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# Sexual selection and the evolution of mechanical sound production in manakins (Aves: Pipridae)

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**Abstract.** I surveyed and described modulated, non-vocal, mechanical sounds of the lek-breeding Neotropical manakins (Pipridae). Variation among manakin species in mechanical sound production, repertoire size, acoustic structure, associated feather specialization, and mechanical sound production mechanisms were analysed comparatively in the context of a phylogenetic hypothesis for the family. Mechanical sound production has probably evolved five or six times independently and been lost once within the 42 species of manakins. Complex mechanical sound repertoires have also evolved independently several times. Acoustic structure of these sounds indicates that at least four different physical mechanisms of mechanical sound production have evolved: short, broad-frequency spectrum pulses; short, low-frequency pulses; aerodynamic vortices; and harmonic oscillations. All well-known mechanical sounds in manakins are associated with obvious wing movements and sexually dimorphic wing feather specializations. Both primary and secondary wing feather specializations have evolved convergently within the family for the production of short, broad-frequency mechanical sound pulses. Two less well-known manakin clades also have tail feather specializations that may function in mechanical sound production. A concentrated-changes test documented that the dynamic patterns of evolution in mechanical sound production in the polygynous manakins are highly unlikely by chance alone. Intersexual selection for acrobatic display may have created subsequent opportunities for the evolution of novel preferences for incidental non-vocal sounds produced by acrobatic movements. Novel female preferences for these mechanical sounds led to further elaboration of these sounds and to the evolution of complex mechanical sound repertoires in independent lineages of the family.

A diversity of avian species produce non-vocal, modulated mechanical sounds as intraspecific communication signals. The production of these sounds is modulated, or willfully controlled, by the bird. These sounds differ from two other classes of non-vocal sounds made by birds: incidental, involuntary physical sounds that have no communication function (e.g. bill snaps made while foraging); and involuntary, non-vocal sounds that may function in communication but that are not modulated by the individual (e.g. wing whistles produced in flight).

Modulated avian mechanical sounds can be produced by the wing feathers, tail feathers, bills or feet (Stettenheim 1976; Manson-Barr and Pye 1985). Information on mechanical sound production by birds is widely dispersed in the literature. With a few notable exceptions (Payne 1973, 1981; Bertram 1977; Winkler & Short 1978), avian mechanical sound production has received little analytical attention. The biophysical mechanisms, evolutionary origin and diversification of this interesting, alternative form of avian communication have received little study.

Darwin (1871) first proposed a causal association between sexual selection by female preference and the evolution of 'instrumental music' in birds, but the role of sexual selection in the evolution of avian mechanical sounds has never been tested. Mechanical sounds that are produced by the wing or tail feathers are often associated with display polygyny (such as grouse, Tetraonidae), acrobatic courtship display (such as snipe, *Gallinago*), very small body size (for example

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todies, *Todus*), or a combination of several of these factors (as in many hummingbirds, Trochilidae). In this study, I present a comparative analysis of mechanical sound variation in a polygynous clade, the manakins (Pipridae), and I test the hypothesis that sexual selection fosters the evolution of mechanical sound production in birds.

The Neotropical manakins (Pipridae) are a family of suboscine passerines that are well known for their sexually dimorphic plumage, lek breeding systems and elaborate courtship displays (Snow 1963a; Sick 1967; Prum 1990a, 1994). Many manakin species produce non-vocal mechanical sounds as part of their lek displays (Snow 1963a; Sick 1967; Prum 1990a). These sounds have been generally hypothesized to be produced by the wings, since most species that produce these sounds have obvious, sexually dimorphic variations in the remiges, or flight feathers (Chapman 1935; Snow 1963a; Sick 1967).

I describe the variation, repertoire, and acoustic structure of the known, non-vocal, modulated, manakin mechanical sounds, and I discuss the variations in wing feather shape, tail feather shape, and display movements that are associated with the production of these sounds. I then analyse this pattern of behavioural and morphological variation within the context of a phylogenetic hypothesis for the family (Prum 1992), and investigate the homology and evolution of manakin mechanical sounds, repertoires, and production mechanisms. Lastly, I test the hypothesis that sexual selection has fostered the evolution of mechanical sound production by examining the correlation between the phylogenetic distribution of mechanical sound production and polygynous lek display within the manakins and their close relatives.

## METHODS

Tape-recordings of manakin mechanical sounds were assembled from my own field recordings and from the collection of the Library of Natural Sounds, Cornell University. I analysed mechanical sounds from 15 species, including all but three species for which mechanical sounds have been described (Table I). When possible, the recordings of mechanical sounds were associated with descriptions of the behaviour of the bird during sound production. I surveyed museum specimens of all manakin species to identify specializations of the wing feathers that might be associated with sound production. Sources of behavioural descriptions and sound recordings are listed in the Appendix.

The acoustic structure of manakin mechanical sounds were analysed using Canary 1.2 (Charif et al. 1995). I analysed the phylogenetic distribution of (1) mechanical sound production, (2) repertoire size, (3) mechanical sound acoustic structure, and (4) associated flight feather specializations using a partially resolved phylogenetic hypothesis for the manakin clade based on a syringeal morphology (Prum 1992) and the MacClade computer program (Maddison & Maddison 1992). MacClade identifies the most parsimonious optimizations (hypotheses of character evolution) for a given trait within a hypothesis of phylogeny. Alternative, equally parsimonious optimizations imply different hypotheses of homology among mechanical sounds produced by various taxa. To examine these alternative hypotheses of homology critically, I present additional analyses of the phylogenetic variation in feather specializations and display movements associated with mechanical sound production, and the hypothesized mechanisms of mechanical sound production for each species. Based on this analysis, a specific, preferred hypothesis for the evolution of manakin mechanical sounds is supported (Fig. 6). I used this hypothesis to investigate: (1) the homology of manakin mechanical sounds; (2) the number of times that mechanical sound production evolved in the manakins; (3) the origin and history of complex mechanical sound repertoires; and (4) the history of evolution and convergence in morphological specializations, acoustic structure and potential mechanisms of mechanical sound production.

These analyses are conducted with a partially resolved, consensus hypothesis of phylogeny (Prum 1992). A partially resolved consensus tree can yield ambiguous hypotheses of character evolution (Maddison & Maddison 1992). These analyses conducted here, however, take into account the ambiguities in the unresolved branches of the manakin phylogeny. None of the hypotheses of character evolution would differ among the possible resolutions of these unresolved nodes.

**Table I.** Distribution and description of known mechanical sounds in manakins (Pipridae)

| Species | Mechanical sounds produced | Repertoire size | Acoustic structure* | Pulse number† | Wing feather specializations‡ | Tail feather specializations | Flight or perched§ |
|---|---|---|---|---|---|---|---|
| *Corapipo gutturalis* | + | 1 | BP | S | 1° | — | F |
| *Corapipo leucorrhoa* | ? | ? | ? |  | 1° | — | ? |
| *Corapipo heteroleuca* | + | 1 | BP | S | 1° | — | F |
| *Corapipo altera* | + | 1 | BP | S | 1° | — | F |
| *Masius chrysopterus* | — |  |  |  | — | — |  |
| *Ilicura militaris* | + | 3 | BP | S, M | 2° | — | F |
| *Machaeropterus deliciosus* | + | 2 | RF | M | 2° | — | P |
| *Machaeropterus regulus* | + | ? | ? | ? | 2° | + | P |
| *Machaeropterus pyrocephalus* | + | 1 | RF? | ? | 2° | + | P |
| *Manacus manacus* | + | 4 | BP | S, M | 1°, 2° | — | F, P |
| *Manacus vitellinus* | + | 4 | BP | S, M | 1°, 2° | — | F, P |
| *Manacus candei* | + | 4? | BP | S, M | 1°, 2° | — | F, P |
| *Chiroxiphia* (4 species) | — |  |  |  | — | — |  |
| *Antilophia galeata* | — |  |  |  | — | — |  |
| *Lepidothrix* (8 species) | — |  |  |  | — | — |  |
| *Xenopipo* (5 species) | — |  |  |  | — | — |  |
| *Dixiphia pipra* | — |  |  |  | — | — |  |
| *Heterocercus flavivertex* | + | 1 | AW | S | 1° | + | F |
| *Heterocercus linteatus* | ? | ? | ? | ? | 1° | + | ? |
| *Heterocercus aurantiivertex* | + | 2 | AW, BP? | S | 1° | + | F |
| *Pipra aureola* | + | ? | BP | S, M | 2° | — | F |
| *Pipra fasciicauda* | + | 2 | BP | S, M | 2° | — | F |
| *Pipra filicauda* | + | 2 | BP, LP | S, M | 2° | — | F |
| *Pipra cornuta* | + | 1? | BP | S, M | 2° | — | F |
| *Pipra mentalis* | + | 2 | BP | S, M | 2° | — | F, P |
| *Pipra chloromeros* | + | 2 | BP | S, M | 2° | — | F |
| *Pipra rubrocapilla* | — |  |  |  | — | — |  |
| *Pipra erythrocephala* | — |  |  |  | — | — |  |
| Ancestor/Outgroup | — |  |  |  | — | — |  |

*AW: aerodynamic whistle; BP: broad-frequency pulses; LP: low-frequency pulse; RF: resonant frequency.
†Number of pulses within a mechanical sound. S: single; M: multiple.
‡1°: primary remiges; 2°: secondary remiges.
§Mechanical sounds produced. F: in flight; P: while perched.

### Concentrated-changes Test

I tested the correlation between lek display and the evolution of mechanical sound production using the concentrated-changes test (Maddison 1990; Maddison & Maddison 1992). This test examines whether evolutionary changes in a dependent variable, mechanical sound production, are statistically correlated with a hypothesized independent variable, polygynous display behaviour, within a clade. To test adequately for a correlation between two traits, there must be sufficient variation in the independent variable (Maddison 1990). Since manakins are primitively lekking and include only one species known to form a pair bond (Marini & Cavalcanti 1993; Prum 1994), it was necessary to expand the test to include close relatives of manakins that lack the derived state of polygynous display behaviour.

The sister groups to the manakins are currently hypothesized to be the cotingas (Cotingidae) and tyrant flycatchers (Tyrannidae) (Superfamily Tyrannoidea; Prum 1990b; Sibley & Ahlquist 1990). The cotingas include 80–100 species, of which about one-third are polygynous, one-third monogamous, and one-third unknown breeding systems (Snow 1982). The tyrant flycatchers include over 375 species which are almost entirely monogamous and lack elaborate display behaviour. Unfortunately a completely resolved hypothesis of phylogeny, which is required for the concentrated-changes test, are not available for these groups. To estimate the effect of these sister groups on the correlation between polygynous display and mechanical sound production in the tyrannoid suboscines, I created two successive, simulated outgroups to the manakins which included 10 and 20 monogamous species, respectively, that lack mechanical sound production. These simulated outgroups are a very conservative estimate of the effect that the much more diverse and predominantly monogamous outgroups would have on the correlation. The topology of the outgroups was generated randomly using MacClade. A resolved hypothesis for the relationships among manakins was chosen arbitrarily from the equally parsimonious resolutions of the data (Prum 1992). I then used the simulation method of the concentrated changes test (with 1000 iterations) to estimate the probability by chance alone of the observed number of evolutionary changes in mechanical sound production among the lineages of the phylogeny characterized by polygynous display (Maddison & Maddison 1992).

## RESULTS

### Distribution and Repertoire Size

Modulated mechanical sounds are documented from 18 species of manakins in six of the 12 genera of the family: *Corapipo*, *Ilicura*, *Machaeropterus*, *Manacus*, *Heterocercus* and *Pipra* (Table I). Modulated mechanical sounds are probably produced by two additional, poorly known species, *Corapipo leucorrhoa* and *Heterocercus linteatus*, which have flight feather specializations that are similar to closely related mechanical sound producing species (see below). Mechanical flight sounds may be produced by a few other species of manakins (for example, *Chiroxiphia* and *Lepidothrix coronata*; M. S. Foster, personal communication) but these sounds are not well documented and are not mentioned in detailed descriptions of the display behaviour of these species. Without additional information, mechanical sound production is considered to be absent in these species.

The phylogenetic distribution of mechanical sound production in the manakins yields several equally parsimonious optimizations for the reconstruction of its evolutionary history (Fig. 1). Mechanical sound production can be interpreted as having either a single origin with several independent losses, or numerous independent origins and losses within the clade. These alternative hypotheses will be compared after the analysis of variation in the acoustic structure, associated feather specializations and display movements, and potential mechanical sound production mechanisms (see Phylogenetic Distribution and Homology).

Mechanical sounds are hypothesized to be distinct elements in a non-vocal sound repertoire if they are produced by a distinct physical movement and are different in acoustic structure (see below). The mechanical sound repertoires of *Machaeropterus*, *Heterocercus flavivertex*, *Corapipo gutturalis* and *Pipra cornuta* are characterized by a single known mechanical sound. In contrast, *Corapipo altera*, *C. heteroleuca*, *Ilicura militaris*,

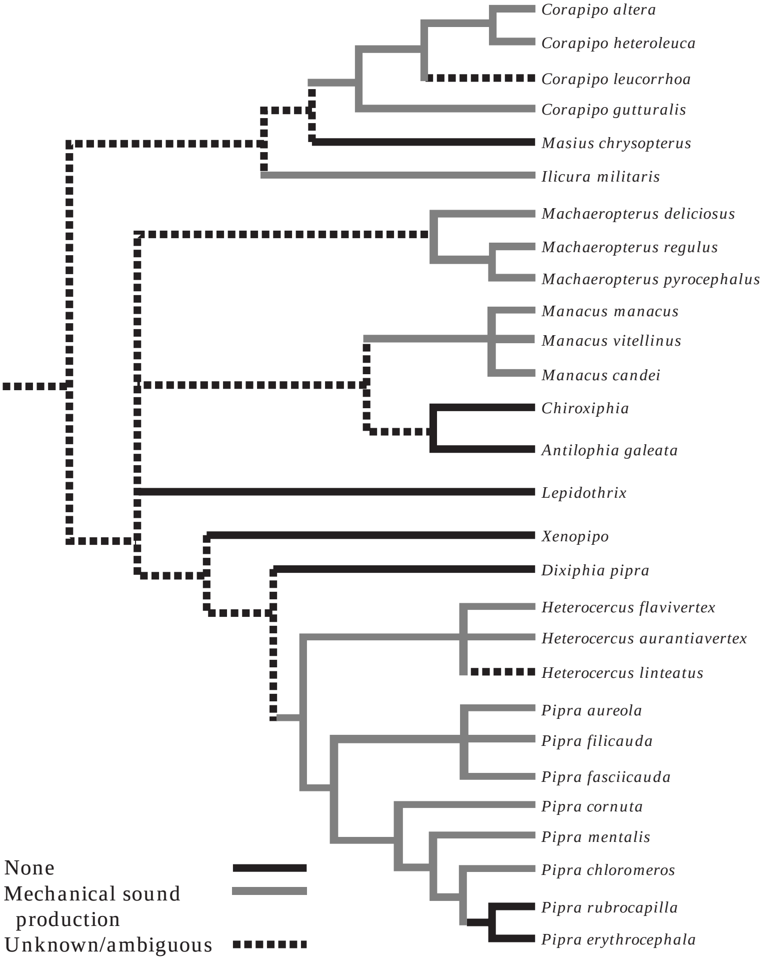

**Figure 1.** Phylogenetic distribution of mechanical sound production in the manakins. Dotted lines indicate that the history of character evolution in these lineages is ambiguous or unknown.

*Manacus*, *Heterocercus aurantiivertex*, the *Pipra aureola* clade, *P. chloromeros* and *P. mentalis* have repertoires of at least two to four distinct mechanical sounds (Table I; Fig. 2).

## Acoustic Structure

The acoustic structure of known manakin mechanical sound can be classified into four qualitatively distinct types: short, broad-frequency pulses; short, low-frequency pulses; aerodynamic ‘whooshes’; and harmonic sounds. Most manakin mechanical sounds are very short pulses of sound with a broad and continuous frequency spectrum from less than 1 kHz to more than 5–10 kHz (Fig. 3). The mechanical sounds of *Corapipo*, *Ilicura*, *Manacus* and *Pipra* are all characterized by short broad-frequency pulses.

Among short, broad-frequency pulses, different taxa differ in whether there are single or multiple pulses within one sound production event. *Corapipo gutturalis* produces only single-pulse mechanical sounds (Fig. 3a). The mechanical sounds of *Ilicura militaris* are characterized by a single pulse or by two to four pulses separated by 33–35 ms (Fig. 3b). The repertoire of all three species of *Manacus* includes a single-pulsed snap (Fig. 3c), and several whirring sounds that incorporate a series of 5–10 identical pulses that are 18–25 ms apart (Fig. 3d, e). *Pipra* species

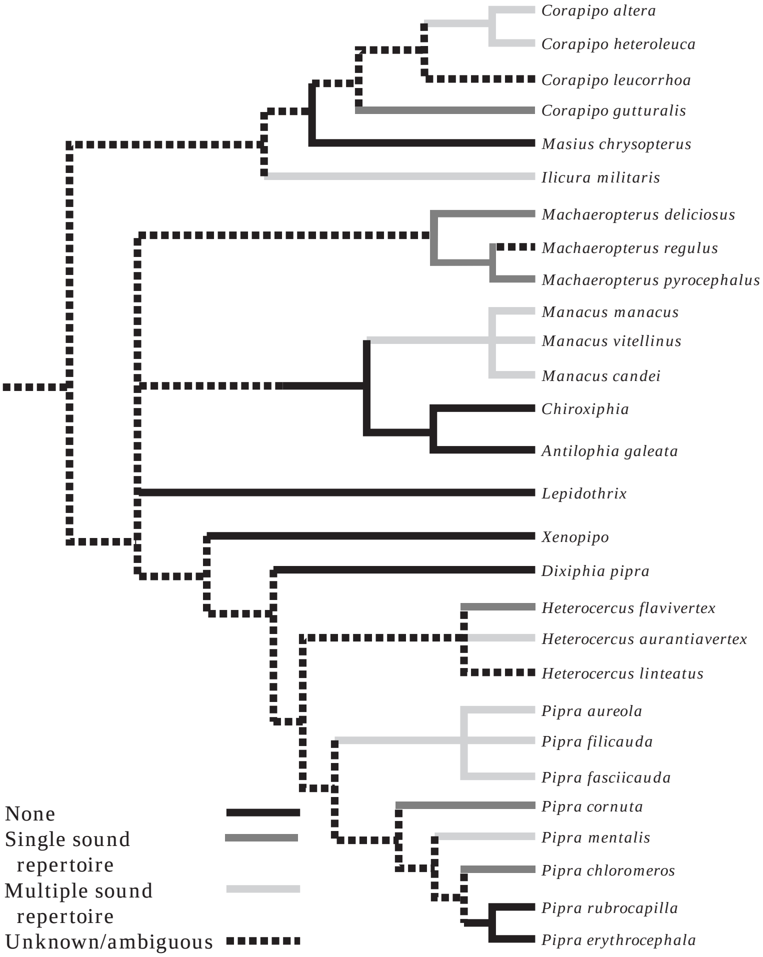

**Figure 2.** Phylogenetic distribution of single and multiple mechanical sound repertoires in the manakins.

produce both single pulse sounds, and sounds with two to four pulses separated by 5–17 ms (Fig. 3f). *Heterocercus aurantiivertex* produces a loud pop note that was not available for spectral analysis but which may be a short, broad-frequency spectrum pulse. *Corapipo altera*, *C. heteroleuca* and *Ilicura militaris* also produce modulated mechanical sound during noisy flights. Recordings of these sounds were not available for analysis, but descriptions of these sounds indicate that they may be composed of a series of short, broad-frequency pulses.

The mechanical ‘kloop’ sound produced by *P. filicauda* is characterized by a short, initial, broad-frequency pulse that is followed by a series of four short, very low-frequency pulses (<250 Hz). Each low-frequency pulse apparently corresponds to a single conspicuous wing beat during flight (Schwartz & Snow 1978). These short low-frequency pulses differ in acoustic structure from all other known manakin mechanical sounds. Similar sounds are not known in *P. aureola* and *P. fasciicauda*.

Two species of *Heterocercus* produce a hissing mechanical sound during a flight display that superficially resembles the ‘whoosh’ of an arrow approaching a target that is followed by a loud thud (Fig. 3g). These sounds are characterized by a prolonged (>0.25 s) band of a broad spectrum of low-frequency sound (0–4 kHz).

In *Machaeropterus deliciosus*, the mechanical sounds have a fundamental frequency of 1.4 kHz

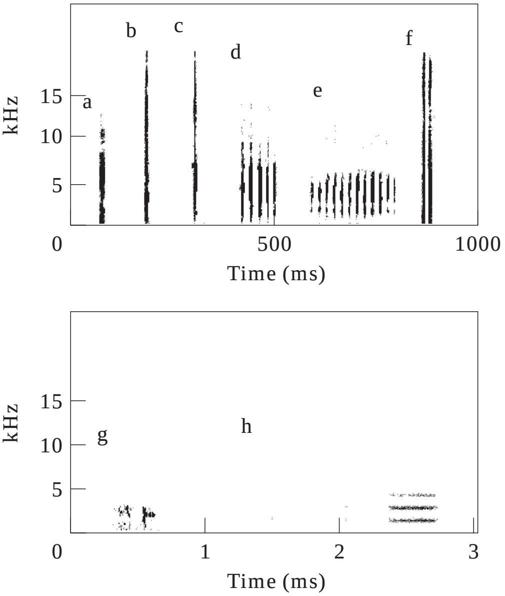

**Figure 3.** Spectrograms of mechanical sounds of manakins. Single, broad-frequency spectrum pulses: (a) *Corapipo gutturalis*, (b) *Ilicura militaris*, (c) *Manacus manacus*. Multiple, broad-frequency spectrum pulses: (d) 'whirr' of *Manacus manacus*, (e) 'whirr' of *Manacus candei*, (f) double-pulsed 'snap' of *Pipra cornuta*. Aerodynamic whistle: (g) *Heterocercus flavivertex*. Harmonic oscillations: (h) *Machaeropterus deliciosus*.

with discrete harmonics that are integer multiples of the fundamental frequency (Fig. 3h). These mechanical sounds include short notes of 20 ms and longer, sustained syllables of 400 ms. Harmonic mechanical sounds are unknown in any other birds. Available recordings of *M. pyrocephalus* include a 175-ms note with a pure fundamental frequency of 3.6 kHz and absolute integer harmonics that is strikingly similar to the known mechanical sounds of *M. deliciosus* in acoustic structure, but field observations indicate that this *M. pyrocephalus* sound is vocal (B. Whitney, personal communication). Recordings of mechanical sounds of *M. regulus* are not available, but they are described as an insect-like buzz (Sick 1959, 1967, 1993; J. Vielliard, personal communication).

## Flight Feather Specializations

All manakin species that produce mechanical sounds have sexually dimorphic specializations of the remiges (Table I; Fig. 4). In *Corapipo*, the outermost primary remiges have slightly thickened and curved rachi, or shafts; the outermost primary is significantly shortened and varies in length among the four species in the genus. In *Ilicura*, *Machaeropterus* and *Pipra*, the rachi of several secondary remiges are thickened and their barbs are stiffened. In *Machaeropterus*, the rachi of the sixth to tenth secondaries are tremendously thickened with reduced barbs; in *M. deliciosus*, the tips of the rachi are twisted. In *Manacus*, the outer four primaries are stiff and their outer webs are attenuate (narrow distally); the secondaries have thickened rachi and stiffened outer webs.

Another feather specialization that is associated with mechanical sound production are the thickened rachi found in the rectrices, or tail feathers, of *Machaeropterus pyrocephalus* and *M. regulus*. It is not known whether these sexually dimorphic rectrices function in mechanical sound production.

The source of the mechanical sounds in *Heterocercus* is unknown. Male *Heterocercus* have significantly longer primaries than females and both sexes have a derived, sexually monomorphic tail specialization, in which the outer rectrices are less than half the length and width of the inner rectrices (Prum et al. 1996). Either morphology could be theoretically associated with mechanical sound production, but only wing shape is sexually dimorphic.

## Display Movements Associated with Mechanical Sound Production

In most manakins, mechanical sounds are produced in flight (Table I). These in-flight mechanical sounds are produced during quick to-and-fro flights between perches (*Ilicura*, *Manacus* and *Pipra*), a sudden hop up from a perch (*Ilicura*, *Manacus*, *Heterocercus aurantiivertex* and *Pipra*), or during elaborate flight displays (*Corapipo*, *Heterocercus* and *Pipra aureola* clade). In *Manacus*, mechanical sounds in the repertoire are produced either while the birds are perched or in short flights between perches or a perch and the ground. *Heterocercus* species produce a unique continuous 'whoosh' mechanical sound while descending rapidly in an elaborate flight display (J. Alvarez, personal communication). Unlike most other manakins, mechanical sounds in *Machaeropterus* are produced while they are

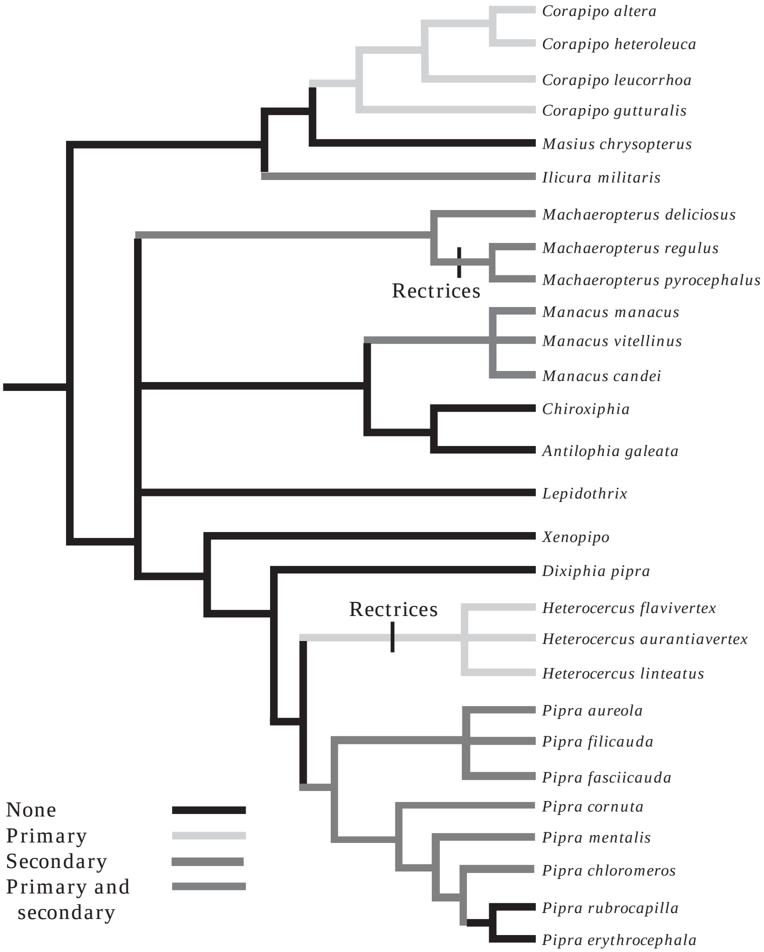

**Figure 4.** Phylogenetic distribution of primary and secondary wing feather specializations in the manakins. The presence of tail feather specializations (rectrices) is marked on two lineages.

perched or immediately after they arrive on a perch.

All well-known manakin mechanical sounds are associated with conspicuous wing flicks or wing movements (Appendix). Mechanical sounds produced in flight are associated with a sudden, rapid closing of the wings (*Ilicura*, *Manacus* and *Pipra*) or a conspicuous and distinctive flapping movement (*Corapipo* and *Pipra aureola* clade). In *Manacus*, the mechanical ‘whirr’ produced while they are perched is associated with a conspicuous ‘fanning’ of the wings. In *Machaeropterus deliciosus*, a mechanical sound is produced while they are perched by suddenly opening the wings above the back. In all of these cases, the association between a mechanical sound, a conspicuous wing movement and a sexually dimorphic specialization of the remiges support the conclusion that these sounds are made by the wings. Unfortunately, the movements associated with mechanical sound production have not been well described for those species with obviously specialized tail feathers: *Machaeropterus regulus*, *M. pyrocephalus* and *Heterocercus*.

## Sound Production Mechanisms

No research has been done on the physical mechanisms of mechanical sound production by bird feathers, but some basic inferences can be

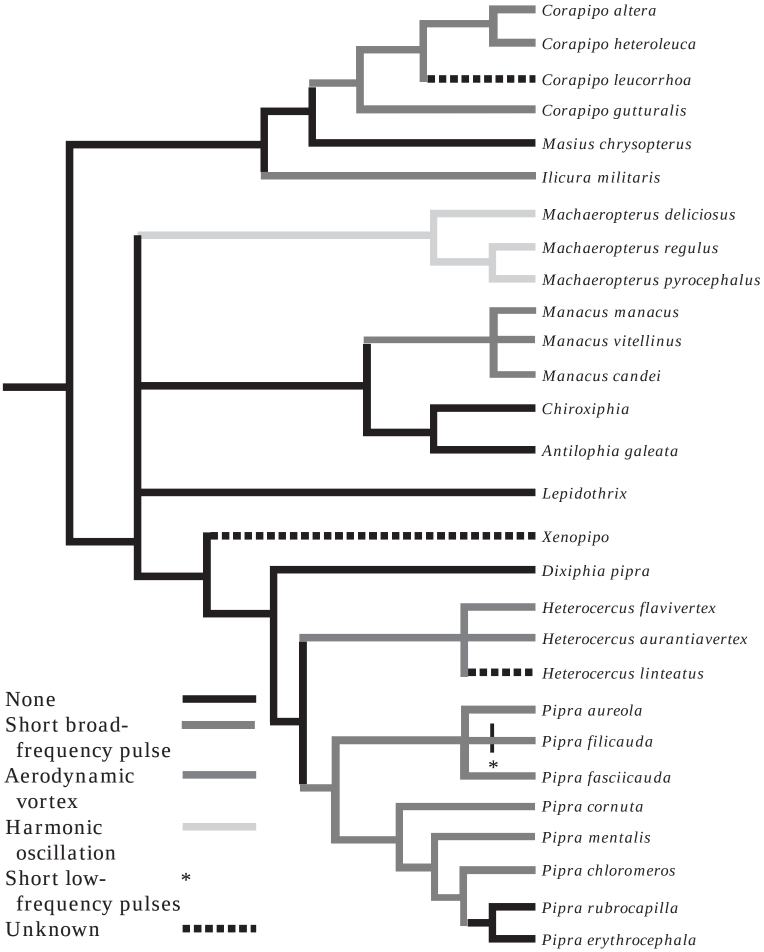

**Figure 5.** Phylogenetic distribution of hypothesized mechanical sound production mechanisms in the manakins. The presence of short, low-frequency pulses in *Pipra filicauda* is marked on that lineage.

made about the diversity of potential mechanical sound production mechanisms from the acoustic structure of the mechanical sound and movements associated with their production.

Short, broad-frequency spectrum pulses are the most prevalent type of mechanical sound in manakins (Table I; Fig. 5). Spectrograms of these sounds are essentially identical in form to percussive sounds (such as a finger snap). Short, broad-frequency pulses that are produced by rapidly opening and closing the wing (as in *Ilicura*, *Manacus* and *Pipra*) are probably produced by rapid clapping, or percussion, of the wing feathers against the body. Other short, broad-frequency pulses are produced by conspicuous wing movements during a sudden stall in flight or the nadir of a dynamic flight display (for example *Corapipo* and the 'klock' in the *Pipra aureola* clade). These mechanical sounds may be produced by a sudden compression of air by the wing or behind the wing when it is fully extended.

Small intervals between short, broad-frequency pulses of mechanical sound imply that these mechanical sounds may be produced by the left and right wings during a single movement (as in *Pipra*). Longer inter-pulse intervals may indicate that the multiple pulses are a result of a series of independent sound-producing movements (for example *Ilicura militaris*, *Manacus* and *Pipra mentalis*).

The short, low-frequency pulses produced by *Pipra filicauda* are like the short, broad frequency pulses of *Corapipo* in that they are produced during wing movements at the nadir of a flight display. These sounds are limited in frequency to below 250 Hz and are produced in multiple pulses. The production mechanism of the low-frequency pulses of *P. filicauda* is probably distinct.

The continuous ‘whoosh’ sounds in *Heterocercus* are produced during dramatic flight displays, and are most likely to be produced by aerodynamic vortices, or whistles, created by air rushing past the remiges or rectrices in flight.

The pure, continuous pitch and harmonic frequencies of the mechanical sounds in *Machaeropterus deliciosus* (and perhaps in *M. pyrocephalus*) indicate that they are produced by harmonic oscillations of the feathers (R. O. Prum & K. S. Bostwick, unpublished data). Aerodynamic vortices or whistles can be eliminated by the lack of rapid movement associated with the production of these sounds.

## Phylogenetic Distribution and Homology

The broad phylogenetic distribution of mechanical sound production in manakins indicates that mechanical sound production could have evolved one to five times independently in the clade with one to six reversals (Fig. 1). The acoustic, behavioural, morphological and functional variation in mechanical sound production among the manakins strongly supports the conclusion that sound production has evolved five or six times independently within the family with only a single loss, or reversal (Fig. 6).

The hypothesis that mechanical sound production evolved in the original common ancestor of the manakins requires a single origin and six independent losses of mechanical sound production to describe the current distribution of this behaviour. This hypothesis requires that all of the heterogeneous mechanical sounds produced by manakins are historical homologues and have diversified from a single, original mechanical sound within the family. When hypotheses of homology or convergence are equally parsimonious, the strength of the initial, or primary, hypothesis of homology is the only available criterion for differentiating the two alternatives (Pinna 1991). The diversity in acoustic structure, associated movements, feather specializations and probable production mechanisms does not support homology among all manakin mechanical sounds (Table I; Figs 2–5). These sounds are non-vocal acoustic signals that are probably produced by the remiges, but they have few other details in common. Furthermore, if all manakin mechanical sounds were homologues, then frequent additional evolutionary changes would have been required in acoustic structure, production mechanisms, and associated wing feather specializations. It is more parsimonious to hypothesize that manakin mechanical sounds that differ significantly in detail are not homologues, but evolved independently within different lineages.

At lower phylogenetic levels, mechanical sounds found in closely related genera could be homologues, but in most cases, differences between these signals do not support their homology. The mechanical sounds in *Corapipo* and *Ilicura militaris* can be parsimoniously hypothesized to be either homologous or independently evolved (Fig. 1). The hypothesis of homology requires that mechanical sound production has been lost secondarily in *Masius chrysopterus*. The mechanical sounds of the two genera are similar in acoustic structure, but *Corapipo* and *Ilicura* have very different wing feather specializations and probably differ in mechanical sound production mechanisms. Although these genera share a large number of display element homologues (Snow & Snow 1985; Prum & Johnson 1987; Prum 1990a), the display elements associated with the production of these mechanical sounds are different. The differences between the two genera indicate that their mechanical sounds are not homologous but convergently evolved. *Corapipo altera*, *C. heteroleuca* and *Ilicura militaris* also produce an additional modulated mechanical sound in flight. These poorly known mechanical sounds are unlikely to be homologous since they are absent in both *Masius chrysopterus* and *Corapipo gutturalis*.

The phylogenetic relationship of *Machaeropterus* to the clade including *Manacus*, *Antilophia* and *Chiroxiphia* is not resolved (Prum 1992). The absence of modulated mechanical sounds in *Antilophia* and *Chiroxiphia*, and the striking differences in the acoustic structure and production mechanism of the mechanical sounds of *Machaeropterus* and *Manacus* indicate that they are probably independently evolved from one another.

**Figure 6.** Best supported hypothesis of evolution of mechanical sound production in the manakins. Variation among lineages in mechanical sound acoustic structure, associated feather specializations, display movements and hypothesized sound production mechanisms supports this optimization of the phylogenetic history for mechanical sound production in manakins (see text).

If the mechanical sound of these two genera were homologous, then that would imply that mechanical sound had been lost in *Antilophia* and *Chiroxiphia*.

*Heterocercus* and *Pipra* are hypothesized to be sister taxa, and both genera produce mechanical display sounds. These sounds differ in acoustic structure, production mechanism and associated feather specializations, and are probably independently evolved in these two sister taxa.

In contrast, the mechanical sounds of the *Pipra aureola* and *P. erythrocephala* clades share similarities in acoustic structure, production mechanism, and feather specializations, and are likely to be homologues. The absence of mechanical sound production in the behavioural repertoires of *P. erythrocephala* and *P. rubrocapilla* constitutes an evolutionary loss of mechanical sound production, which initially evolved in the common ancestor of the genus *Pipra*.

## Concentrated-changes Test

Five or six independent derivations and one loss in mechanical sound production are probably required to explain the variation in mechanical sound production in manakins. The manakins are primitively polygynous and lekking (Prum 1990a, 1994). Only one manakin species has a pair bond (Marini & Cavalcanti 1993). Using two successive, simulated outgroups of 10 and 20 non-lekking species that lack mechanical sound production (Maddison & Maddison 1992), the probability of the observed correlation between polygynous display and the evolution of mechanical sound production is less than 0.022.

In the absence of resolved phylogenies of the outgroups, these simulated outgroups are a very conservative estimate of the effect of variation in the breeding system of tyrannoids on the observed correlation. If a resolved phylogeny for the more than 400 non-lekking outgroup taxa that lack mechanical sound production were included in the test, the strength of the correlation between display polygyny would become incalculable. The proposed correlation would be further strengthened by the observation of three to five additional derivations of mechanical sound production in cotingas that are all positively correlated with display polygyny. Mechanical sound production is known in three genera of cotingas (*Rupicola*, *Phoenicircus* and *Cotinga*), and is suspected in two others because of their sexually dimorphic wing feather specializations (*Chirocylla* and *Laniisoma*). *Rupicola*, *Phoenicircus* and *Cotinga* are all polygynous and have elaborate arena or lek display breeding systems (Snow 1982; Trail & Donoghue 1991). The breeding systems of *Chirocylla* and *Laniisoma* are unknown, but they are both most closely related to polygynous genera (Snow 1982; Prum & Lanyon 1989).

## DISCUSSION

### Mechanical Sound Production in Manakins

Alternative, non-vocal modes of acoustic communication have had a dynamic evolutionary history in the polygynous manakin clade. The phylogenetic distribution and acoustic structure of manakin mechanical sounds, and the variation in associated feather specializations indicates that mechanical sound production has evolved five or six independent times and has been lost once within the 42 species in the family (Fig. 6). In addition, diverse repertoires of multiple mechanical sounds have evolved independently numerous times (Fig. 2). In some lineages (such as *Ilicura* and *Manacus*), multiple sound repertoires apparently evolved in the same lineage as the origin of mechanical sound production, whereas in other cases (as in *P. filicauda*) complex repertoires evolved and diversified subsequent to the origin of mechanical sound production in earlier, ancestral lineages.

Many manakin mechanical sounds are convergent in their acoustic structure. Short, broad-frequency pulses have apparently evolved independently four times. *Ilicura*, *Manacus* and *Pipra* have also convergently evolved sounds that incorporate rapid repetitions of these pulses. Unique, low-frequency pulses have evolved in *P. filicauda*. Longer, sustained mechanical sounds are found in *Heterocercus* and *Machaeropterus*. The former is probably produced by an aerodynamic whistle, and the latter are resonant sounds produced by harmonic oscillations of some kind.

Of the six instances of mechanical sound production in manakins, three involve primary feather specializations, two involve thickening and reinforcement of the secondary feathers, and one case involves both. Both primary and secondary feather specializations are independently associated with the production of short, broad-frequency pulses, the most prevalent type of mechanical sound in manakins.

All manakins that produce mechanical sounds have sexually dimorphic wing feather specializations. Mechanical sounds in *Machaeropterus regulus*, *M. pyrocephalus* and *Heterocercus* are also associated with specialized tail feathers. Without additional observations, it appears unlikely that the thickened rectrices in *Machaeropterus* function in sound production, given that the closely related *M. deliciosus* produces a homologous, resonant mechanical sound without any tail feather specializations. Additional observations or experimental work will be required to identify the source of mechanical sounds in *Heterocercus*.

Most manakin mechanical sounds are additions to an acoustic repertoire of vocal sounds. In contrast, *M. deliciosus* use their resonant mechanical sounds as the exclusive lek advertisements calls (Willis 1966; personal observations; K. Bostwick, personal communication). The only known vocalizations in *M. deliciosus* are simple alarm calls or intermale aggressive calls (personal observations; K. S. Bostwick, personal communication). Like other manakins, *M. regulus* has both a prominent vocal advertisement call in addition to its mechanical display sounds (personal observations; B. Whitney, personal communication). The extreme reduction in vocal function is derived in *M. deliciosus*. The loss of vocal function with corresponding elaboration of mechanical sound production is an extreme example of the evolution of alternative acoustic communication function. Interestingly, the genus *Machaeropterus* is characterized by a reduction in syringeal muscle complexity (Prum 1992). In particular, *M. deliciosus* has almost no syringeal musculature (Prum 1992).

## Sexual Selection and Mechanical Sound Evolution

All manakin mechanical sounds are sexually dimorphic elements of polygynous courtship display repertoires. The concentrated-changes test indicates that the correlation between polygynous display behaviour and the origin of mechanical sound production in manakins and related tyrannoids is much stronger than would be expected by chance alone. Only 30 monogamous species without mechanical sounds among the near sister taxa of manakins are required to render the observed association significant. In fact, the cotingas and tyrant flycatchers include an order of magnitude more of such species.

Polygyny itself is not hypothesized to be causally related to the evolution of mechanical sound production. Rather, the simplest explanation of the observed phylogenetic association is that intersexual selection, which is a consequence of lek polygyny, has caused the frequent convergent evolution of mechanical sound production in manakins. The observed association could be a consequence of some other difference between manakins and tyrant flycatchers, such as diet or foraging mode. However, the close logical association between the independent variable (breeding system) and the dependent variable (mechanical sound production) in this analysis makes any other selective explanation less likely.

The causal association between sexual selection and the evolution of mechanical sound production is further strengthened by the observation that mechanical sounds have continued to diversify after the origin of mechanical sound production in most lineages. For example, the ‘whirr’ of *Manacus candei* from northern Central America differs significantly in a greater number of pulses (seven to nine) than the ‘whirrs’ of *M. vitellinus* or *M. manacus* populations (three to five pulses) throughout the rest of the Neotropics. After the ‘whirr’ sound evolved in the ancestor of *Manacus*, it has continued to diversify among species in the genus. Similar interspecific variation is also documented in *Pipra*. Furthermore, once mechanical sound production has evolved, the majority of manakin lineages have evolved multiple mechanical sound repertoires (Fig. 2). In an extreme case (*Machaeropterus deliciosus*), the mechanical sound advertisement has evolved to replace the primitive, vocal mode of acoustic advertisement and apparently resulted in a loss of syringeal complexity associated with vocalization (Prum 1992).

The probable role of sexual selection in the evolution of mechanical sound production in manakins allows us to examine more specifically the mechanism by which this novel mode of communication has arisen. Sexual selection on polygynous display behaviour often results in selection for novel preferences for new morphological traits. For example, phylogenetic patterns in manakin display elements and plumages indicate that novel display elements evolve before the morphological traits that are prominently featured in those displays (Prum 1990a). The evolution of a novel display provides opportunities for the evolution of female preferences for novel plumage traits that would be featured in that display.

Similarly, female choice for acrobatic male display elements in manakins may have created incidental acoustic variations among males that were a consequence of these movements. Rapid flight, hops, rapid changes in flight direction, or sudden stops or ‘stalling’ in flight can produce incidental sounds. Such sounds may occur more frequently in small-bodied birds with high wing loadings like manakins. The evolution of novel preferences for specific variations of these incidental non-vocal sounds could have led to the evolution of modulated mechanical sounds. As predicted by this model, manakin mechanical sounds are produced by conspicuous, acrobatic movements in five of six mechanical sound producing lineages. Since these elaborate physical display elements have probably evolved by intersexual selection, it is reasonable to hypothesize that the associated mechanical sounds have a similar evolutionary origin.

This analysis identified one unambiguous case of the loss of mechanical sound production in

**Table II.** Distribution of modulated mechanical sound production in the passerine birds (Passeriformes), and its association with three other traits

| Family | Genus | Polygynous display | Aerial flight–song display | Small body size | References |
|---|---|---|---|---|---|
| Eurylaimidae | *Smithornis* | * | * | | 1–3 |
| | *Neodrepanis* | | | * | 4 |
| Cotingidae | *Phoenicircus* | * | * | | 5 |
| | *Rupicola* | * | * | | 6 |
| | *Cotinga* | * | * | | 6 |
| | *Gymnoderus* | * | | | 14 |
| | *Chirocylla* | * | | | 6 |
| | *Laniisoma* | * | | | 6 |
| Pipridae | (See Table I) | * | | | |
| Alaudidae | *Mirafra* | | * | | 3, 7–9 |
| | *Certhilauda* | | * | | 3 |
| Meliphagidae | *Prosthoderma* | | | | 10 |
| Sylviidae | *Cistocola* | | * | * | 3, 11 |
| Paradisaeadae | *Macgregoria* | * | | | 12 |
| | *Lycocorax* | * | | | 12 |
| | *Manucodia* | | | | 12 |
| | *Ptiloris* | * | | | 12 |
| | *Astrapia* | * | | | 12 |
| | *Paradisaea* | * | | | 12, 13 |
| Ptilonorhynchidae | *Chlamydera* | * | | | 12 |

*Indicates that mechanical sounds in that genus are associated with that trait.
1: Lawson 1961; 2: Brossert & Erard 1986; 3: Keith et al. 1992; 4: personal observations; 5: Trail & Donohue 1991; 6: Snow 1982; 7: Serle 1943; 8: Payne 1973, 1981; 9: Bertram 1977; 10: Onley 1986; 11: Lynes 1930; 12: Gilliard 1969; 13: Frith 1982; 14: S. Robinson, personal communication.

manakins, the *Pipra erythrocephala–rubrocapilla* clade. The explanation for this loss in not clear. *Pipra erythrocephala* and *P. rubrocapilla* have similar display repertoires, display sites, and habitats to other *Pipra* species. However, these two species have a derived, smaller body size than other species of *Pipra*; selection for smaller body size may have resulted in a loss of mechanical sound production ability. In any case, this result indicates that sexual selection may result in the loss of behavioural complexity as well as create behavioural diversity.

## Mechanical Sound Evolution in Other Birds

A thorough review of mechanical sound production in birds is difficult because description of these behaviours are obscurely placed in natural history literature. Furthermore, many observers have not commented on whether these sounds are modulated or merely incidental to other movements. Based on current information (e.g. Stettenheim 1976; Manson-Barr & Pye 1985), however, this alternative, non-vocal mode of acoustic communication is relatively rare among passerines and other birds. The dynamic patterns of mechanical sound production evolution in manakins are highly unusual among birds.

Among the more than 5000 species of passerine birds (Passeriformes), reports of modulated mechanical sounds could be found for only 19 genera in seven families (Table II). It is difficult to infer the number of times mechanical sound production has evolved in these groups without detailed phylogenetic hypotheses, but these cases probably constitute between 9 and 18 independent origins of mechanical sound production. This simple survey implies that between one-third and one-quarter of instances of mechanical sound evolution in the passerine birds are members of the tiny manakin clade that includes less than one-hundredth of the species in the order.

As in the manakins, sexual selection on acrobatic, polygynous display behaviour is associated with most other instances of mechanical sound production in passerine birds. Among the 18 other genera of passerines that are known to produce modulated mechanical sounds, 10 genera are lekking, highly polygynous, or suspected of being polygynous (Table II). Thus, intersexual selection is the most generalized causal explanation of the evolution of mechanical sound production in passerines.

In at least some of the other six non-polygynous genera of passerines with mechanical sound production, mechanical sound production is still sexually dimorphic and may have evolved by inter- or intrasexual selection (Table II). In *Mirafra*, *Certhilauda* (Alaudidae) and *Cistothorus* (Sylviidae), males establish pair bonds and produce mechanical wing sounds during extended aerial flight-song displays. These species all live in open, grassy habitat, and these mechanical sounds have probably evolved through inter- or intrasexual selection on incidental noises produced during prolonged flight-song displays. Male *Neodrepanis* (Eurylaimidae) produce a modulated wing sound with specialized primaries (personal observation). *Neodrepanis* breed in an established pair bond (personal observation) but they have sexually dimorphic ornamental plumage and caruncles. Mechanical sound production in *Neodrepanis* may have evolved from sexual selection on variation in flight sounds that are an incidental consequence of very small body size (<7 g).

Outside of the passerines, most of the conspicuous, well-known examples of mechanical sound production are also found in polygynous groups with elaborate courtship display and no paternal care: for example, grouse (Tetraonidae), woodcock (*Scolopax*) and snipe (*Gallinago*, Scolopacidae), hummingbirds (Trochilidae) and the lyre-tailed honeyeater (*Melichneutes*, Indicatoridae). Others examples of mechanical sound production occur in sexually dimorphic advertisements that are associated with aerial courtship display: for example, piping guans (*Pipile*, *Aburria*, Cracidae). The cases of sexually monomorphic mechanical sound production, as in todies (Todidae), are a rare exception (Kepler 1977). Most of these species have relatively high wing loadings (mass per wing area) that are associated with explosive but inefficient flight (Rayner 1988). This inefficiency may result in incidental noises that can become subject to subsequent sexual selection.

Like the majority of manakin mechanical sounds, mechanical sounds in many other birds are short, broad-frequency spectrum pulses. Within passerines, *Neodrepanis*, *Smithornis*, *Mirafra* and *Cistothorus* have this acoustic structure, and among non-passerines, the mechanical sounds of hummingbirds and todies are also composed of short pulses (Kepler 1977). Aerodynamic vortices, or whistles, that are convergent with the manakin *Heterocercus* have evolved in the cotingas *Rupicola* and *Phoenicircus* (Trail & Donohue 1991), and probably in the many ‘rustling silk’ sounds of the birds of paradise (Gilliard 1969). The resonant, harmonic mechanical sounds found in *Machaeropterus* manakins are apparently unique in acoustic structure and production mechanism.

The best known example of an avian mechanical sound is drumming, a territorial and courtship communication that evolved in the woodpeckers and piculets (excluding the wryneck, *Jynx*; Short 1982). Drumming apparently evolved as a consequence of selection for a novel communication function on variation in incidental noises produced by bark and dead-wood foraging.

## Conclusions

Intersexual selection has apparently caused the evolutionary origin and diversification of alternative acoustic communication mechanisms in manakins and other birds. Intersexual selection has had a similar role in the evolution of alternative modes of communication in other animals. For example, several genera of moths produce ultrasonic intersexual advertisements by wing movements (Bailey 1991). Ultrasound production in moths probably evolved from primitive pheromone-dispersing wing movements. As in manakins, sexual selection on incidental noises produced during pheromone advertisement led to the evolution of an entirely novel mode of communication (Bailey 1991). Bailey hypothesized that insect acoustic behaviour has evolved by sexual selection on incidental sounds produced by other, primitive advertisement, displacement or combat behaviours.

These general evolutionary patterns across phyla demonstrate the importance of mate choice in the diversification of communication behaviour. This process proceeds unpredictably by taking advantage of incidental properties of primitive behaviours. Derived forms of communication are then contingent upon incidental opportunities presented by primitive behaviours. In this manner, sexual selection can produce a historical cascade of increasing complexity in communication behaviour.

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## APPENDIX

List of available citations (**C**) about display behaviour for each species of the Pipridae, and sources of mechanical sound recordings (**R**) analysed for known mechanical sound producing species (MSs). Classification follows Prum (1992) except with the recognition of *Corapipo altera* and *C. heteroleuca* as distinct species from *C. leucorrhoa*. *LNS*: Cornell University Laboratory of Ornithology Library of Natural Sounds.

*Corapipo gutturalis*. (**C**) Davis 1949; Davis 1982; Prum 1986; Théry 1990. (**R**) R. O. Prum; T. H. Davis, LNS uncatalogued.
*Corapipo leucorrhoa*. No information available.
*Corapipo heteroleuca*. (**C**) Aldrich & Bole 1937; Skutch 1969; Slud 1967; Wetmore 1972.
*Corapipo altera*. (**C**) L. Roselli, personal communication. (**R**) LNS 25668-9, 25809.
*Masius chrysopterus*. (**C**) Prum & Johnson 1987. (**R**) R. O. Prum.
*Ilicura militaris*. (**C**) Sick 1959, 1967; Snow & Snow 1985. (**R**) LNS 32188.
*Machaeropterus deliciosus*. (**C**) Willis 1966; Orejuela et al. 1982; R. O. Prum, unpublished observations. (**R**) K. Bostwick, R. O. Prum.
*Machaeropterus regulus*. (**C**) Sick 1959, 1967; Skutch 1969; R. O. Prum, unpublished observation.
*Machaeropterus pyrocephalus*. (**C**) Sick 1959, 1967. (**R**) LNS 12868, 13393 (possible MSs).
*Manacus manacus*. (**C**) Snow 1962a; Lill 1974a, b. (**R**) LNS 7311, 29313, 29322, 38860, 38902; R. O. Prum.
*Manacus vitellinus*. (**C**) Chapman 1935; Wetmore 1972. (**R**) LNS 27256, 28214.
*Manacus candei*. (**R**) LNS 7306-8, 28159.
*Chiroxiphia linearis*. (**C**) Aldrich & Bole 1937; Slud 1957; Wetmore 1972; Foster 1977a; McDonald 1989; Trainer & McDonald 1993.
*Chiroxiphia lanceolata*. (**C**) Friedmann & Foster 1955; Wetmore 1972.
*Chiroxiphia pareola*. (**C**) Gilliard 1959; Snow 1963a, 1971.
*Chiroxiphia caudata*. (**C**) Sick 1942; Snow 1976; Foster 1977b, 1981.
*Antilophia galeata*. (**C**) Sick 1959, 1967; Marini & Cavalcanti 1993; R. O. Prum, unpublished observations.
*Lepidothrix serena*. (**C**) Prum 1985; Théry 1990.
*Lepidothrix suavissima*. No information available.
*Lepidothrix isidorei*. No information available.
*Lepidothrix coeruleocapilla*. No information available.
*Lepidothrix coronata*. (**C**) Skutch 1969; R. O. Prum, unpublished observations.
*Lepidothrix nattereri*. No information available.
*Lepidothrix vilasboasi*. No information available.
*Lepidothrix iris*. No information available.
*Xenopipo unicolor*. No information available.
*Xenopipo flavicapilla*. No information available.
*Xenopipo holochlora*. No information available.
*Xenopipo uniformis*. No information available.
*Xenopipo atronitens*. (**C**) Sick 1959, 1967, 1993.
*Dixiphia pipra*. (**C**) Snow 1961; R. O. Prum, unpublished observations.
*Heterocercus linteatus*. (**C**) Sick 1959, 1967, 1993.
*Heterocercus flavivertex*. (**C**) Prum et al. 1996. (**R**) R. O. Prum.
*Heterocercus aurantiivertex*. (**C**) J. Alvarez, personal communication; R. O. Prum, unpublished observations.
*Pipra aureola*. (**C**) Snow 1963b.
*Pipra fasciicauda*. (**C**) Robbins 1983, 1985.
*Pipra filicauda*. (**C**) Schwartz & Snow 1978. (**R**) LNS 28535.
*Pipra cornuta*. (**C**) Snow 1977; R. O. Prum, unpublished observations. (**R**) R. O. Prum.
*Pipra chloromeros*. (**C**) Niethammer 1956; J. Tello, personal communication. (**R**) LNS 12831, 17838, 18165; J. Tello.

*Pipra mentalis*. (**C**) Skutch 1949, 1969. (**R**) LNS 7316, 7318, 28430, 31394.

*Pipra erythrocephala*. (**C**) Snow 1962b; Lill 1976.

*Pipra rubrocapilla*. (**C**) Sick 1959, 1967.

## REFERENCES

Aldrich, J. W. & Bole, B. P., Jr. 1937. Birds and mammals of the western slope of the Azuero Peninsula. *Scient. Publs Cleveland Mus. nat. Hist.*, **7,** 1–196.

Bailey, W. J. 1991. *Acoustic Behaviour of Insects: An Evolutionary Perspective*. London: Chapman & Hall.

Bertram, B. C. R. 1977. Variation in the wing-song of the flappet lark. *Anim. Behav.*, **25,** 165–170.

Brossert, A. & Erard, C. 1986. *Les Oiseaux des Régions Forestières du Nord-Est du Gabon. Vol. 1*. Paris: Soc. Natn. Protect. Natr.

Chapman, F. M. 1935. The courtship of Gould's manakin (*Manacus vitellinus vitellinus*) on Barro Colorado, Canal Zone. *Bull. Am. Mus. nat. Hist.*, **68,** 471–525.

Charif, R. A., Mitchell, S. & Clark, C. W. 1995. *Canary. Version 1.2*. Ithaca, New York: Cornell Laboratory of Natural Sound.

Darwin, C. 1871. *The Descent of Man, and Selection in Relation to Sex*. London: John Murray.

Davis, T. A. W. 1949. Display of white-throated manakins *Corapipo gutturalis*. *Ibis*, **91,** 146–147.

Davis, T. H. 1982. A flight-song display of the white-throated manakin. *Wilson Bull.*, **94,** 594–595.

Foster, M. S. 1977a. Odd couples in manakins: a study of social organization and cooperative breeding in *Chiroxiphia linearis*. *Am. Nat.*, **11,** 845–853.

Foster, M. S. 1977b. Social organization and behaviour of the swallow-tailed manakin, *Chiroxiphia caudata*. *Natn. Geogr. Soc. Res. Rep.*, **1977,** 313–320.

Foster, M. S. 1981. Cooperative behaviour and social organization of the swallow-tailed manakin (*Chiroxiphia caudata*). *Behav. Ecol. Sociobiol.*, **9,** 167–177.

Friedmann, H. & Foster, F. D., Jr. 1955. A contribution to the ornithology of northeastern Venezuela. *Proc. U. S. natn. Mus.*, **104,** 463–524.

Frith, C. B. 1982. Displays of Count Raggi's bird of paradise *Paradisaea raggiana* and congeneric species. *Emu*, **81,** 193–201.

Gilliard, E. T. 1959. Notes on the courtship behaviour of the blue-backed manakin (*Chiroxiphia pareola*). *Am. Mus. Novit.*, **1942**, 1–19.

Gilliard, E. T. 1969. *Birds of Paradise and Bowerbirds*. Garden City, New York: Natural History Press.

Keith, S., Urban, E. K. & Fry, C. H. 1992. *The Birds of Africa. Vol. IV*. Boston: Academic Press.

Kepler, A. K. 1977. *Comparative Study of Todies: with Emphasis on the Puerto Rican Tody,* Todus mexicanus. Cambridge, Massachusetts: Nuttall Ornithological Club.

Lawson, W. J. 1961. Probable courtship behaviour of the broadbill *Smithornis capensis*. *Ibis*, **103,** 289–290.

Lill, A. 1974a. Sexual behaviour of the lek-forming white-bearded manakin (*M. manacus trinitatus* Hartert). *Z. Tierpsychol*, **36,** 1–36.

Lill, A. 1974b. Social organization and space utilization in the lek-forming white-bearded manakin, *M. manacus trinitatus* Hartert. *Z. Tierpsychol.*, **36,** 513–530.

Lill, A. 1976. Lek behaviour in the golden-headed manakin, *Pipra erythrocephala*, in Trinidad (West Indies). *Adv. Ethol.*, **18,** 1–83.

Lynes, H. 1930. Review of the genus *Cisticola*. *Ibis*, **6** (Supplement), 1–673.

McDonald, D. B. 1989. Cooperation under sexual selection: age graded changes in a lekking bird. *Am. Nat.*, **134,** 709–730.

Maddison, W. P. 1990. A method for testing the correlated evolution on polytomous binary characters: are gains or losses concentrated on certain branches of a phylogenetic tree? *Evolution*, **44,** 539–557.

Maddison, W. P. & Maddison, D. R. 1992. *MacClade*. Sunderland, Massachusetts: Sinauer.

Manson-Barr, P. & Pye, J. D. 1985. Mechanical sounds. In: *A Dictionary of Birds* (Ed. by B. Campbell & E. Lack), pp. 342–344. Staffordshire, England: Poyser.

Marini, M. A. & Cavalcanti, R. B. 1993. Foraging behaviour, diet, and possible monogamy of a sexually dichromatic manakin, *Antilophia galeata*. *Auk*, **109,** 911–913.

Niethammer, G. 1956. Zur Vogelwelt Boliviens (Teil II: Passeres). *Bonn. zool. Beitr.*, **7,** 84–150.

Onley, D. J. 1986. A method of ageing the tui (*Prosthederma novaeseelandiae*) and its use in assessing body measurements. *Notornis*, **33,** 45–49.

Orejuela, J. E., Cantillo, F. G. & Alberico, M. 1982. Observaciones del comportamiento reproductivo del saltarín *Allocotopterus deliciosus* (Familia Pipridae, Aves) en Nariño, Colombia. *Cespedesia* (Supplement 3) **42–43,** 69–79.

Payne, R. B. 1973. Wingflap dialects in the flappet lark *Mirafra rufocinnamomea*. *Ibis*, **115,** 270–274.

Payne, R. B. 1981. Persistance of local wingflap dialects in flappet larks, *Mirafra rufocinnamomea*. *Bull. Br. Ornithol. Club*, **101,** 507–511.

Pinna, M. C. 1991. Concepts and tests of homology in the cladistic paradigm. *Cladistics*, **7,** 367–394.

Prum, R. O. 1985. Observations of the white-fronted manakin (*Pipra serena*) in Suriname. *Auk*, **102,** 384–387.

Prum, R. O. 1986. The displays of the white-throated manakin *Corapipo gutturalis* in Suriname. *Ibis*, **128,** 91–102.

Prum, R. O. 1990a. Phylogenetic analysis of the evolution of display behaviour in the neotropical manakins (Aves: Pipridae). *Ethology*, **84,** 202–231.

Prum, R. O. 1990b. A test of the monophyly of the manakins (Pipridae) and of the cotingas (Cotingidae) based on morphology. *Occ. Pap. Mus. Zool. Univ. Michigan*, **723,** 1–44.

Prum, R. O. 1992. Syringeal morphology, phylogeny, and evolution of the neotropical manakins (Aves: Pipridae). *Am. Mus. Novit.*, **3043,** 1–65.

Prum, R. O. 1994. Phylogenetic analysis of the evolution of alternative social behaviour in the manakins (Aves: Pipridae). *Evolution*, **48,** 1657–1675.

Prum, R. O. & Johnson, A. E. 1987. Display behaviour, foraging ecology, and systematics of the goldenwinged manakin (*Masius chrysopterus*). *Wilson Bull.*, **87,** 521–539.

Prum, R. O. & Lanyon, W. E. 1989. Monophyly and phylogeny of the *Schiffornis* group (Tyrannoidea). *Condor*, **91,** 444–461.

Prum, R. O., Kaplan, J. A. & Pierson, J. D. 1996. Display behavior and natural history of the yellow-crowned manakin (*Heterocercus flavivertex*: Pipridae). *Condor*, **98,** 722–735.

Rayner, J. M. V. 1988. Form and function in avian flight. *Curr. Ornithol.*, **5,** 1–66.

Robbins, M. B. 1983. The display repertoire of the band-tailed manakin (*Pipra fasciicauda*). *Wilson Bull.*, **95,** 321–342.

Robbins, M. B. 1985. Social organization of the band-tailed manakin (*Pipra fasciicauda*). *Condor*, **87,** 449–456.

Schwartz, P. & Snow, D. W. 1978. Display and related behaviour of the wire-tailed manakin. *Living Bird*, **17,** 51–78.

Serle, W. 1943. Notes on East African birds. *Ibis*, **85,** 55–82.

Short, L. S. 1982 Woodpeckers of the World. Cinnaminson, New Jersey: Delaware Museum of Natural History.

Sibley, C. G. & Ahlquist, J. E. 1990. Phylogeny and classification of birds. New Haven, Connecticut: Yale University Press.

Sick, H. 1942. Die Balz von *Chiroxiphia caudata. Orn. Monatsber.* **50,** 18.

Sick, H. 1959. Die Balz der Schmuckvogel (Pipridae). *J. Ornithol.*, **100,** 269–302.

Sick, H. 1967. Courtship behaviour in manakins (Pipridae): a review. *Living Bird*, **6,** 5–22.

Sick, H. 1993. *Birds in Brazil*. Princeton, New Jersey: Princeton University Press.

Skutch, A. F. 1949. Life history of the yellow-thighed manakin. *Auk*, **66,** 1–24.

Skutch, A. F. 1969. Life histories of Central American birds. III. *Pacif. Coast Avifauna*, **35,** 1–580.

Slud, P. 1957. The song and dance of the long-tailed manakin, *Chiroxiphia linearis*. *Auk*, **74,** 333–339.

Slud, P. 1967. The birds of Costa Rica. *Bull. Am. Mus. nat. Hist.*, **128,** 1–430.

Snow, B. K. & Snow, D. W. 1985. Display and related behaviour of male pin-tailed manakins. *Wilson Bull.*, **97,** 273–282.

Snow, D. W. 1961. The displays of manakins *Pipra pipra* and *Tyranneutes virescens*. *Ibis*, **103,** 110–113.

Snow, D. W. 1962a. A field study of the black-and-white manakin, *Manacus manacus*, in Trinidad, West Indies. *Zoologica*, **47,** 65–104.

Snow, D. W. 1962b. A field study of the golden-headed manakin, *Pipra erythrocephala*, in Trinidad, West Indies. *Zoologica*, **47,** 183–198.

Snow, D. W. 1963a. The display of the blue-backed manakin, *Chiroxiphia pareola*, in Tobago, West Indies. *Zoologica*, **48,** 167–176.

Snow, D. W. 1963b. The display of the orange-headed manakin. *Condor*, **65,** 44–48.

Snow, D. W. 1971. Social organization of the blue-backed manakin. *Wilson Bull.*, **83,** 35–38.

Snow, D. W. 1975. The classification of the manakins. *Bull. Br. Ornithol. Club*, **95,** 20–27.

Snow, D. W. 1977. The display of the scarlet-horned manakin *Pipra cornuta*. *Bull. Br. Ornithol. Club*, **97,** 23–27.

Snow, D. W. 1982. *The Cotingas*. Ithaca, New York: Cornell University Press.

Stettenheim, P. 1976. Structural adaptations in feathers. *Proc. Int. Ornithol. Congr.*, **16,** 385–401.

Thery, M. 1990. Display repertoire and social organization of the white-fronted and white-throated manakins. *Wilson Bull.*, **102,** 123–130.

Trail, P. W. & Donahue, P. 1991. Notes of the behaviour and ecology of the red-cotingas (Cotingidae: *Phoenicercus*). *Wilson Bull.*, **103,** 539–551.

Trainer, J. M. & McDonald, D. B. 1993. Vocal repertoire and its relation to male–male cooperation. *Condor*, **95,** 769–781.

Wetmore, A. 1972. *The Birds of Panama*. Part 3. Washington: Smithsonian Press.

Willis, E. O. 1966. Notes on a display and nest of the club-winged manakin. *Auk*, **83,** 475–477.

Winkler, H. & Short, L. L. 1978. A comparative analysis of acoustical signals in pied woodpeckers (Aves, *Picoides*). *Bull. Am. Mus. nat. Hist.*, **160,** 1–109.