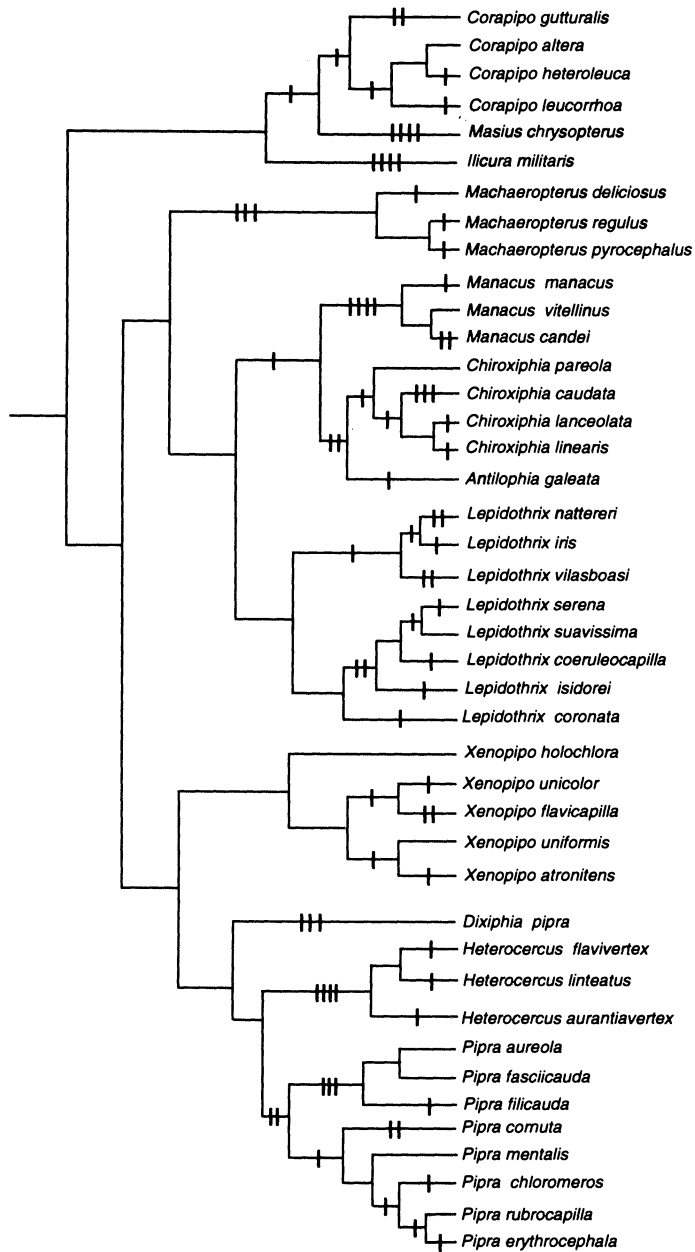
FIG. 4.—The hierarchical phylogenetic distribution of character changes for secondary sexual plumage traits on a hypothesis of phylogeny for the Neotropical manakins (Pipridae). Hatchmarks across a branch indicate a hypothesized plumage trait character state change, either development or loss. Phylogenetic hypothesis is based on the combined analysis of characters from syringeal morphology and plumage (see the text). Plumage trait characters are described in the appendix, and their distributions are detailed in table 1.

diversity in plumage traits and limited hierarchical complexity. There are only two examples of elaborate secondary sexual ornamentation: the brilliant red in a single species of *Pyrocephalus* and the twisted and lengthened tail plumes in two species of *Alectrurus*. In contrast, manakins have numerous brilliant secondary sexual plumages and at least four independent instances of derived tail feathers used in intersexual display (in *Ilicura, Chiroxiphia, Heterocercus,* and *Pipra fili-cauda*).

The statistical analysis of the distribution of plumage characters within the manakins indicates that plumage characters are significantly skewed in distribution toward the terminal branches or tips of the phylogenetic tree (fig. 4). The mean branch rank of each plumage character change was 1.91 (n = 76, SD = 1.42). Only 11 of 500 bootstrap samples of the simulated character changes had means as small as the observed mean (P < .025). This result supports the hypothesis that the male plumage characters in manakins have evolved by an unconstrained process that has led to rapid diversification in traits and trait repertoires and to the "erasure" of history of earlier trait homologies.

DISCUSSION

Alternative mechanisms of intersexual selection support different predictions about phylogenetic patterns in the evolution of trait diversity and trait repertoires. Comparative tests of these macroevolutionary predictions are presented here as an addition to proximate, experimental, and population-level tests of sexual selection mechanisms. These macroevolutionary predictions were deduced from current microevolutionary genetic models and are not yet formulated as explicit mechanistic models. Additional theoretical research is necessary to develop explicit macroevolutionary models of intersexual selection that incorporate the evolution of preferences, traits, trait repertoires, speciation, and extinction within polygynous clades.

These analyses indicate that macroevolutionary patterns in manakin traits conform well to the predictions of the Fisherian mechanism. Manakin display elements, plumage traits, and trait repertoires are very diverse. Trait repertoires are composed of multiple, hierarchically distributed (i.e., historically nested) traits that have evolved independently at various times in the history of manakin lineages. Convergence in manakin traits is low in comparison with morphological and behavioral data sets of a similar size (Sanderson and Donoghue 1988; de Queiroz and Wimberger 1993). In comparison with the predominantly monogamous tyrant flycatchers (Tyrannidae), manakins exhibit an order of magnitude more diversity in display and plumage traits among an order of magnitude fewer species. The differences in diversity and hierarchical complexity of traits between the two clades supports the conclusion that the male traits of tyrant flycatchers and manakins have evolved by constrained and unconstrained evolutionary processes, respectively.

The within-clade analysis of the distribution of manakin plumage traits indicates that derived plumage traits are significantly skewed toward the terminal branches or "tips" of the phylogeny (fig. 4). Extant plumage traits have not constrained

the evolution of subsequent trait diversity in manakins. The phylogenetic distribution of manakin display elements was not distinguishable from a null distribution of traits, and these traits are not significantly skewed in their phylogenetic distribution (fig. 2). Based on this test, a null hypothesis of character change cannot be rejected in favor of either the constrained or unconstrained process hypotheses. Since these predictions are probabalistic, there may be trait distributions that are inconclusive. However, this behavioral data set is biased by a lack of information for many species (Prum 1990a); additional data for poorly known taxa would probably lower the mean branch rank for these data. Neither data set showed any skew toward the basal branches of the tree, as would be predicted by a constrained process of diversification.

The phylogenetic patterns of hierarchical complexity (fig. 1A) and unconstrained, tip-biased distribution (fig. 1D) in traits are not mutually exclusive or contradictory. Both patterns can occur independently (as illustrated in fig. 1 for simplicity), but they are also possible, simultaneous outcomes of an unconstrained evolutionary process that leads to the accumulation of repertoire diversity through time, such as the Fisherian mechanism.

The repertoire diversity and the complex, hierarchical phylogenetic distribution of secondary sexual traits in manakins do not conform to the macroevolutionary predictions of the indicator mechanisms. Indicator mechanisms provide numerous opportunities for constraints on trait differentiation, which were not observed in the manakins. Indicator mechanisms can yield diversification within a lineage through successive switching to new traits (Schluter and Price 1993), but this process should not result in diverse trait repertoires, like those observed in manakins, since natural selection should eliminate previous traits from the population. Further, a trait-switching process should be ultimately constrained by the evolution of particularly robust, high-fidelity indicators within lineages. Multiple indicator traits may evolve in a lineage if the costs of the preferences are not additive (Iwasa and Pomiankowski 1994). However, this process requires that each successive trait contribute additional and independent information about quality (Iwasa and Pomiankowski 1994). The progressive evolution of increasing quality information within a repertoire appears unlikely. Furthermore, under these conditions, the evolution of novel Fisherian traits would be more likely than the origin of new indicator traits that require a substantial initial quality correlation that is independent of previous traits in the repertoire. Under the conditions that permit evolution of multiple indicator traits, Fisherian traits should predominantly contribute to trait diversity.

All three mechanisms of direct natural selection on preferences—mate choice efficiency, species isolation, and sensory drive—could yield complex repertoires of hierarchically distributed traits if each novel trait contributes successively to increases in female fitness. Detailed analyses of repertoire evolution and field experiments would be required to examine these hypotheses in detail, but the fitness contributions of successive, derived traits are not obvious (e.g., fig. 3).

Several lines of evidence indicate that natural selection for species isolation is unlikely to have contributed significantly to macroevolutionary patterns in manakin traits. First, many lineages have diverged in allopatry. Further, most closely

related manakins share many homologous traits that should be eliminated by selection for species isolation. Finally, measures of sexual selecton in the field demonstrate that sexual selection within populations is intense (Snow 1962; Lill 1974; Payne 1984; McDonald 1989) and likely to preclude any potential natural selection for species isolation.

Direct selection predicts that trait diversity should be associated with variation in predation and mate search costs. No relevant data exist on these costs in manakins, and further research is required to test this hypothesis critically. However, a simplistic survey indicates that the predicted relationship does not exist in manakins. Many manakin species with divergent trait repertoires live sympatrically in the same microhabitats (see below) and probably have similar predators and mate search costs. Direct selection on mate choice efficiency is also likely to be weak in manakins (and many other lek species) because individuals are long-lived and leks are traditional sites that may be occupied for decades (e.g., Snow 1962; Lill 1974; McDonald 1989); females are likely to be familiar with available display sites and incur minimal energetic costs in searching for mates.

The sensory drive mechanism predicts adaptive differentiation and convergence in traits among lineages in relation to the psychophysical characteristics of the habitat. Despite some evidence that variation in light exposure among male territories may influence female choice in *Corapipo gutturalis* (Théry and Veherencamp 1995), there is little apparent macroevolutionary support for sensory drive in manakins. Behavioral and plumage traits are shared by species in clades (e.g., *Manacus, Chiroxiphia,* and *Pipra*) that are found in vastly different habitats, from aseasonal tropical rain forests in Amazonia to highly seasonal dry tropical woodlands in Mexico (Prum 1990*a,* 1994). Multiple manakin species are frequently found displaying microsympatrically. For example, I observed active lek territories of five manakin species with divergent repertoires within a <1-km^2, second-growth forest patch in Amazonian Ecuador (*Pipra erythrocephala, Pipra filicauda, Chiroxiphia pareola, Machaeropterus regulus,* and *Lepidothrix coronata;* Ecuador: Napo Province, Nueva Avila, Rio Guataraco, 400 m; October 1986). Additional research is required to examine psychophysically variation in manakin display sites and determine whether manakin plumage and display traits have adapted accordingly. While sensory drive may provide some constraints or biases on the form of manakin display, it appears unlikely to be a generalized mechanism for the evolution of hierarchical trait diversity in manakins.

A very broad sensory bias could result in a diverse radiation of traits limited only by the frequency of origin of bias-exploiting traits. A narrow sensory bias function would be unlikely to yield diverse, hierarchically distributed patterns in traits unless novel biases and coincidentally corresponding novel traits arose frequently. Convergent evolution by sensory bias would be determined by the persistence of the bias and the frequency of origin of matching traits. Currently, there is no experimental evidence on the existence or the breadth of sensory biases in birds. However, sensory biases have been hypothesized in clades of frogs and fishes (Basolo 1990; Ryan et al. 1990; Kirkpatrick and Ryan 1991; Ryan 1991). (An alternative resolution of the phylogeny of the swordtails supports an alternative explanation for one of these cases; Meyer et al. 1994.) Proposed examples of sensory bias consist of narrow bias functions that explain only a portion

of secondary sexual diversification within these clades. For example, in *Physalae-mus* frogs, the proposed sensory bias explains only a restricted component of vocal diversification in the group; each species still prefers a species-specific, primary portion of its own call to the calls of all other species (Ryan et al. 1990). The restricted nature of the best-documented sensory biases does not support the hypothesis that a broad sensory bias has fostered diversification of manakin traits.

The macroevolutionary patterns in manakin traits are consistent with the predictions of the Fisherian and broad sensory bias mechanism, but they are not consistent with the predictions of the indicator, direct selection, species isolation, or sensory drive mechanisms. The diverse repertoires and hierarchically distributed traits in the lekking manakin clade indicate that Fisherian selection may have played an important role in the diversification of secondary sexual traits in other groups of polygynous animals.

These findings do not imply that indicator and direct selection mechanisms do not occur in manakins or other highly polygynous groups. Rather, they indicate that these adaptive processes are not a predominant cause of differentiation in traits and repertoires among lineages. As in the study of adaptation (Gould and Lewontin 1979), a proximate function for a trait does not demonstrate that that trait evolved through selection for that function. A Fisherian trait could evolve into a quality indicator following the depletion of genetic variation for the trait and the retention of some quality-correlated phenotypic variation in the trait (e.g., Dominey 1983). Likewise, an indicator trait could evolve into a Fisherian trait through the erosion of its quality correlation by the origin of novel genetic variation for the trait itself or loss of variation in quality. Proximate evidence for an indicator function for a trait within a population cannot constitute evidence that an indicator mechanism is responsible for its evolutionary origin. Furthermore, investigations of sexual selection on traits within populations need to examine whether the traits under study originated within that lineage or evolved in an earlier ancestor. Macroevolutionary tests that focus on patterns of trait evolution can provide an alternative means of assessing the contributions of various sexual selection mechanisms to trait diversity.

Female preference costs that can constrain trait evolution may be rare in lekking species that have no paternal investment and provide a minimum of opportunities for constraining selection on female preferences. Indicator and direct selection mechanisms are more likely to predominate as the length of the pair bond and paternal investment increase and the potential costs and benefits of variation in male quality increase. Accordingly, most tyrant flycatchers, in contrast to manakins, have an extensive pair bond that is likely to produce significant constraints on the evolution of trait diversity and hierarchical complexity within the group.

APPENDIX

MANAKIN PLUMAGE CHARACTERS

Manakin plumage traits were based on observations of museum study skins of all species in the family in the collections of the University of Kansas Natural History Museum and the American Museum of Natural History. Character state variation was polarized based on outgroup comparison to the cotingas (Cotingidae) and tyrant flycatchers (Tyrannidae) and by ontogenetic criteria (Wiley 1981). All male manakins first have entirely green, female-like plumage and molt into adult plumage over 1–4 yr. Primitive and derived characters states are described as states 0, 1, 2, or 3, respectively. Unordered multistate characters are indicated in boldface type. Character state distributions are shown in table 1.

1—Erectable, white throat patch: 0 = absent; 1 = present.
2—V-shaped, white throat patch: 0 = absent; 1 = present.
3—Inverted V-shaped, white throat patch: 0 = absent; 1 = present.
4—Outer (tenth) extremely attenuate primary: 0 = absent; 1 = present.
5—Hidden white wing patch: 0 = absent; 1 = present.
6—Yellow wing and tail patches: 0 = absent; 1 = present.
7—Black lateral crown horns: 0 = absent; 1 = present.
8—Plush forecrown: 0 = absent; 1 = yellow present; 2 = red present. **Unordered.**
9—Red hindcrown: 0 = absent; 1 = present.
10—Elongated, pin-shaped central tail feathers: 0 = absent; 1 = present.
11—Red rump patch: 0 = absent; 1 = present.
12—Secondaries 7–10 with thickened rachis: 0 = absent; 1 = moderately thickened; 2 = extremely thickened. **Ordered.**
13—Rusty brown breast: 0 = absent; 1 = present.
14—Striped brown-and-white breast: 0 = absent; 1 = present.
15—Red crown: 0 = absent; 1 = present.
16—Yellow crown with central red stripe: 0 = absent; 1 = present.
17—Legs orange or yellow: 0 = absent; 1 = present.
18—Outer primaries attenuate: 0 = absent; 1 = present.
19—Black cap and wings with contrasting collar: 0 = absent; 1 = white collar present; 2 = yellow collar present. **Unordered.**
20—Yellow belly and chest: 0 = absent; 1 = present.
21—Blue back: 0 = absent; 1 = present.
22—Long central tail feathers: 0 = absent; 1 = moderately elongated; 2 = very long; 3 = extremely long.
23—Red back and crown, with forecrest curling over bill: 0 = absent; 1 = present.
24—Mostly black male plumage: 0 = absent; 1 = wings and tail; 2 = mostly black.
25—Blue belly: 0 = absent; 1 = present.
26—White forecrown: 0 = absent; 1 = present.
27—Sky blue rump: 0 = absent; 1 = present.
28—Yellow central chest spot: 0 = absent; 1 = present.
29—Blue crown: 0 = absent; 1 = present.
30—White crown: 0 = absent; 1 = present.
31—Yellow rump: 0 = absent; 1 = present.
32—Yellow crown: 0 = absent; 1 = present.
33—Opalescent crown: 0 = absent; 1 = present.

34—White rump: 0 = absent; 1 = present.
35—White or yellow iris: 0 = absent; 1 = present.
36—Red iris: 0 = absent; 1 = present.
37—White axillaries and underwing coverts: 0 = absent; 1 = present; 2 = bright white present.
38—Inverse-graduated tail (*Heterocercus*): 0 = absent; 1 = present.
39—Erectable crown: 0 = absent; 1 = red; 2 = yellow; 3 = orange. **Unordered.**
40—Deep olive green above: 0 = absent; 1 = present.
41—Elongated tail feather rachi: 0 = absent; 1 = present.
42—Red or yellow head: 0 = absent; 1 = red; 2 = yellow. **Unordered.**
43—Distinctly colored thighs: 0 = absent; 1 = red; 2 = yellow. **Unordered.**
44—Scarlet horns on hindcrown: 0 = absent; 1 = present.

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