

## PHYLOGENETIC ANALYSIS OF THE EVOLUTION OF ALTERNATIVE SOCIAL BEHAVIOR IN THE MANAKINS (AVES: PIPRIDAE)

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*Abstract.*—Phylogenetic analyses of lekking, lek spatial organization, and cooperative and coordinated lek display in the manakins (Aves: Pipridae) demonstrate that variation in social behavior in the group has a strong, phylogenetic component. Two of the three classes of social behavior examined also show significant phylogenetic constraints. Current adaptive plasticity models are insufficient to explain the phylogenetic variation in these behaviors in the manakins. These findings support the conclusion that vertebrate reproductive social behavior has an evolutionary history, and that it is not determined solely by adaptive individual plasticity to current conditions. The evolution of social behavior, particularly through sexual selection, can have historical consequences that can limit subsequent behavioral adaptation.

*Key words.*—Adaptation, cooperation, lek behavior, manakins, Pipridae, phylogenetic constraint.

Received September 14, 1993. Accepted January 10, 1994.

According to the predominant paradigm, reproductive social behavior of animals is determined by the distribution of ecological resources, the asymmetry in reproductive investment between the sexes, and the variance in reproductive success within the sexes (e.g., Lack 1968; Emlen and Oring 1977; Wittenberger 1981; Oring 1982; Krebs and Davies 1991; Davies 1992). Most models of the evolution of social behavior, particularly in vertebrates, are essentially ahistorical. They view variations in reproductive social behavior of populations as the result of adaptive individual plasticity, in which each individual has the capacity to exhibit an entire range of social behaviors and adopts a specific behavior in response to current ecological conditions and social selection pressures (Emlen and Oring 1977; Wittenberger 1981; Oring 1982; Krebs and Davies 1991; Davies 1992). An alternative view is that these traits evolve largely through natural and sexual selection on genetic variation for behavior and that they are not determined solely by adaptive plasticity.

Investigations of the correlation between ecology and behavior of single species or a set of populations are insufficient to document the historical process of evolution of social behavior in a diverse group. Phylogenetic methods have been developed that can explicitly test historical predictions of alternative mechanisms of behavioral change (Hennig 1966; Wiley 1981; Dobson 1985; Felsenstein 1985; Coddington 1988; Donoghue 1989; Maddison 1990; Prum 1990a; Brooks and McClennan 1991; Harvey and Pagel 1991). The

evolutionary and plasticity mechanisms of social behavior determination yield some distinctive predictions about phylogenetic patterns in social behavior within clades. Plasticity models are consistent with the observation of extensive variation in social behavior among species and populations, and even within populations, because (1) ecological variables may vary extensively among species and populations, (2) individual assessments of current conditions may vary, and (3) behavioral plasticity is hypothesized to be unconstrained by genetic variation for specific social behaviors. Plasticity mechanisms could result in coherent phylogenetic patterns in social behavior only if there were significant, phylogenetically coincident uniformity in ecological conditions among species and higher lineages. Evolutionary mechanisms are consistent with a wide variety of phylogenetic patterns in social behavior. Evolutionary mechanisms could result in very rapid diversification with little phylogenetic pattern or slow diversification with significant phylogenetic coherence in social behavior. Evolutionary mechanisms could also lead to phylogenetic constraints—a limitation in the expected amount or direction of change (McKittrick 1993)—which can limit subsequent evolution in social behavior (Gould and Lewontin 1979; Cheverud et al. 1985; Gould 1989; McKittrick 1993). Highly conserved phylogenetic patterns and phylogenetic constraints would be unlikely to occur in social behaviors that are determined solely by adaptive individual plasticity.

In vertebrates, phylogenetic patterns in the

evolution of alternative forms of reproductive social behavior have just begun to be explored. Investigations of the evolution of parental care (Gittleman 1981; Rhijn 1984, 1990; McKittrick 1992; Ligon 1993), interspecific nest parasitism (S. M. Lanyon 1992) and cooperative breeding (Edwards and Naeem 1993; Ligon 1993) support a reevaluation of adaptive individual plasticity as an explanation for the diversity of these breeding systems.

Among the most interesting classes of alternative social behavior are lek breeding, and coordinated and cooperative lek display, which occur in animals undergoing extreme sexual selection. In a lek breeding system, males contribute only gametes to reproduction and may form territorial aggregations where they display to attract potential mates (Bradbury 1981; Wiley 1991). In general, the phylogenetic history of the evolution of lek behavior and variations in lek spatial organization are poorly understood. Only recently have attempts been made to identify the number of independent origins of lek behavior in behaviorally diverse groups such as birds (Payne 1984; Höglund 1989; Oakes 1992). Phylogenetic patterns in the variation in lek spatial organization have not yet been documented in any groups. In birds, the overwhelming pattern is that most species of lekking birds belong to clades of species which also breed in polygynous arena systems, strongly indicating a phylogenetic component to this form of breeding behavior (Payne 1984; Höglund 1989).

Most current models hypothesize that lekking and lek spatial organization are determined by proximate individual strategies that are adaptive solutions to current ecological and sociobiological conditions (Emlen and Oring 1977; Bradbury 1981; Oring 1982; Bradbury and Gibson 1983; Foster 1983; Beehler and Foster 1988; Wiley 1991). All of these models are ahistorical in view, and none considers whether the evolution or distribution of this alternative social behavior is influenced by phylogenetic or genetic components. Alternatively, Quellar (1987) has provided a nonadaptive genetic model for the evolution of lek size through arbitrary or "Fisherian" female mate preferences. Documenting the history of the origin and diversification of lek breeding systems is an important part of a general solution to the "paradox of the lek," which is central to current research on sexual selection (Kirkpatrick and Ryan 1991).

Another alternative social behavior found in

a few polygynous species with extreme sexual selection is coordinated display, in which pairs or groups of males engage in synchronized, mutual display that can be competitive or cooperative in function (Sick 1942; Slud 1957; Gilliard 1959; Snow 1963a,b, 1971a; Hogan-Warburg 1966; Skutch 1969; Rhijn 1973; Watts and Stokes 1971; Foster 1977a,b, 1981, 1985; Balph et al. 1980; LeCroy et al. 1980; Avery 1984; Prum 1985; Robbins 1983, 1985; Bradbury and Davies 1987; Prum and Johnson 1987; McDonald 1989a,b; Wiley 1991). In fully cooperative systems, the subordinate males in a partnership or group contribute to the attraction of females to the group, but the dominant males in these associations receive most or virtually all the copulations (Rhijn 1973; Foster 1977a, 1981, 1985; McDonald 1989a,b). This form of premating cooperation is distinct from other forms of communal or cooperative breeding in which there are long-term social relationships among a reproductive pair and other individuals (e.g., Brown 1987). Previous investigations of coordinated display and premating cooperation in polygynous species have modeled this behavior on the basis of individual plasticity and have not considered the historical patterns in the evolution of the behavior (Foster 1985; McDonald 1989a,b).

In this paper, I analyze phylogenetic patterns in the evolution of these alternative social behaviors in a clade of polygynous, Neotropical passerine birds: the manakins (Pipridae). Many of the 40 or more species of manakins are known for their strongly, sexually dimorphic plumage, lek breeding behavior, and elaborate male courtship displays (Snow 1963c; Sick 1967; Prum 1990a,b, 1992). The display repertoires vary among manakin species, but most display elements are homologues shared by groups of species or genera (Prum 1990a). Manakins also vary extensively in the social and spatial organization of their leks. In previous papers, I have produced a well-resolved phylogenetic hypothesis for the manakins based on morphology of the syrinx, the avian vocal organ (Prum 1992), and I have analyzed the phylogenetic patterns and evolution of manakin display elements (Prum 1990a). Here, I analyze the evolution of three classes of alternative social behavior within the family: (1) lekking, (2) lek size and spatial organization, and (3) coordinated and cooperative display. I will compare the phylogenetic patterns of variation in these behaviors to the expected patterns based

on the plasticity and evolutionary mechanisms to determine which models provide a better explanation of social behavior determination in manakins.

#### MATERIALS AND METHODS

The analysis includes 12 genera in the restricted, monophyletic family of manakins (Pipridae; Prum 1990b, 1992). Six genera from the traditional, polyphyletic manakin assemblage are excluded: *Schiffornis*, *Piprites*, *Tyrannetes*, *Neopelma*, *Neopipo*, and *Sapayoa* (e.g., Snow 1975, 1979). These six genera are not manakins, and their inclusion in the family has confounded previous analyses of the behavioral evolution of the group (Snow 1963c, 1975; Sick 1967; Prum and Lanyon 1989; Prum 1990b, 1992). The immediate sister group of the manakins is the monophyletic cotingas (Cotingidae), and the next outgroup is the tyrant flycatchers (Tyrannidae) (Sibley and Ahlquist 1985, 1990; Prum 1990b). The cotingas and tyrannids will be used as outgroups in the analysis, but the monophyly of the tyrannids will not be assumed (Sibley and Ahlquist 1985, 1990; Prum 1990b). Here, I use a revised phylogenetic classification of the Pipridae in which there are several taxonomic changes (Prum 1992): (i) *Xenopipo* is expanded to include four species in the paraphyletic genus *Chloropipo*, (ii) the *serena* species group is removed from the polyphyletic genus *Pipra* and placed in *Lepidothrix*, and (iii) the species *pipra* is also removed from *Pipra* and placed in the presently monotypic genus *Dixiphia*.

For the phylogenetic analyses of character evolution within the manakins, I use an independent hypothesis of phylogeny for the manakins based on characters from the morphology of the syrinx (Prum 1992). Syringeal morphology was used in that analysis because syringeal characters are phylogenetically informative in suboscine birds (Lanyon 1984a,b, 1985, 1986, 1988a,b,c; Prum and Lanyon 1989; Prum 1990b, 1993), and syringeal characters were hypothesized to be more independent of display behavior than other morphological character systems such as plumage (which is prominently featured during display) and osteology and limb musculature (which may be correlated with physical aspects of display). The syringeal hypothesis of phylogeny was highly congruent with an independent data set of derived manakin display elements (Prum 1990a).

Behavioral information for this analysis was gathered from the literature and from my own

field observations (table 1). The sources of behavioral information about each manakin species are summarized in the Appendix. I superimposed variations in three classes of social behavior on the syringeal hypothesis of phylogeny: (1) lekking, (2) lek spatial organization, and (3) coordinated and cooperative male display. The most parsimonious hypotheses for the evolution of each trait were identified visually and confirmed using MacClade (Maddison and Maddison 1992) with the syringeal hypothesis of phylogeny as an input tree. All conclusions about the evolution of social behavior classes were unaffected by accelerated or delayed transition assumptions.

Although similarities in these social behavior traits could be treated as homologues among some species at a finer level of analysis, I have defined these behaviors as distinct classes that are characterized by thresholds of organization. These behavioral grades are not strictly historical entities (i.e., ontological "individuals" *sensu* Hull 1976) and would not be appropriate as systematic characters for phylogenetic reconstruction. Including these social behavior traits in the original data set used in phylogenetic reconstruction as if they were appropriate systematic characters does not alter the phylogenetic hypothesis used in these analyses.

Adaptive plasticity models are consistent with the observation of extensive intraspecific and interspecific variation in these social behaviors within a clade, but they are inconsistent with the observation of significant phylogenetic coherence or phylogenetic constraints in behavior. Evolutionary models are consistent with a diversity of historical patterns including strongly coherent phylogenetic patterns and phylogenetic constraints, which are not expected through plasticity mechanisms. A highly variable pattern of social behavior could arise by either plasticity or evolutionary mechanisms, whereas highly conserved phylogenetic patterns or phylogenetic constraints in social behavior could not arise by plasticity mechanisms alone.

#### RESULTS

##### *Lek Behavior*

In a lek breeding system, males do not establish any lasting pair bond with females. Rather, they defend nonresource-based, display territories and contribute only gametes to reproduction. A lek has been defined as an aggregation of such advertisement territories (Bradbury 1981).

TABLE 1. Summary of distribution of alternative social behavior variables in the manakins (Pipridae). See the text for details. Sources of behavioral data for each species are listed in the Appendix. Classification follows Prum (1992). Abbreviations: +, present; -, absent; ?, unknown.

Species	Lek behavior present	Males/lek	Territory diameter (m)	Class of lek	Coordinate display
<i>Ilicura militaris</i>	+	2-3	20-30	dispersed	none
<i>Masius chrysopterus</i>	+	3	25-40	dispersed	complex
<i>Corapipo gutturalis</i>	+	6-8	25	dispersed	none
<i>C. leucorroha</i>	+	?	?	dispersed	none
<i>Machaeropterus deliciosus</i>	+	2-4	20	dispersed	none
<i>M. regulus</i>	+	3-5	20-30	dispersed	simple(?)
<i>M. pyrocephalus</i>	+	?	?	dispersed	simple(?)
<i>Lepidothrix serena</i> (Suriname)	+	2-4	30-40	dispersed	simple(?)
<i>L. serena</i> (French Guiana)	+	5-8	4-6	concentrated	simple(?)
<i>L. suavissima</i>	?	?	?	?	none
<i>L. coronata</i>	+	3-5	10-20	concentrated	simple(?)
<i>L. nattereri</i>	?	?	?	?	?
<i>L. vilasboasi</i>	?	?	?	?	?
<i>L. iris</i>	?	?	?	?	?
<i>L. isidorei</i>	?	?	?	?	?
<i>L. coeruleocapilla</i>	?	?	?	?	?
<i>Manacus manacus</i>	+	6-50	1-5	concentrated	none
<i>M. vitellinus</i>	+	5-10	0.5-1	concentrated	none
<i>M. candei</i>	+	5+	1-5	concentrated	none
<i>Chiroxiphia caudata</i>	+	4-6	?	cooperative	comp. cooperative
<i>C. pareola</i>	+	2+	30-40	cooperative	comp. cooperative
<i>C. lanceolata</i>	+	2	?	cooperative	comp. cooperative
<i>C. linearis</i>	+	2+	25-100	cooperative	comp. cooperative
<i>Antilophia galeata</i>	-	-	-	-	none
<i>Xenopipo unicolor</i>	?	?	?	?	?
<i>X. flavicapilla</i>	?	?	?	?	?
<i>X. holochlora</i>	?	?	?	?	?
<i>X. uniformis</i>	?	?	?	?	?
<i>X. atronitens</i>	?	?	?	?	?
<i>Dixiphia pipra</i>	+	3-5	30	dispersed	none
<i>Heterocercus linteatus</i>	?	?	?	?	?
<i>H. flavivertex</i>	+	1	20-30	solitary	none
<i>H. aurantiavertex</i>	+	1	20	solitary	none
<i>Pipra aureola</i>	+	3	20	dispersed	complex
<i>P. fasciicauda</i>	+	10	20-40	dispersed	complex
<i>P. filicauda</i>	+	?	20-35	dispersed	complex
<i>P. cornuta</i>	+	2	20	dispersed	none
<i>P. chloromeros</i>	+	?	?	dispersed	none
<i>P. mentalis</i>	+	4-9	> 3	dispersed	none
<i>P. erythrocephala</i>	+	5-16	3	concentrated	none
<i>P. rubrocapilla</i>	+	?	?	concentrated	none

Lek behavior is known from field studies and observations in 27 of the 40 manakin species (table 1). Twelve species are behaviorally too poorly known to categorize. Only one species of manakin is known not to breed in any form of lek or arena system. In *Antilophia galeata*, males are highly territorial and closely aggregated, but females build their nests inside male territories and have an extended pair bond with the male (Marini and Cavalcanti 1993). Females perform all of the parental care, and it is not known whether males are polygynous. In two species of

*Heterocercus*, males are apparently polygynous, but their advertisement territories are solitary and isolated from one another (R. O. Prum unpubl. obs.). The five species of *Xenopipo* include some sexually monochromatic species that have been suspected of being monogamous (Sick 1967; Snow 1975), but they are behaviorally too poorly known to categorize. The behaviorally poorly known species of *Lepidothrix* (formerly in the genus *Pipra*) are all likely to be lek breeding, as are the two behaviorally known species in the genus: *serena* and *coronata*.

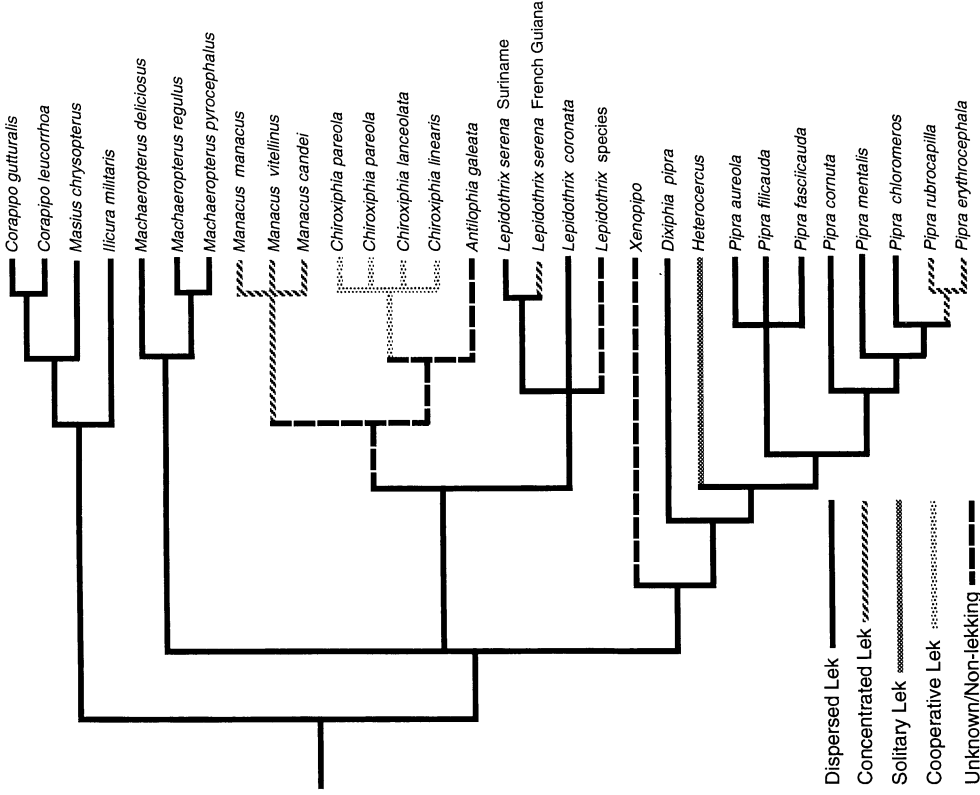


FIG. 2. Phylogenetic analysis of the evolution of lek spatial organization in the manakins (Pipridae). Phylogenetic hypothesis follows Prum (1992). Observed classes of lek spatial organization are dispersed, concentrated, solitary, and cooperative. Dispersed leks are primitive to the manakin clade. Concentrated leks have evolved convergently three times. Cooperative leks and solitary leks have each evolved once.

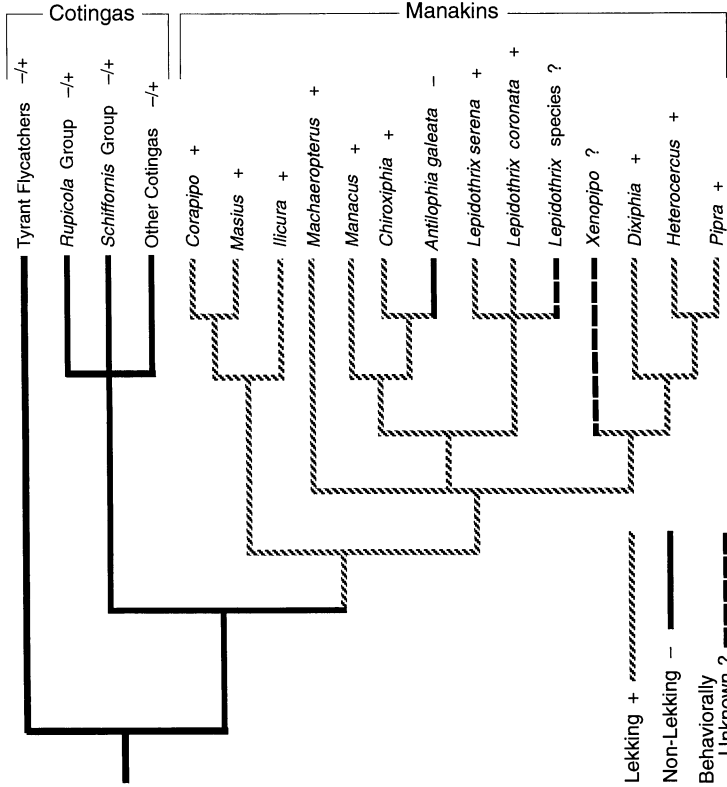


FIG. 1. Phylogenetic analysis of the evolution of lekking in manakins (Pipridae), cotingas (Cotingidae), and tyrannids (Tyrannidae). Phylogenetic hypothesis follows Sibley and Ahlquist (1985, 1990), Prum and Lanyon (1989), and Prum (1990a, b, 1992, unpubl. data). Lekking had a single origin in the common ancestor of the manakin clade and was lost once in *Antilophia galeata*. The cotingid and tyrannid outgroups are composed of both monogamous and lekking taxa, but all lekking taxa have several successive, monogamous sister groups (Snow and Snow 1979; Snow 1982; Prum and Lanyon 1989; Prum 1990b; Prum unpubl. obs.), and monogamy is primitive to both outgroups.

The phylogenetic pattern in the presence and absence of lek behavior indicates that lek breeding evolved only once in the common ancestor of all manakins, independently of other cotingas and flycatchers (fig. 1). All lekking tyrannids and cotingas share derived evolutionary novelties with several, successive lineages of nonlekking tyrannoids (Lanyon 1985; Sibley and Ahlquist 1985, 1990; Prum and Lanyon 1989; Prum 1990b, unpubl. data), indicating that monogamy is the primitive breeding system within the cotinga-manakin clade (fig. 1). Within the manakins, lek-breeding behavior has been lost only in *A. galeata*, resulting in male nest territory defense, an extended pair bond, and perhaps monogamy (Marini and Cavalcanti 1993). Strictly defined lek behavior has also been lost in *Heterocercus*, in which solitary male display territories have evolved, but this appears to be a derived form of lek spatial organization and is not considered an evolutionary loss of lekking (see below). If any of the behaviorally poorly known manakin species is shown to be nonlekking (e.g., *Xenopipo*), the phylogenetic distribution of lek behavior in the family would still support the conclusion that lek behavior is primitive to the entire family.

#### *Lek Spatial Organization*

Manakin species vary extensively in the size of lek territories and the number of males per lek (table 1). Variation in lek spatial organization is a theoretical continuum, but based on the documented variation in manakins (table 1), I have defined four major classes of lek spatial organization (fig. 2): (1) *concentrated lek*, small territories of 1–5 m in diameter usually with five or more males per lek; (2) *dispersed lek*, male territories of 10–40 m in diameter with 2–7 adja-

cent male territories in a lek; or (3) *solitary lek*, male territories of 10–30 m in diameter that are isolated from other territories (outside of sight or hearing range); (4) *cooperative lek*, an area in which a single dominant male and associated cooperative partners display. These categories do not attempt to incorporate variation in distance between leks, which is poorly documented in manakins.

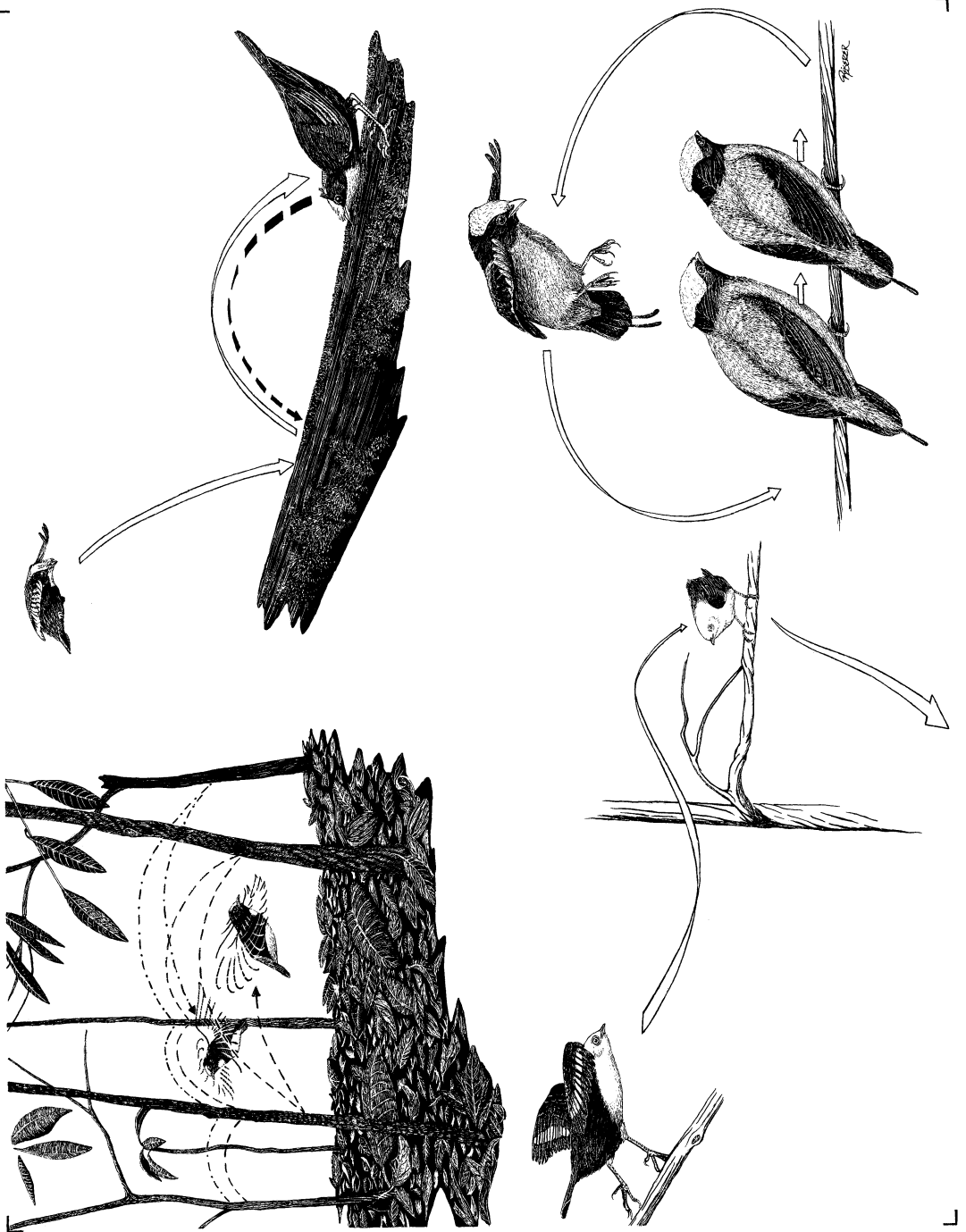
Although solitary advertisement territories have not been previously considered leks, they are the extreme in a continuum of dispersion of male advertisement territories. According to these results, solitary display territories in manakins are derived from leks in *Heterocercus*, and they are included in this analysis of evolution of lek spatial organization as a distinct class of true lek.

Lek spatial organization in *Chiroxiphia* is difficult to categorize because cooperative relationships between males break down the meaningful limits of individual territoriality which define the spatial classes of leks. Leks in *Chiroxiphia* have been defined as either (1) the assemblage of widely dispersed display perches occupied by several male partnerships (*linearis*, Foster 1977a), or (2) the restricted set of display perches on which a dominant male and associated partners display (*linearis*, McDonald 1989a,b; *caudata*, Foster 1981). The latter definition emphasizes the similarity in spatial distribution to other dispersed lek species but defines a lek within which the female does not exercise mate choice. In contrast, the former defines a much larger lek that encompasses a larger set of males among which a female may effectively choose a mate. Cooperative space use in *Chiroxiphia* is distinct enough to require an additional class of lek type. Here, I define a cooperative lek as the restricted display area of a single, cooperative male partnership. In choos-

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FIG. 3. Coordinated display behavior of four species of manakins. **Upper left.** *Pipra serena*. A pair of males chases one another from vertical perch to vertical perch in either buzzy or direct to-and-fro flights (Prum 1985; Théry 1990). Uncoordinated forms of these displays are primitively present in the genus (Prum 1990a). **Upper right.** *Masius chrysopterus*. One male waits on the display log, while a second male flies to the log and performs the log-approach display (white arrows). While the approaching male rebounds down the log, the waiting male also rebounds in the opposite direction (dark dotted arrows). The display is then repeated with the roles reversed (Prum and Johnson 1987). The log-approach display is primitively present in the *Masius-Corapipo* clade, but the rebound-hop from a stationary position on the log is derived in *Masius* (Prum 1990a). **Lower left.** *Pipra fasciicauda*. One male waits on the display perch (right), as the second flies to the perch and performs the S-curved flight display (left). As the flying male arrives, the waiting male drops from the perch and gives a distinctive vocalization (Robbins 1983). The S-curved flight display is primitive to the genus *Pipra*, whereas the coordinated drop from the perch with distinctive vocalization is derived in the *Pipra aureola* clade (Prum 1990a). **Lower right.** *Chiroxiphia caudata*. Two to four males on the same perch each flutter in succession from one end of the perch to the other, as the remaining male(s) slide along the perch. This cartwheel display is derived in *Chiroxiphia* (Prum 1990a).



ing the restricted definitions for cooperative lek and solitary lek, it should be recognized that, to exercise mate choice, females must select among more than one available lek.

The overwhelming phylogenetic pattern among manakin species and genera is that variation in the classes of lek spatial organization has a strong, historical component (fig. 2). All known, lekking manakin species share their form of spatial organization with at least one other sister species or have the primitive form of lek. The simplest historical hypothesis for the evolution of lek spatial organization is that dispersed leks with large male territories and few males per lek evolved in the common ancestor of the family. Concen-

trated leks with more males and smaller lek territories were secondarily derived in the genus *Manacus*, in the *Pipra erythrocephala-rubrocapilla* clade, and in a population of *Lepidothrix* (formerly *Pipra*) *serena*. Solitary polygynous display territories evolved in *Heterocercus* from primitive, dispersed leks. Cooperative leks evolved a single time in *Chiroxiphia*. Known variation in manakin lek spatial organization can be explained by these six evolutionary events.

In general, intraspecific variation in lek spatial organization is poorly documented. Significant intraspecific variation in several lek size variables have been documented in populations of *Manacus manacus* (Olson and McDowell 1983;



FIG. 4. Phylogenetic analysis of coordinated and cooperative display behavior in the manakins (Pipridae). Three classes of coordinated behavior are recognized: simple, complex, and complex-cooperative. Coordinated behavior has had five independent origins in the family, and has never been lost. All forms of coordinated behavior are phylogenetically independent of one another within the manakins.



table 1). This variation is correlated with the order of magnitude difference in population density between islands and the mainland, and significant changes in character of the habitat. However, even under this extreme demographic and ecological variation, *Manacus* populations maintained the concentrated or "classical" lek spatial organization at both sites (Olson and McDowell 1983).

Prum (1985) and Théry (1990) documented significant variation in lek spatial organization among populations of *L. serena*. Prum (1985) observed dispersed leks in Suriname, whereas Théry (1990) described a unique "two-spot" concentrated lek for this species in French Guiana, in which males display at either of two concentrated leks in apparent response to ambient light conditions. This level of variation is unique in manakins and practically all lek birds.

#### *Coordinated and Cooperative Display*

Coordinated male display behavior is interactive, synchronous display incorporating two or more males. This behavior is distinct from simultaneous display by males at separate territories on the same lek. Coordinated display may have a competitive function in establishing dominance among males, or it may have a cooperative function in attracting potential mates to the group, or both (Foster 1977a, 1981, 1985; Avery 1984; Bradbury and Davies 1987; Wiley 1991). Coordinated display can be recognized ethologically, whereas cooperative forms of coordinated display behavior can be distinguished only with additional sociobiological information. Here, I use "cooperative" display to refer only to coordinated displays that function in attracting mates to a group of males with an established dominance relationship. Only coordinated display that functions to attract females to mate requires the cooperative reproductive investment of nonmating, coordinated males.

Coordinated display behavior has been observed in *Masius chrysopterus*, *Lepidothrix serena*, *L. coronata*, *Chiroxiphia linearis*, *C. lanceolata*, *C. pareola*, *C. caudata*, *Pipra aureola*, *P. fasciicauda*, *P. filicauda*, and, anecdotally, in *Machaeropterus regulus* and *Machaeropterus pyrocephalus*. In *L. serena* and *L. coronata*, coordinated displays are performed by nonpermanent male pairs and consist of synchronized interactive performances of solitary display elements (fig. 3, upper left) (Prum 1985; Skutch

1969; Théry 1990). In *Masius* (Prum and Johnson 1987) and the *P. aureola* clade (Snow 1963a; Schwartz and Snow 1978; Robbins 1983), coordinated display consists of the combination of primitive solitary display elements and novel, derived display elements that are unique to coordinated display (fig. 3, upper right, lower left) (Prum 1990a). The highly derived, coordinated display of *Chiroxiphia* is known only from that genus, and no primitive homologues of the display are known (fig. 3, lower right) (Prum 1990a). The display behavior of *Machaeropterus regulus* and *Machaeropterus pyrocephalus* is too poorly known to be well characterized (Sick 1967; Skutch 1969).

The social function of coordinated display behavior in *Lepidothrix*, *Machaeropterus*, and *Masius* is not known, though it is most likely competitive and unrelated to mate attraction (Skutch 1969; Prum 1985, pers. obs.; Prum and Johnson 1987; Théry 1990). In the *P. aureola* clade, coordinated display may be associated with the attraction of mates but is not obligatory for female visits or copulation (Robbins 1983, 1985). Coordinated behavior appears to function in establishing dominance relationships among males that influence the inheritance of display territories. In the *P. aureola* clade, coordinated behavior may serve a marginally cooperative role in addition to its competitive function (Robbins 1983, 1985). In *Chiroxiphia*, coordinated display is virtually obligatory for attracting mates and is cooperative in nature (Foster 1977a, 1981; McDonald 1989a,b). Males form long-term display partnerships or teams, and the dominant member of the partnerships copulates with visiting females (Foster 1977a, 1981; McDonald 1989a,b).

Because the social function of coordinated behavior is poorly understood in many genera, I have defined three classes of coordinated behavior in manakins based primarily on an ethological analysis of the evolution of manakin display elements (Prum 1990a): (1) *simple coordinated display* involves two or more males that perform synchronized versions of the typical solitary display elements (present in *Lepidothrix*); (2) *complex coordinated display* incorporates novel elements in the synchronized performance that are not performed solitary (present in *Masius chrysopterus* and the *P. aureola* clade); and (3) *complex-cooperative display* is a virtually obligatory, complex coordinated display that serves in mate attraction and results in differential mating suc-

cess among coordinated males (present in *Chiroxiphia*). Coordinated behavior in *Machaeropterus regulus* and *Machaeropterus pyrocephalus* is too poorly known to categorize but will be conservatively classified as simple coordinated display.

The phylogenetic distribution of coordinated display behavior indicates that it had five evolutionarily independent origins within the family (fig. 4). The known coordinated displays of *Masius*, *Lepidothrix*, *Machaeropterus*, the *P. aureola* clade, and *Chiroxiphia* are all unique and phylogenetically independent. In the *P. aureola* clade, *Chiroxiphia* and the *Machaeropterus regulus-pyrocephalus* clade, coordinated display behavior is uniformly present in all species within a monophyletic group. Additionally, coordinated display behavior is found in both of the behaviorally known species of *Lepidothrix*, and may be present in more species in the genus. In only one of five cases, (*Masius chrysopterus*), is coordinated behavior restricted to a single species. In three of five cases (*Masius*, *Pipra*, and *Chiroxiphia*), coordinated display behavior has been evolutionarily elaborated to incorporate novel display elements that are not performed in the solitary repertoire (Prum 1990a). Cooperative display has further evolved at least once in *Chiroxiphia* and perhaps a second instance, marginally, in the *P. aureola* clade.

#### DISCUSSION

##### *Phylogenetic Patterns in Social Behavior*

Phylogenetic patterns in the three classes of alternative manakin social behavior that I examined document that variation in reproductive social behavior of manakins has a strong historical component. These results imply that evolutionary mechanisms have had an important role in the determination of social behavior in manakins and that plasticity mechanisms alone cannot explain the phylogenetic patterns in manakin behavior. Detailed ecological data are not available to test directly the alternative explanation that phylogenetic patterns in manakin social behavior are determined by adaptive plasticity to phylogenetically coincident variation in ecological and social conditions. However, plasticity models of these social behaviors are so sensitive to variation in ecological factors that they would require highly detailed similarity in ecology and social conditions among manakin populations and species to explain the observed phylogenetic patterns.

Plasticity models for the determination of lekking and lek size are based on proximate ecological and social factors such as home range size (Bradbury 1981), female habitat-use patterns (Bradbury and Gibson 1983), and spatial distribution of the most attractive males (Beehler and Foster 1988). It is unlikely that such factors would be conserved sufficiently over an entire continent to produce the observed stability in lek behavior within wide ranging species and genera. Lekking manakins are found in almost all classes of Neotropical forest including: humid lowland terra firme; subtropical mossy forests; highly seasonal deciduous forests; gallery forests in dry campo cerrado; seasonally inundated varzea; and bamboo (e.g., Meyer de Schauensee and Phelps 1978; Parker et al. 1982; Hilty and Brown 1986; Ridgely and Gwynne 1989; Stiles and Skutch 1989; Sick 1993). Many behaviorally uniform manakin clades are found over a wide variety of these habitats, or over a large distribution of a single habitat type. For example, the four cooperative species of *Chiroxiphia* and the three or more concentrated lek species of *Manacus* are found in seasonal tropical dry forests and aseasonal humid forests in Central America, Amazonia, southern Brazil, and northern Argentina. Various aspects of social behavior in these and other manakin clades do not vary and are apparently resistant to change over diverse and wide-ranging habitats. Many aspects of manakin social behavior are too phylogenetically consistent for adaptive plasticity to provide a complete explanation of their variation.

A single case of significant interspecific variation is present in *Lepidothrix serena*. In Suriname, I documented dispersed leks in which males defended their territories throughout the day (Prum 1985). In French Guiana, Théry (1990) observed a unique "two-spot" concentrated lek in which males defend territories on two different leks, depending on the time of day and in apparent response to changes in light. Such extensive variation is unknown in any other species of manakin or lekking bird. Additional research is needed to clarify whether this variation is due to the origin of a novel form of concentrated-mobile lek in *L. serena* populations of French Guiana, or to the evolution of greater plasticity in lek spatial organization in the genus *Lepidothrix*. Evidence from a closely related species supports the former hypothesis. The only other behaviorally known species of the genus, *Lepidothrix coronata*, has consistently dispersed leks

throughout its range from Central America to Amazonian Ecuador and Peru (Skutch 1969; R. O. Prum, pers. obs.).

A strong phylogenetic component to lekking and lek spatial organization is certainly not restricted to manakins. Most species of lekking birds belong to diverse clades in which lekking is primitive (Payne 1984; Höglund 1989). The largely lekking birds of paradise (Paradisaeidae) show a pattern of taxonomic coherence in lek spatial characteristics that is very similar to the manakins. Although a detailed phylogenetic hypothesis is not available for the birds of paradise, four of the six presumably monophyletic, polygynous genera that include more than one behaviorally known species are uniform for type of lek spatial organization: *Ptiloris*, *Epimachus*, *Parotia*, and *Diphylodes* (Beehler and Pruett-Jones 1983). The other two, *Astrapia* and *Paradisea*, include five or seven species, respectively, with concentrated, dispersed, or solitary leks (Beehler and Pruett-Jones 1983). Assuming the monophyly of current genera, this variation constitutes significant phylogenetic consistency in social behavior of the birds of paradise. A detailed phylogenetic hypothesis for birds of paradise and behavioral information for more poorly known species are required to reconstruct the history of lek organization in the family, but it is likely that the extensive variation in lek spatial organization of the birds of paradise can be explained by relatively few evolutionary events.

Comparative analyses of other vertebrate social behaviors have documented similar phylogenetic patterns in breeding system (Gittleman 1981; McKittrick 1992; S. M. Lanyon 1992; Ligon 1993; Edwards and Naem 1993). The emerging generalization is that the behaviorally hypervariable species that are the basis of the adaptive plasticity paradigm are highly unusual (e.g., Davies 1992). Phylogenetic patterns in behavior document that social systems in vertebrates evolve as do other aspects of phenotype and that they are not merely proximately determined by adaptive individual response to the environment. A historical perspective on the behavioral diversification of a group is required for a complete understanding of the behavioral evolution of any specific member of that group.

#### *Phylogenetic Constraints in Social Behavior*

Lekking and cooperative display have evolved phylogenetic constraints that may limit future behavioral diversification within manakin lin-

eages. These constraints document that the evolution of vertebrate social behavior may have historical consequences that can limit subsequent opportunities for behavioral adaptation. These constraints should not occur by plasticity mechanisms alone, which further supports the conclusion that plasticity models are insufficient to describe the documented patterns of variation.

Only a single instance of the loss of true lek behavior was identified in manakins. In this species (*Antilophia galeata*), females nest inside male territories but perform all the parental care duties (Marini and Cavalcanti 1993). The loss of lek behavior in *A. galeata* may be a result of selection associated with the evolution of its unique, derived habitat preference within the family. This species is common to abundant in moist riparian forests within dry savanna woodlands (campo cerrado) in southern and central Brazil, and eastern Bolivia and Paraguay (Marini and Cavalcanti 1993). Sometime during the evolution of this derived habitat preference, *Antilophia* populations became restricted to narrow strips of habitat along rivers and streams. These populations may have become concentrated so densely that male territories that primitively contained no resources came to include critical limited resources for females, such as nesting sites. Females would then have been selected to establish long-term pair bonds with males, resulting in the loss of lekking in the species.

Although complex social behaviors, such as lekking, may be facultative in some vertebrate species (e.g., Leuthold 1966), this analysis of manakins, Höglund (1989), and McKittrick (1992) provide strong support for the conclusion that lek behavior and the loss of direct male parental care is strongly constrained in manakins and other birds. Nest territorial defense by males and an extensive pair bond have reevolved only once among behaviorally known species of manakins in the roughly 14 to 35-My history of the manakin clade (Sibley and Ahlquist 1985). The only instance of the "loss" of lek behavior in birds identified by Höglund (1989) was in the blue bird of paradise, *Paradisea rudolphi* (Paradisaeidae), which is actually a solitary lek species (Gilliard 1969; Beehler and Pruett-Jones 1983). McKittrick (1992) did not identify a single example of the reevolution of male parental care in birds. Phylogenetic studies indicate that lek behavior and the correlated loss male parental care are strongly constrained once they are evolved. Interspecific brood parasitism (S. M. Lanyon 1992)

and cooperative breeding (Edwards and Naeem 1993) in birds exhibit similar patterns of phylogenetic constraint that further support the hypothesis that evolution of alternative breeding systems can limit subsequent adaptation in social behavior.

Bull and Charnov (1985) described how evolutionary elaboration of a derived state can contribute to its irreversibility. As an example, they cited the elaborately sexually dimorphic flowers of dioecious plants, which can provide a irreversible barrier to the reevolution of monoecy in many lineages. Similarly, elaboration of social behavior and morphology following the origin of lekking could contribute to the evolution of phylogenetic constraints on reversibility. In manakins, derived secondary sexual plumages, display elements, wing morphologies used for mechanical noise production, and the competitive and cooperative social interactions among males all evolved and diversified following the origin of lek behavior in the group. Because these traits may make a male less suited for direct or indirect parental care, evolution of these extreme, derived characters may constitute to an effective, functional barrier to the evolutionary reversal in lek behavior in many clades. Because these secondary sexual traits evolved through sexual selection, sexual selection mechanisms can apparently contribute directly to the evolution of phylogenetic constraints in social behavior. Selective inferiority of intermediates also contributes to evolutionary irreversibility between two states (Bull and Charnov 1985). Sexual selection through female mate preferences can provide a strong selective force against intermediate male social behaviors, and further contribute to constraints on the reversal of a lekking system to male parental care (Lande 1980, 1981, 1982; Kirkpatrick 1982; Quellar 1987).

#### *Consequences for the Study of Social Behavior Evolution*

These findings about manakins have several important consequences for the study of the evolution of vertebrate breeding systems and for models of sexual selection on social behavior. Future theoretical and ecological models of the evolution of breeding systems must take into account that establishment of lek behavior and other alternative social systems can have historical consequences that limit subsequent adaptation in social behavior. If lekking and coordinated and cooperative display evolve as a consequence

of sexual selection, as all current models propose (Emlen and Oring 1977; Bradbury 1981; Oring 1982; Bradbury and Gibson 1983; Foster 1983, 1985; Quellar 1987; Beehler and Foster 1988; Wiley 1991), then sexual selection can produce strong phylogenetic constraints on future adaptive change in social behavior. This conclusion is particularly interesting in regards to honest-advertisement and good-genes models of female choice, which hypothesize that female mate preferences are adaptive (e.g., Zahavi 1975, 1977; Andersson 1982, 1986; Hamilton and Zuk 1982; Kodric-Brown and Brown 1984; Pomiankowski 1988; Heywood 1989; Price et al. 1993).

The phylogenetic patterns and constraints on social behavior in manakins and other vertebrates strongly indicate that social behavior has a genetic component that is not included in current adaptive plasticity models. Current plasticity models may have identified the selection pressures that affect social behavior. But the explanatory power of these models is limited because they do not include the possibility that social behaviors evolve and are not merely adaptive strategies. Plasticity models should be expanded to include explicit genetic components to social behavior variation, which can themselves evolve through natural selection and sexual selection. Quellar (1987) has provided such a model of lek size based on female preferences in an arbitrary, Fisherian sexual selection mechanism and has demonstrated that these models are theoretically tractable and potentially testable. Theoretical models that incorporate selection on both genetic variation for social behavior and adaptive plasticity are required for further theoretical progress on social behavior evolution.

Future studies of evolution in social behavior must take into account the history of behavioral diversification in a group before testing evolutionary hypotheses. Completely ahistorical models of social behavior evolution may yield unrealistic conclusions when applied to species in which that social behavior is plesiomorphic. For example, Théry (1992) concluded that variation in lek size characteristics and home range sizes of four sympatric species of manakins were consistent with predictions of both the female-choice (Bradbury 1981) and hot-spot (Bradbury and Gibson 1983) models of lek spatial organization. However, the female-choice and hot-spot plasticity models cannot adequately explain the consistent history of lek spatial organization among

the clades of manakins that include these species. Similarly, autecological studies of single lekking species from diverse lekking clades cannot accurately investigate the evolutionary origins of lekking in early history of these taxa.

Phylogenetic methods can be used to identify the events in the history of the behavioral diversification of groups that require evolutionary explanation and to establish appropriate comparative tests of macroevolutionary predictions about these events. Analyses of ecological hypotheses concerning evolutionary transitions in social behavior should compare the relevant traits of species that have the derived behavior and their closely related sister taxa that primitively lack that behavior (Coddington 1988). Although ahistorical comparative analyses may accurately identify the cause of a behavioral transition, the greater the amount of time since the initial evolution of the derived social behavior, the greater the likelihood is that current ecological or social conditions have changed since the behavior's origin and that current conditions do not reflect those at the time the behavior evolved. For manakins and a large majority of the lekking birds, the proximate answer to the "paradox" of why they breed in leks is because their parents did; the ultimate answer lies in the ancient past when these behaviors initially evolved. Comparisons of the few lekking species that belong to largely monogamous clades to their primitively monogamous sister taxa are more likely to yield productive tests of ecological hypotheses about the evolution of lek behavior (e.g., *Mionectes*, Tyrannidae; Snow and Snow 1979).

Although the evolution of a social behavior may have occurred in the past, ahistorical studies may correctly identify an evolutionary explanation of a behavioral transition without correctly identifying the historical instance itself. For example, Snow (1971b, 1976) hypothesized that frugivory in manakins and other lekking birds released males from all parental care, and established sexually competitive conditions which fostered the subsequent evolution of lek behavior. This hypothesis is supported by the observation that manakins are largely frugivorous (Snow 1962a,b, 1976; Skutch 1967, 1969; Worthington 1982; Prum 1985, 1986; Prum and Johnson 1987; R. O. Prum unpubl. obs.), that frugivory is primitive in the group, and thus evolved before or coincident with the evolution of lekking in manakins. Snow's ecological model remains generally well supported given that many

clades of lekking birds are primitively frugivorous, or have highly precocial young that require little parental care.

#### *Lek Terminology*

A practical consequence of this analysis on social behavior evolution in manakins deals with lek terminology. Concentrated and dispersed leks are often referred to as "classical" and "exploded" leks, respectively (Bradbury 1981; Beehler and Pruett-Jones 1983; Bradbury and Gibson 1983; Foster 1983; Théry 1992). These terms originally come from Gilliard's (1963, 1969) hypothesis that larger leks were evolutionary derived from more concentrated or "classical" leks, and therefore literally "exploded" in size. Gilliard's hypothesis has not been tested previously in the birds of paradise (Gilliard 1963, 1969; Beehler and Pruett-Jones 1983) or any other polygynous birds, but the terms "exploded" and "classical" lek have advanced the notion that larger, more dispersed lek territories are derived in polygynous birds. This phylogenetic analysis indicates that the opposite is true in the manakins. Dispersed leks are primitive within the family, and concentrated, solitary, and cooperative leks are independently derived. The terms "exploded" and "classical" should be abandoned in favor of unbiased modifiers that describe lek spatial dispersion without implying a specific evolutionary mechanism or polarity. Alternative terms such as "dispersed" and "solitary" lek may be criticized as oxymorons (implying that males are simultaneously "grouped" and "dispersed"). These terms, however, are evolutionarily neutral and unify these conceptually related forms of polygynous, advertisement territories in a single comparable vocabulary. This unification is scientifically advantageous because "dispersed" and "solitary" leks are interesting for precisely the same reason as concentrated leks: females may choose mates without receiving direct benefits from mate choice, such as a high-quality territory or parental care. Furthermore, a unified terminology will aid in recognition that solitary arena-display breeding systems may be historically related to other forms of lek behavior.

#### *Evolution of Coordinated and Cooperative Display*

Although coordinated display is relatively common among manakins, its phylogenetic distribution in the family indicates that this behav-

ior is not typical of, or plesiomorphous to, the entire group. Coordinated display behavior had five independent origins within the manakins (fig. 4). Coordinated display has further evolved to incorporate novel, derived display elements in at least three of five cases and has also evolved into one marginal form and one virtually obligatory form of premating cooperation. These coordinated and cooperative display behaviors are also apparently phylogenetically constrained. In four of five cases, these derived, alternative social behaviors are present in all behaviorally known species within a clade; the additional case occurs in a single species (*Masius chrysopterus*). No case of the loss of coordinated or cooperative behavior was identified. As with lek behavior itself, the phylogenetic persistence of these alternative social behaviors supports the hypothesis that sexual selection has resulted in constrained novelties in male social behavior.

Unfortunately, because each case of coordinated behavior is phylogenetically independent, these data cannot reflect on the history of potential transitions between classes of coordinated behavior, that is, whether cooperative display evolves from competitive, coordinated display. Snow (1963a) hypothesized that the complex coordinated display of the *Pipra aureola* clade was an intermediate stage in the evolution of obligate cooperative display in *Chiroxiphia*, based on the implicit assumption that the two genera were closely related. Although the coordinated behavior in the *P. aureola* clade is marginally cooperative and similar to *Chiroxiphia*, this analysis demonstrates that coordinated display behavior in these two genera are historically unrelated and had independent origins.

Foster (1977a, 1981) hypothesized that the elements of coordinated display in manakins evolved through female preference for ritualized aggressive displacement among males. Comparative analysis of the coordinated display elements in the display repertoires of *Lepidothrix serena* and *L. coronata*, *Masius chrysopterus*, and the *P. aureola* clade demonstrates that, ethologically speaking, these coordinated displays have evolved through the synchronization and, in the latter two cases, elaboration of primitive display elements that are performed in the solitary display repertoire of these or the sister species (Prum 1990a). These coordinated display elements are not ritualized aggressive displays. It is not possible to determine whether the cartwheel display performed by cooperating male *Chiroxiphia* is

derived from some primitive element within the clade (Prum 1990a). However, the pattern among the other three testable cases contradicts Foster's hypothesis and supports the prediction that coordinated display elements in *Chiroxiphia* were derived from primitive elements of solitary display.

Coordinated and cooperative display among males is rare in birds. Putatively cooperative display behavior has been reported only in wild turkey (*Meleagris gallopavo*, Meleagridae; Watts and Stokes 1971; Balph et al. 1980), ruff (*Philomachus pugnax*, Scolopacidae; Hogan-Warburg 1966; Rhijn 1973), Goldie's bird of paradise (*Paradisea decora*, Paradisaeidae; LeCroy et al. 1980), and, perhaps, black-and-gold cotinga (*Tijuca atra*, Cotingidae; Snow 1982). All of these species breed in lek or arena-display systems, demonstrating that coordinated display evolves through extreme sexual selection. Interestingly, coordinated behavior has evolved five times independently in the small manakin clade but is known in only four other species among the more than 9000 species of birds. Foster (1985) hypothesized that cooperative display is determined by adaptive plasticity in response to spatial proximity among males, length of the pair bond, and rate of male disruption of display. More theoretical work is required to develop genetic models that explain both the phylogenetic patterns in coordinated and cooperative display, and the unusually high frequency of evolution of this behavior in manakins.

#### ACKNOWLEDGMENTS

This research was supported by a grant from the Graduate Research Fund of the University of Kansas. The research was aided by discussions with R. Gomulkiewicz, M. Nachman, M. C. McKittrick, S. M. Goodman, R. B. Payne, and G. F. Barrowclough. L. Kinkel, S. Williamson, L. Rosselli, and J. Tello shared their field observations on manakins. R. Holt, R. Mumme, and an anonymous reviewer made constructive criticisms on the manuscript.

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## APPENDIX.

List of the available sources of information about social behavior for each species of the Pipridae. Classification follows Prum (1992).

Species	Sources
<i>Corapipo gutturalis</i>	Davis 1949a; Davis 1982; Prum 1986; Théry 1990, 1992
<i>C. leucorrhoea</i>	Aldrich and Bole 1937; Skutch 1967; Slud 1967; Wetmore 1972; L. Roselli pers. comm. 1988
<i>Masius chrysopterus</i>	Prum and Johnson 1987
<i>Ilicura militaris</i>	Sick 1959, 1967; Snow and Snow 1985
<i>Machaeropterus deliciosus</i>	Willis 1966; Orejuela et al. 1982; Prum unpubl. obs.
<i>M. regulus</i>	Sick 1959, 1967; Skutch 1969; Prum unpubl. obs.
<i>M. pyrocephalus</i>	Sick 1959, 1967
<i>Lepidothrix serena</i>	Prum 1985; Théry 1990, 1992
<i>L. suavissima</i>	no information available
<i>L. isidorei</i>	no information available
<i>L. coeruleocapilla</i>	no information available
<i>L. coronata</i>	Skutch 1969; Prum unpubl. obs.
<i>L. nattereri</i>	no information available
<i>L. vilasboasi</i>	no information available
<i>L. iris</i>	no information available
<i>Manacus manacus</i>	Snow 1962a; Lill 1974a,b; Olson and McDowell 1983
<i>M. vitellinus</i>	Chapman 1935; Wetmore 1972
<i>M. candei</i>	S. Williamson pers. comm. 1991
<i>Chiroxiphia linearis</i>	Aldrich and Bole 1937; Wagner 1945; Slud 1957; Wetmore 1972; Foster 1977b; McDonald 1989a,b
<i>C. lanceolata</i>	Friedmann and Foster 1955; Wetmore 1972
<i>C. pareola</i>	Gilliard 1959; Snow 1963b, 1971a
<i>C. caudata</i>	Sick 1942; Lamm 1948; Snow 1976; Foster 1977b, 1981
<i>Antilophia galeata</i>	Sick 1959, 1967; Marini and Cavalcanti 1993; unpubl. obs.
<i>Xenopipo unicolor</i>	no information available
<i>X. flavicapilla</i>	no information available
<i>X. holochlora</i>	no information available
<i>X. uniformis</i>	no information available
<i>X. atronitens</i>	Sick 1959, 1967, 1993
<i>Dixiphia pipra</i>	Snow 1961; Théry 1992; Prum unpubl. obs.
<i>Heterocercus linteatus</i>	Sick 1959, 1967, 1993
<i>H. flavivertex</i>	Prum unpubl. obs.
<i>H. aurantiavertex</i>	Prum unpubl. obs.
<i>Pipra aureola</i>	Snow 1963a
<i>P. fasciicauda</i>	Robbins 1983, 1985
<i>P. filicauda</i>	Schwartz and Snow 1978
<i>P. cornuta</i>	Snow 1977; Prum unpubl. obs.
<i>P. chloromeros</i>	Niethammer 1956; L. Kinkel pers. comm. 1988
<i>P. mentalis</i>	Skutch 1949, 1969
<i>P. erythrocephala</i>	Snow 1962b; Lill 1976
<i>P. rubrocapilla</i>	Sick 1959, 1967