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Delayed Plumage Maturation and Orderly Queues for Status: A Manakin Mannequin Experiment

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Abstract

Lek-mating male long-tailed manakins (*Chiroxiphia linearis*) move through three distinct, unambiguously age-specific, predefinitive (subadult) plumages, and do not attain the definitive ('adult') male plumage until their fourth year. Males form orderly, generally age-graded queues for rank in leks. The top-ranking (alpha and beta) males cooperate in courtship display, although only alphas copulate. Taxidermic model experiments tested the function of the 3-yr delay in plumage maturation. Reaction to a model manakin in female-like, first-year predefinitive plumage was stronger than that to a treatment control or a neutral species but weaker than that to a model manakin in definitive plumage. Reaction to the model manakins resembled mobbing choruses directed at model snakes, indicating that the reaction was a response to a potential threat. The results did not support female mimicry, juvenile mimicry, molt constraints or predator crypticity hypotheses for delayed plumage maturation. Decisive rejection of the first two hypotheses would require further experiments with model females and models of the other predefinitive stages. Nevertheless, none of the four hypotheses is sufficient to explain age-specific plumage stages. The results were, however, consistent with a status-signaling hypothesis that suffices to explain successive age-specific plumages. The reaction to models was often by non-alpha males, who had no opportunity for copulations. The presence of the models, therefore, appeared to pose a threat to the system of male-male alliances rather than a risk of stolen copulations. By choosing with high discrimination among leks (queues), females appear to enforce orderly male queuing. The predefinitive plumages, therefore, seem to function as age-specific badges of status that indicate a male is a queue entrant. The plumages mediate but do not eliminate aggression during the several years of becoming established in lek assemblages.

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Introduction

In a number of sexually dichromatic species of passerine birds, males do not attain the definitive male plumage in the breeding season following hatch. I use the term 'definitive' rather than 'adult', to avoid any implications concerning reproductive maturation. Likewise, I use the term predefinitive (FOSTER 1987)

rather than 'subadult' (ROHWER 1978) to describe any plumages worn by males during breeding seasons before they attain the definitive plumage. Most previous studies have focused on migratory, north temperate passerines, none of which delays plumage maturation for more than 1 yr.

Males of neotropical, frugivorous long-tailed manakins, *Chiroxiphia linearis* (Pipridae), delay plumage maturation for 3 yr (FOSTER 1987; McDONALD 1989 b). The transitional, predefinitive plumages form a distinctly age-graded series that allows human observers to distinguish age classes without ambiguity (McDONALD, unpubl.). No other genus in the family Pipridae has a delay of more than 1 yr; the congeneric swallow-tailed manakin, *Chiroxiphia caudata*, has a 2-yr delay (FOSTER 1987).

The problem of delayed plumage maturation (DPM) in long-tailed manakins is of particular interest because of the social context. They have both a lek mating system and male-male cooperation in courtship display. As in other lek mating systems (BRADBURY & ANDERSSON 1987), both male-male interactions (intrasexual selection) and female choice (intersexual selection) influence patterns of mating success (McDONALD 1989 a, b). Male-male interactions critical to the establishment of dominance and later mating success might depend upon interactions influenced by a male's age or status. Further, male-male cooperation in courtship display entails a complex network of male-male associations that persist for many years (McDONALD 1989 b). Long-term interactions of this sort provide ample opportunity for advantages conferred by transitional plumages acting as signals. For example, predefinitive plumage might reduce or eliminate aggression against the bearer during a protracted period of queuing for status in a lek.

The possible function of DPM during the breeding season has generated a number of both adaptive and nonadaptive hypotheses. To test various alternative hypotheses (predictions outlined below, summarized in Table 1), I presented taxidermic models of definitive (plumage of males ≥ 4 yr old) and predefinitive male long-tailed manakins at lek arenas in my long-term study area in Monteverde, Costa Rica. The reaction to models during trial experiments reminded me of mobbing choruses directed at potential predators such as owls or snakes. To test the hypothesis that the reaction to the models was one example of a more general response to potential threats, I also presented snakes made of modeling clay, with the same protocol used for presenting the taxidermic models and treatment controls. I also presented two types of control treatments — a stand of the same sort used in presenting the avian models, and a Swainson's thrush (*Catharus ustulatus*), as a representative neutral species.

Four major adaptive hypotheses and one nonadaptive hypothesis have been proposed to explain DPM. (1) ROHWER (1977) proposed that predefinitive plumage might function as a reliable signal of lower status that would mediate aggression against less competitive younger males. The hypothesis received support from a comparative analysis of DPM in north temperate passerines (LYON & MONTGOMERIE 1986). A prediction of this hypothesis is that males should be less aggressive toward predefinitive models than toward definitive models, but could be aggressive toward both model types. (2) ROHWER (1978) and FOSTER (1987) proposed a female mimicry hypothesis, whereby males in female-like

predefinitive plumages would gain opportunities for stolen copulations, or access to resources from which established males would exclude younger males but not females. Under this hypothesis, the reaction of males to models in female-like predefinitive plumage should resemble the reaction to females visiting the lek arena, thereby allowing predefinitive males access to lek arenas for stolen copulations or for learning from the behavior of successful males. Because lek arenas do not contain food resources, the hypothesis that female mimicry provides access to resources is not germane to long-tailed manakins. (3) The juvenile mimicry hypothesis of FOSTER (1987) is an adaptive hypothesis for DPM not applicable to north temperate species. Foster suggested that the later predefinitive plumages of male *Chiroxiphia* manakins constitute juvenile mimicry, whereby older predefinitive males, capable of posing a reproductive threat via stolen copulations, might mimic younger predefinitive males incapable of posing such a threat. Each of these first three hypotheses proposes a signaling function for predefinitive plumage. (4) SELANDER (1965) and PROCTER-GRAY & HOLMES (1981) hypothesized that predefinitive plumages might maintain crypticity, thereby reducing the risk of predation attributable to bright, definitive plumages. The hypothesis makes no prediction concerning reaction of males to models, but predicts higher predation pressure on males in definitive plumage. (5) As a nonadaptive hypothesis, ROHWER & BUTCHER (1988) proposed that DPM might increase overwinter survival at the cost of being maladaptive during the breeding season. Molt constraints, they suggested, might keep many north temperate passerines from attaining a more adaptive breeding plumage. This hypothesis is very unlikely to apply to long-tailed manakins, because several complete molts precede the attainment of definitive plumage.

It is tempting to seek a single comprehensive explanation for the functional significance of DPM. Studies of tropical species (e.g. GRANT 1990) broaden the ecological context, and provide additional evidence that the function of DPM may vary, depending on the mating system or the ecological context.

Materials and Methods

Natural History and Study Area

Long-tailed manakins are nonmigratory. I have studied a color-banded population in my 80-ha study area in Monteverde, Costa Rica (10°18'N, 84°48'W) since 1982 (MCDONALD 1989 b, 1993). Males cooperate in courtship displays that include unison 'toledo' calls to attract females, and dual-male backwards leapfrog dances (MCDONALD 1989 a, b). I define a 'lek' as the assemblage of males affiliated with a particular alpha male, and use 'lek arena' or 'perch-zone' to describe the physical location of display sites, which may include several dance perches. Courtship displays can occur in every month of the year except Nov., but activity is consistently high from Mar. to Jul. Each lek comprises an alpha male, to whom almost all copulations accrue, a beta male, who is the alpha male's primary partner for courtship display to females, and a variable number of auxiliary males, some of which may be affiliated with more than one lek. The network of male-male associations is complex, and associations persist for as much as 10 yr. Males are generally 7 yr of age or older before attaining beta status and move through the ranks in fairly orderly succession (MCDONALD 1989 b, 1993). The variance of male mating success is higher than any other yet reported for birds (MCDONALD 1989 b).

The units of replication were 10 different lek arenas within the study area. Each lek arena had a different alpha male, and the experiments took place at the primary dance perch. Although five of the beta males maintained affiliations with other leks included in the experiment, none simultaneously held the beta rank in any other lek. During the period of the experiment, 51 color-banded males were seen at the experimental lek arenas, and only a few unbanded males.

Males move through three age-specific predefinitive plumages before attaining the definitive plumage in their fourth year. Evidence from 56 color-banded predefinitive males (MCDONALD 1989 a, unpubl.) suggests a modification of the sequence described by FOSTER (1987) for this species. One year after hatch, males are all green, with a variable amount of red in the cap ('redcap'). Two yr after hatch, males have red caps and a black face ('black-face'). Three yr after hatch, males have slight to extensive blue in the back, but always retain at least a trace of green in wings or body ('blue-back'). Four yr after hatch, males have the fully red, black and blue definitive plumage. A simple, year-to-year developmental heuristic therefore summarizes the sequence: (1) add red (usually), (2) add black, (3) add blue, (4) take away green. FOSTER's (1987) suggested sequence differed in proposing that the first predefinitive plumage comprised males in black-face as well as redcap plumage, the second comprised males with $\frac{1}{2}$ blue in the back, and the third comprised males with $\frac{2}{3}$ blue in the back. No male in my study was consistent with FOSTER's sequence, while being inconsistent with the sequence presented here. The difference may be attributable to geographic variation in maturation schedules, or to FOSTER's having to rely on inferences from museum specimens in the absence of known-age birds.

Taxidermic Models and Experimental Treatments

Two males (window-killed mortalities) were prepared as taxidermic models in normal sitting postures. The leg wires were left long enough to wrap around a short stick, which could then be attached to saplings within 2 m of the dance perch. One of the models was in the redcap predefinitive plumage. The other was in the definitive plumage. Ideally, each repetition of a treatment would have employed a different model, to allow for reactions dependent upon the individual model, but collection of further models was not feasible. I also prepared a Swainson's thrush as a taxidermic model. I used bright green modeling clay with yellow stripes to produce a model snake, which somewhat resembled the snakes *Leptophis mexicanus*, *Oxybelis fulgidus* and *Bothrops lineatus*, all of which occur in the study area.

The treatments were of five types: (1) a stand of the same type to which the taxidermic models were attached, placed in the same location used during the taxidermic model presentations (stand-only treatment control, St); a taxidermically prepared Swainson's thrush (neutral species control, Th); (3) a

Table 1: Predictions of hypotheses tested

DPM hypotheses	Treatment reaction ranks; other predictions
Signal function	
Status signaling	St ^a) < Rc < De
Juvenile mimicry	St = Rc < De; males tolerate first-year but not older predefinitives.
Female mimicry	St = Rc < De; reaction to Rc resembles reaction to visiting females.
Crypticity	no predicted ranking; predation pressure greater on definitive males.
Molt constraints	no predicted ranking; no complete molts intervene between predefinitive and definitive stages.
Other hypotheses	
Wheooo chorus as threat response	Sn, reaction to model snake, qualitatively similar to, but possibly stronger than, reaction to other treatments that represent a threat to lek members.

^a) Symbols for reaction to treatments: St: reaction to stand-only treatment control; Rc: reaction to redcap predefinitive mount; De: reaction to definitive mount.

taxidermic model of a male in the redcap, predefinitive plumage, Rc; (4) a taxidermic model of a definitive male, De; (5) a model snake, Sn. All treatments were placed 1–2 m from the dance perch and observed for 1 h. For each of the five treatments, a temporal control observation (1 h) preceded the treatment observation (1 h). During the temporal control hour, with no treatment present, the same variables were monitored as during the presentations. The temporal control, therefore, assessed the background activity level at the time of the presentation. Predicted reactions of lek males to the five treatments are listed in Table 1.

Experimental Design and Analysis

I presented the five treatments in randomly assigned order at 10 different lek arenas (experimental units). One constraint on random assignment was that all the snake and thrush treatments took place in 1991, while the redcap and stand-only treatments took place in 1990. The two model manakin treatments and the stand-only treatments control were presented three times at each of the 10 lek arenas, and the mean of the three presentations was used. The snake and Swainson's thrush treatments were presented once at each lek arena. No more than one presentation occurred at a lek arena on any day, and an interval of 1–3 wk separated repeated presentations of the same treatment.

Control and treatment observations began upon the appearance of one or more lek members within the vicinity of the dance perch (≤ 25 m from the dance perch), as detected by either sighting or vocalization. The initiation criterion was intended to ensure that males would have the opportunity to respond to a treatment, were one present. If no males approached during an h of readiness for the temporal control observation or within an h following the presentation of the treatment, the run was aborted, and conducted on a subsequent day. Aborted runs occurred only six times in 116 presentations. The manakin model presentations and stand-only treatment controls took place between 3 May 1990 and 18 June 1990. The thrush, snake and further definitive male presentations took place between 18 May 1991 and 23 June 1991. Five lek arena substitutions were made in 1991 because of decreased activity at the lek arenas used in the 1990 presentations. Substitutes were matched with previously used lek arenas according to the similarity of their temporal control scores, and I tested for a lek arena (block) effect. To assess differences between years, I presented the definitive model at five lek arenas (one of the 1990 lek arenas plus four not previously used) during the 1991 presentations.

Table 2: Variables analyzed

Abbreviation	Description
$M \geq 3$	no. min ≥ 3 males present
$1/P$	inverse of closest approach during hour
≤ 5 m	no. min ≥ 1 male ≤ 5 m from mount/perch
Wheooo	total no. wheooo vocalizations
Whee	total no. whee vocalizations
Chorus	no. min with ≥ 10 wheooo or whee calls

Observers monitored behavior from blinds 8–12 m from the dance perch. Tape recorders or video cameras recorded vocalizations and observer comments. Following pilot experiments in 1989 and 1990, I monitored six variables, describing male proximity to the dance perch and attendance at the lek arena, male vocalizations, and the duration of multimale chorusing (Table 2). I used the inverse of the variable describing male proximity ($1/P$), so that the hypotheses in Table 1 called for one or more treatments to have higher values (stronger reactions) than controls on all variables. The 'wheooo' call is an onomatopoeic description of a two-syllable whistle, and the 'whee' call is a brief and sharp utterance of the first syllable. A synoptic tape of 15 functionally distinct vocalizations in the vocal repertoire, including the wheooo, whee, toledo and chitter calls, is at the Laboratory of Natural Sounds of the Cornell Laboratory of Ornithology (Accession No. 49097). A 'chorus minute' was defined as one in which ≥ 10 wheooo or whee calls occurred. A 'swoop' was defined as a rapid flight that dipped to within 0.5 m of the model or stand. A 'hover' was defined as a hovering flight within 0.5 m of the model or stand.

I used principal components analysis (SAS JMPTM) to reduce the number of variables, some of which were highly correlated. I used only the first principal component (PC1) for producing the scores used in statistical tests. I transformed the raw PC1 scores into percentiles, and calculated ratios of treatments to their matched temporal controls. The ratio, T/C, of a treatment's PC1 percentile score, T, to the PC1 percentile score, C, of its matched temporal control h was designed to filter out the effect of background variability. The null expectation was for a T/C ratio of 1.0 (behavior during treatment equals that during temporal control hr). I ranked the T/C ratios of treatments within each of the experimental units (10 lek arenas). I used PAGE's (1963) L-test, based on summed ranks, to test an ordered hypothesis of treatment effects against an unordered null hypothesis. For individual pairwise comparisons of treatments, I used a Wilcoxon signed-rank test (HOLLANDER & WOLFE 1973), based on the difference between T/C ratios across the 10 experimental units. The maximum possible test statistic, R^+ (sum of positive signed ranks for 10 items), was 55 ($= \sum_{i=1}^{10} i$). To test differences in reaction to the thrush model with respect to female visitation, I used a G-test for independence (SOKAL & ROHLF 1981). I used a sequential Bonferroni correction (HOLM 1979) to correct for the fact that I conducted several tests of differences among various treatment combinations. All tests were single-tailed unless noted otherwise. For the definitive model treatments, comparison of the 10 1990 T/C scores ($\bar{x} = 3.4$; SE = 0.9) and the five 1991 scores ($\bar{x} = 2.1$; SE = 0.9) indicated that the years did not differ ($W = 32$, $p = 0.37$, two-tailed Wilcoxon rank sum test; $p < 0.05$ achievable by $W < 23$ or $W > 57$, possible range 15–65; HOLLANDER & WOLFE 1973).

Results

Differences among Treatments

Fig. 1 shows loadings of the six variables for the first two principal components. All six variables loaded positively on PC1, which can be interpreted as a measure of overall response, including close approach and a high number of wheooo vocalizations. Table 3 shows the mean values of T and C (percentile-transformed PC1 scores for each treatment and its matched temporal control) at the 10 lek arenas.

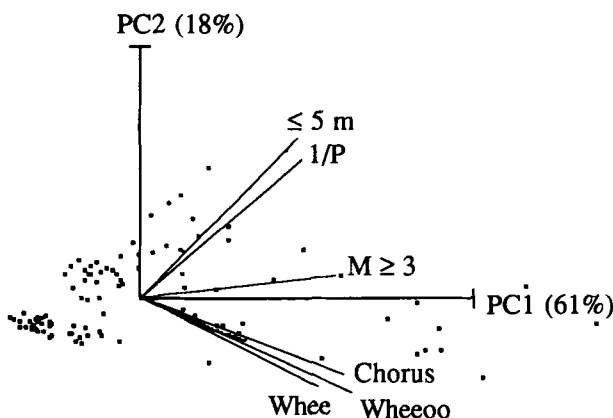


Fig. 1: Scores of the treatment/lek arena combinations on principal component 1 (PC1) and PC2, as shown by the scattered points, and loadings of the variables (Table 2), as shown by labeled vectors. Numbers following axis labels are the percentage of the variance described by the given principal component

Predictions of the alternative hypotheses for the function of the predefinitive plumage are listed in Table 1. I expected little reaction to the stand-only treatment control, St. Only the status-signaling hypothesis predicted a stronger reaction to

Table 3: Values of T (treatment h) and C (temporal control h) for five treatments at 10 experimental units

		Br	F ^{a)}	H ^{a)}	La	LI	N ^{a)}	O5	T ^{a)}	Y2	Z ^{a)}	\bar{X}	SE	min.	max.
Treatment															
St ^{b),c)}	T	0.06	0.07	0.12	0.03	0.05	0.20	0.17	0.12	0.27	0.12	0.12	0.02	0.03	0.27
	C	0.06	0.08	0.14	0.04	0.06	0.14	0.20	0.14	0.38	0.08	0.13	0.03	0.04	0.38
Th ^{d)}	T	0.20	0.01	0.37	0.03	0.32	0.03	0.08	0.33	0.45	0.22	0.20	0.05	0.01	0.45
	C	0.06	0.01	0.16	0.10	0.11	0.15	0.05	0.19	0.34	0.25	0.14	0.03	0.01	0.34
Rc ^{b),c)}	T	0.34	0.23	0.30	0.14	0.04	0.36	0.16	0.56	0.99	0.35	0.35	0.09	0.04	0.99
	C	0.13	0.14	0.16	0.03	0.06	0.13	0.18	0.33	0.38	0.15	0.17	0.03	0.03	0.38
De ^{c)}	T	0.30	0.30	0.11	0.30	0.07	0.70	0.16	0.39	0.87	0.19	0.34	0.08	0.07	0.87
	C	0.08	0.16	0.05	0.04	0.11	0.08	0.06	0.23	0.32	0.12	0.12	0.03	0.04	0.32
Sn ^{d)}	T	0.64	0.69	0.73	0.53	0.40	0.19	0.69	0.80	0.73	0.16	0.56	0.07	0.16	0.80
	C	0.13	0.28	0.06	0.13	0.01	0.17	0.14	0.25	0.30	0.02	0.15	0.03	0.01	0.30

^{a)} Lek arenas for which substitutions were made in 1991; ^{b)} Treatment presented in 1990 only; ^{c)} Scores based on means of three presentations to each lek; ^{d)} Treatment presented once to each lek, in 1991 only.

the redcap model, Rc, than to the stand-only. Under all three signaling hypotheses a weaker reaction was expected to the redcap model than to the definitive model, De. The remaining hypotheses provided no prediction of relative reaction to the two models. Thus, the three signaling hypotheses (status signaling, female mimicry, and juvenile mimicry) predicted an ordered reaction to the treatments, St, Rc, and De. Using the ranked data matrix of T/C ratio scores with the L-test of PAGE (1963), I accepted an ordered alternative hypothesis ($St \leq Rc \leq De$; $L = 136$, $p < 0.005$, following Bonferroni adjustment), against a null hypothesis of no difference among treatments. Fig. 2 shows the ratio scores, T/C, for all five treatments. Note that the stand-only treatment control treatment had a mean T/C ratio of 0.96, the only mean less than unity.

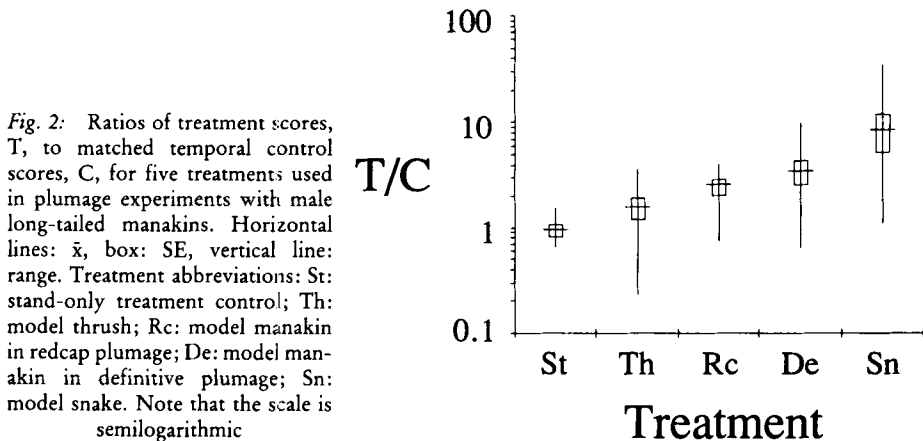


Fig. 2: Ratios of treatment scores, T, to matched temporal control scores, C, for five treatments used in plumage experiments with male long-tailed manakins. Horizontal lines: \bar{x} , box: SE, vertical line: range. Treatment abbreviations: St: stand-only treatment control; Th: model thrush; Rc: model manakin in redcap plumage; De: model manakin in definitive plumage; Sn: model snake. Note that the scale is semilogarithmic

Because Page's L-test requires only one strict inequality, the ordered outcome ($St \leq Rc \leq De$) was consistent with all three signal hypotheses (Table 1) for the function of the predefinitive plumage. The definitive model elicited a signifi-

cantly stronger reaction than did the redcap model (Wilcoxon signed-rank test; $R^+ = 49$ [of 55 possible]; $p = 0.014$ following Bonferroni adjustment), as required by all three signal hypotheses. Under the female mimicry hypothesis, reaction to the redcap model should not have differed significantly from the control treatment, as males never gave wheeoo calls to females during 5816 h of observation between 1983 and 1991. The juvenile mimicry hypothesis also proposes that first-year males should not be a threat. Reaction to the redcap model, however, differed significantly from that to the stand-only treatment control (Wilcoxon signed-rank test; $R^+ = 53$ [of 55 possible]; $p = 0.009$ following Bonferroni adjustment).

Similar Reaction to Model Snake and Manakin Models

Males usually reacted quite strongly to the manakin models (Fig. 2). The wheeoo chorus minutes occurred almost invariably as multimale assemblages, and all identified males were previously known affiliates of the experimental leks. Lek members spent > 13 min within 5 m of the model, engaged in > 4 chorus min, and gave > 107 wheeoo (Table 4). In contrast, during the thrush and stand-only treatments, males spent < 7 min within 5 m of the treatments, engaged in < 2 chorus min, and gave < 60 wheeoo calls.

Table 4: Mean values of variables across all experimental units

	≤ 5 m	Wheeoo	Chorus
Treatment			
St	5.9	16.3	0.5
Th	6.3	51.2	1.9
Rc	13.4	111.6	4.7
De	18.6	107.7	4.7
Sn	12.1	172.9	7.9

The response to the redcap model did not involve confusion over the sexual identity of the model, despite overlap in the plumage of some first-year males and some females. Color-banded females ($n = 6$) have had red in the cap that equaled or exceeded the amount present in the redcap model. Nevertheless, during nonexperimental observations, males responded appropriately to such females by doing dual-male leapfrog dances (McDONALD 1989 a). Conversely, they did not display for young males with no or little red in the cap. An attempted copulation with the redcap model immediately followed a copulation with a live female, during a pilot experiment. The alpha copulator was unusually young (5 yr old). The partners had little history of prior performance, and the partnership dissolved later in the season, whereas most successful partnerships persist until the death of the alpha or beta male. In none of 30 other presentations of the redcap model did males display to it, attempt to mount it, or contact it. The copulation attempt was accompanied by vigorous pecking never observed under nonexperimental conditions.

Reactions of Males Other Than the Alpha Male

During 11 of the 75 h-long presentations of the manakin models, identified males made one or more swoops or hovers at the model. Six of the 11 cases involved only males other than the alpha. In one of those six cases, the beta male swooped and hovered at the definitive model during dual-male dance display for a live female; the alpha male did not react visibly to the model. In another case, also during a dance for a female, the beta male pecked as well as swooped at the definitive model, while the alpha only swooped. In the four remaining cases, alpha males were the only ones to swoop or hover, but they never pecked.

Context-dependent Reaction to the Thrush

Six leks had strong ($T/C > 1.0$) thrush reactions, while four had weak ($T/C < 1.0$) reactions. A sample of scheduled observations at times other than the experiment indicated that the leks with strong thrush reaction also had higher female visitation rates (55/201 2-h observations had female visits) than did the leks with weak thrush reaction (4/60 2-h observations had female visits; $G_{adj} = 7.99$, $p < 0.01$ following Bonferroni adjustment). This appeared not to be due to generally low reactivity of the leks with weak thrush reaction, because reactions to the definitive model at those leks were stronger (mean $T/C = 2.7$ vs. 1.7, calculated for the five leks to which both Th and De were presented in 1991).

Discussion

Models Perceived as a Threat

Reaction to the model snake was the strongest of those to the experimental treatments (Fig. 2, Table 4). The wheooo chorus minutes elicited by the snake treatments were qualitatively and quantitatively similar to those elicited by the model treatments (Table 4). I therefore take the response to the bird models as constituting a mobbing chorus toward a potential threat. CHAPMAN (1935) found that male golden-collared manakins (*Manacus vitellinus*) also reacted strongly to model males. The reaction of Chapman's males, however, was far more vigorous than that of the males in this experiment, including vigorous pecking that damaged the models.

Other species, including orange-billed nightingale-thrushes (*Catharus aurantiirostris*), golden-crowned warblers (*Basileuterus culicivorus*), rufous-and-white wrens (*Thryothorus rufalbus*), and stripe-tailed hummingbirds (*Eupherusa eximia*), joined the mobbing chorus at the model snake. These species had been noted as appearing during the model bird presentations, but had not joined the chorus. Although the presence of these species produced a qualitative sense of a stronger reaction to the snake, their activity did not enter into the variables of PC1 and therefore did not directly affect the T/C scores of Fig. 2.

Female and Juvenile Mimicry Hypotheses

Stronger reaction to the redcap model than to the stand-only treatment control runs counter to the female mimicry hypothesis. In only one of 31

presentations of the redcap model did the males respond as to a female. The single exception occurred under unusual circumstances, and the vigorous pecking accompanying attempted copulation with the model suggests that the males did not treat the model as a normal female. The reactions support the hypothesis (McDONALD 1989 b) that males generally recognize females by behavioral as well as plumage cues. CHAPMAN (1935) found a variable response to model females whose plumage had been altered to include male-like elements (black feathers) or elements of the plumage of males of other species (red caps). He similarly posited that sexual recognition depended partly upon behavioral cues provided by predefinitive males or females.

Only the first predefinitive plumage is likely to permit female mimicry, since females never have the black patches seen in the two subsequent predefinitive plumage stages. The benefit, if any, would be close observation of a dance display. Because males often perform all the elements of the display in multimale assemblages when no females are present (McDONALD 1989 a, b), this seems a very minor benefit. Given the lack of a clear benefit, the female mimicry hypothesis receives little support, even regarding the only predefinitive stage to which it could apply. However, both to settle the issue of sexual recognition and to test the female mimicry hypothesis more rigorously, presentation of female models would be desirable.

This experiment did not assess the difference in reaction to different predefinitive plumages, as would be required for a decisive test of the juvenile mimicry hypothesis of FOSTER (1987). Nevertheless, three factors argue against the juvenile mimicry hypothesis. First, even the first predefinitive plumage (the redcap model) provoked wheooo chorus minutes that more closely resembled the response to the definitive model or the snake model than to the other two treatments (Fig. 2, Table 4). The juvenile mimicry hypothesis requires that the earlier plumages provoke little or no aggressive reaction. Again, a rigorous test of the hypothesis would require comparison to model females. Second, the sequence proposed by FOSTER (1987) would make it difficult for other males to assess the age of predefinitive males with certainty, and facilitate deceptive mimicry. In contrast, the sequence presented here yields distinct, unambiguously age-specific stages, making it impossible for males to deceive others about their age. Third, no predefinitive male, even at age three, is ever likely to be a threat via stolen copulations. In eight years of study only 5 of 166 copulations were by males < 8 yr old, none was by a predefinitive male, and females can and do show unrestricted and acute discrimination even among alpha males (McDONALD 1989 b, 1993). As I argue below, a more plausible explanation of the threat posed by 'strange' males (the models) is not via stolen copulations but via disruption of orderly male queues.

Predator Crypticity

Might predefinitive plumage promote crypticity and reduce predation? Predation can be a major risk for brightly plumaged males with elaborate courtship displays. TRAIL (1987) saw 56 predation attempts on male cock-of-the-rock (*Rupicola rupicola*), during 254 d of observing 55 males. Attackers included

six species of raptors, one species of mammal, and one species of snake. Two males were killed by raptors, and two by snakes. In at least three times as many male-observation days my assistants and I have seen only one possible predation attempt on definitive males. The attack, if it was one, was a swooping approach by an emerald toucanet (*Aulacorhynchus prasinus*), and did not appear to be a critical threat. This lack of attempted predation exists despite the gaudy plumage, predictable locations, and attention-grabbing displays of definitive males. GÖT-MARK (1992) suggested that bright male plumage may warn of unprofitable prey. Such an antipredator function is more likely in species with aerial displays and light, maneuverable males. Both cock-of-the-rock and sage grouse (*Centrocercus urophasianus*), another species in which predation at leks has been observed (HARTZLER 1974), have terrestrial displays by heavy, highly clustered males. While crypticity could provide a slight benefit, it seems unlikely to have been a major force in the evolution of multiple predefinitive plumages in long-tailed manakins. Male long-tailed manakins do not appear to be toxic (DUMBACHER et al. 1992), as a mouse (*Peromyscus nudipes*) ate one of my models.

Molt and Energetic Constraints

If molt constraints were the primary factor promoting DPM in this species, one would expect a single predefinitive plumage until the benefits (in mating success) outweighed the costs, or upon the completion of a full molt. The fact that three successive years produce distinctly different predefinitive plumages is difficult to reconcile with such a hypothesis. Further, both the second (black-face) and third (blue-back) stages include full development of that element of the plumage most likely to be costly — the iridescent red cap (HILL 1992). Even in the first-year (redcap) plumage, the red is the first element present. Given that the element likely to be the most costly is incorporated first, the energetic constraints hypothesis becomes less attractive. Nevertheless, decisive rejection would require quantifying the relative energetic costs of red, black, blue and green plumage elements.

Status Signaling

Stronger reaction to the redcap model than to the stand-only treatment control, while probably inconsistent with the female mimicry hypothesis, is fully consistent with a status-signaling hypothesis. The differential reaction supports the hypothesis that the redcap plumage serves a role in moderating aggression towards its bearer. Two factors may explain why the response was as strong as it was.

1. Lack of behavioral context: When accompanied by suitable behavior, predefinitive plumages may serve as honest signals of lower status, and facilitate admission of unfamiliar young males as newcomers to leks. A live male's plumage would normally be accompanied by a suite of behaviors and vocalizations. Indeed, the submissive chitter call is given almost exclusively by predefinitive males as a reaction to aggression by definitive males (McDONALD, unpubl.). Without appropriate submissive behavior, even a predefinitive male may pose a threat to members of the lek, as I will argue below. By the time males acquire

definitive plumage, they have interacted with lek members for several years. Individual recognition among lek members is then likely to be based on behavior and vocalizations, not requiring a badge of lowly status. Because courtship might also require appropriate behavior from females, decisive rejection of the female mimicry hypothesis would require presentation of female models or live, tethered females, as well as a demonstration that predefinitive males either cannot adopt female-like behaviors or would gain nothing by doing so. Because males appear unable to secure copulations by force or subterfuge (McDONALD 1989 a), sneak strategies (GROSS & CHARNOV 1980) seem unlikely to be important.

2. Orderly queues: The nature of the threat posed by unfamiliar males might also diminish the difference in reaction. One might suppose that the major threat posed by intruders would be via stolen copulations. If that were the case, we would expect the most reactive males to be alphas, to whom most copulations accrue (162 of 166; McDONALD 1993).

Nevertheless, the strongest reactions (e.g., swoops, pecks) to the models most often came not from the alpha but from the beta male or one of the other lek members. These males did not stand to lose copulations, which would (in the absence of intruders) accrue only to the alpha male anyway. What might be threatened, however, is the stability of incipient partnerships in the lek assemblage. In a queue, individuals near the front of the queue stand to lose from any change in the ordering (MAYNARD SMITH 1983), but individuals at the bottom might benefit from a reshuffling. However, if the benefit for which the queue forms can be withheld by an external agent as a response to disorder, then even the last in line should benefit from maintaining and even helping to enforce orderliness. Although MAYNARD SMITH argued that external enforcement of orderly queues in nonhuman animals was unlikely, long-tailed manakins may provide just such a case, with females as enforcers that choose among queues (leks).

The relative lack of agonism among males noted in this species (FOSTER 1987; McDONALD 1989 b) may be due in large part to female ability to enforce orderliness. Support for this hypothesis comes from the fact that during nonexperimental observations females remained at dance displays by more than two males ($n = 10$, including one bout of 94 successive triple-male leapfrogs), but left when one (or occasionally both) of the higher-ranking males chased away the lowest-ranking male ($n = 9$). On only two occasions did females remain at a perch following vigorous male-male chases. Lack of an orderly queue criterion for female choice might also help explain the stronger agonism by male *Manacus vitellinus* toward experimental models (CHAPMAN 1935).

The sort of status signaling provided by age-specific plumages may facilitate orderly alignment of the end of queues. Because considerable variation exists within the distinct, age-specific predefinitive plumages (McDONALD, unpubl.), an intriguing possibility exists for fine-tuning the signal function of the plumages within cohorts (JACKSON et al. 1988). Among cohorts, the broad pattern of age-specific plumages would function as reliable badges of age and status. Within cohorts, brighter males might signal superior condition to duller males. Further, if red is the most costly element, its early acquisition increases the scope for

reliable status signaling within cohorts. Some support for this idea comes from the fates of known-age males whose plumage brightness was recorded at the blue-back stage. Of 21 such males hatched before 1987, 7 were bright, while 14 were average or dull. By the end of the study period 6 of the 7 bright males had danced at least once for a female, while only 6 of the 14 duller males had done so ($G_{adj} = 3.52$, $p = 0.06$, G-test, SOKAL & ROHLF 1981). A plausible alternative hypothesis is that the considerable variability within predefinitive stages aids individual recognition (JACKSON et al. 1988) until individuals can be recognized by behavior, vocalizations or more subtle morphological characteristics.

Differing Nature of Threats Posed by Models

Inter- and intraspecific differences in response to models may arise because of the differing nature of the threat posed by intruders (models). In most territorial systems, including leks, intruding males could cause immediate loss of reproductive success to the territory holder, either by taking over the territory or by copulating with females. In the dual-male display system of long-tailed manakins, solitary males do not pose such a threat.

The nature of the threat posed by intruders may explain the difference between the results of this study and those of ENSTROM (1992) in a model experiment with orchard orioles, *Icterus spurius*. ENSTROM found that breeding males attacked predefinitive models more strongly than they did definitive models, the opposite of the results of this study. Predefinitive orchard orioles do breed and thus constitute a present reproductive threat to breeders. Predefinitive male long-tailed manakins do not. ENSTROM noted that the age-specificity of predefinitive plumage in orchard orioles may then make it safer for established males to attack predefinitive intruders more strongly.

A possible reason for sporadic reaction to the model thrush, leading to its higher T/C ratio compared to the stand-only treatment (Fig. 2) is that females may be less likely to approach a dance perch in the presence of heterospecifics. For the males with high visitation rates it may therefore pay to mob neutral species. For the males at leks with low visitation success, such mobbing may not pay. Conversely, the stronger reaction to the definitive model at unsuccessful perches may be a consequence of less firmly established alliances and dominance relations, making the queue more vulnerable to disruption by strangers.

Differing Functions for Delayed Plumage Maturation

In a recent paper, THOMPSON (1991) showed a prealternate (HUMPHREY & PARKES 1959) molt to a more adult female-like plumage in male painted buntings (*Passerina ciris*). Such a molt supports an adaptive function of predefinitive plumage in the breeding season, as opposed to the hypothesis that energetic constraints force first-year males to retain maladaptive juvenile-like plumages. STUTCHBURY (1991) also rejected the molt constraints hypothesis in purple martins (*Progne subis*). While THOMPSON's results provide intriguing support for a female mimicry hypothesis, the results of the present experiment allow tentative rejection of the female mimicry hypothesis, as did STUTCHBURY's experiments. STUTCH-

BURY found no evidence for subordination signaling in the martins. In long-tailed manakins, however, the results supported the hypothesis that predefinitive plumage mediates aggression by established males against younger males seeking to establish relationships within a lek assemblage. Given the differing social systems and ecology of the three species, it should not be surprising to find that the functions of predefinitive plumage may also differ.

GRANT (1990) discussed the function of multiyear delays in plumage maturation in tropical Darwin's cactus finches (*Geospiza fortis*). An intriguing difference in sequence and context is apparent. GRANT showed that the sequence of successive predefinitive stages was highly variable (i.e., not age-specific), and was heritable. The variability was explained by a tradeoff between increased viability of slowly maturing males, and increased reproductive success in the first year for rapidly maturing males. The same sort of tradeoff is unlikely in long-tailed manakins, because males rarely copulate before age 8, although within-cohort tradeoffs between dominance establishment and survival may occur. The interspecific difference again points to the importance of social, behavioral and ecological context when searching for functional explanations of DPM (ANDERSSON 1983; ROHWER & BUTCHER 1988). The costs and benefits of predefinitive plumage can depend upon the social system in the breeding or the nonbreeding season, and upon constraints imposed by tradeoffs that may differ in different ecological contexts.

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Literature Cited

- ANDERSSON, M. B. 1983: On the functional significance of conspicuous seasonal plumages in birds. *Anim. Behav.* **31**, 1262—1264.
- BRADBURY, J. W. & ANDERSSON, M. B., eds. 1987: *Sexual Selection: Testing the Alternatives*. Wiley, Chichester.
- CHAPMAN, F. M. 1935: The courtship of Gould's manakin (*Manacus manacus vitellinus*) on Barro Colorado Island, Canal Zone. *Bull. Am. Mus. Nat. Hist.* **68**, 471—525.
- DUMBACHER, J. P., BEEHLER, B. M., SPANDE, T. F., GARRAFFO, H. M. & DALY, J. W. 1992: Homobatrachotoxin in the genus *Pitohui*: chemical defense in birds? *Science* **258**, 799—802.

- ENSTROM, D. A. 1992: Breeding season communication hypotheses for delayed plumage maturation in passerines: tests in the orchard oriole, *Icterus spurius*. *Anim. Behav.* **43**, 463—472.
- FOSTER, M. S. 1987: Delayed maturation, neoteny and social system differences in two manakins of the genus *Chiroxiphia*. *Evolution* **41**, 547—558.
- GOTMARK, F. 1992: Anti-predator effect of conspicuous plumage in a bird. *Anim. Behav.* **44**, 51—55.
- GRANT, B. R. 1990: The significance of subadult plumage in Darwin's finches, *Geospiza fortis*. *Behav. Ecol.* **1**, 161—170.
- GROSS, M. R. & CHARNOV, E. L. 1980: Alternative male life histories in bluegill sunfish. *PNAS USA* **77**, 6937—6940.
- HARTZLER, J. E. 1974: Predation and the daily timing of sage grouse leks. *Auk* **91**, 532—536.
- HILL, G. E. 1992: Proximate bases of variation on carotenoid pigmentation in male house finches. *Auk* **109**, 1—12.
- HOLLANDER, M. & WOLFE, D. A. 1973: *Nonparametric Statistical Methods*. Wiley, New York.
- HOLM, S. 1979: A simple sequentially rejective multiple test procedure. *Scand. J. Stat.* **6**, 65—70.
- HUMPHREY, P. S. & PARKES, K. C. 1959: An approach to the study of molts and plumages. *Auk* **76**, 1—31.
- JACKSON, W. M., ROHWER, S. & WINNEGRAD, R. L. 1988: Status signaling is absent within age and sex classes of Harris' sparrows. *Auk* **105**, 424—427.
- LYON, B. E. & MONTGOMERIE, R. D. 1986: Delayed plumage maturation in passerine birds: reliable signaling by subordinate birds? *Evolution* **40**, 605—615.
- MAYNARD SMITH, J. 1983: Game theory and the evolution of cooperation. In: *Evolution from Molecules to Men*. (BENDALL, D. S., ed.) Cambridge Univ. Press, Cambridge, pp. 445—456.
- McDONALD, D. B. 1989a: Correlates of male mating success in a lekking bird with male-male cooperation. *Anim. Behav.* **37**, 1007—1022.
- — 1989b: Cooperation under sexual selection: age-graded changes in a lekking bird. *Am. Nat.* **134**, 709—730.
- — 1993: Demographic consequences of sexual selection in the long-tailed manakin. *Behav. Ecol.*, in press.
- PAGE, E. B. 1963: Ordered hypotheses for multiple treatments: a significance test for linear ranks. *J. Am. Stat. Assoc.* **58**, 216—230.
- PROCTER-GRAY, E. & HOLMES, R. T. 1981: Adaptive significance of delayed attainment of plumage in male American redstarts: tests of two hypotheses. *Evolution* **35**, 742—751.
- ROHWER, S. 1977: Status signalling in Harris sparrows: some experiments in deception. *Behaviour* **61**, 107—129.
- — 1978: Passerine subadult plumages and the deceptive acquisition of resources: test of a critical assumption. *Condor* **80**, 173—179.
- — & BUTCHER, G. S. 1988: Winter versus summer explanations of delayed plumage maturation in temperate passerine birds. *Am. Nat.* **131**, 556—572.
- SELANDER, R. K. 1965: On mating systems and sexual selection. *Am. Nat.* **99**, 129—141.
- SOKAL, R. R. & ROHLF, F. J. 1981: *Biometry*. 2nd ed. Freeman, New York.
- STUTCHBURY, B. J. 1991: The adaptive significance of male subadult plumage in purple martins: plumage dyeing experiments. *Behav. Ecol. Sociobiol.* **29**, 297—306.
- THOMPSON, C. W. 1991: The sequence of molts and plumages in Painted Buntings and implications for theories of delayed plumage maturation. *Condor* **93**, 209—235.
- TRAIL, P. 1987: Predation and antipredator behavior at Guianan Cock-of-the-Rock leks. *Auk* **104**, 496—507.

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