

**AGE AND SEXUAL DIFFERENCE IN SPATIAL
DISTRIBUTION AND MOBILITY IN
MANAKINS (PIPRIDAE): INFERENCES
FROM MIST-NETTING**

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Natal and breeding dispersal in birds occurs predominantly in females (reviewed by Greenwood 1980). This sexual bias is widespread in monogamous (Chabrzyk and Coulson 1976), communally breeding (Woolfenden and Fitzpatrick 1978), and promiscuous species such as manakins (Lill 1974). Long term studies of color-marked manakins suggest that territorial males are sedentary (Snow 1962a, b, Lill 1976, Robbins 1983). Non-resident adult males visit different leks for the possibility of becoming established in a new lek, or moving up in lek hierarchy. Females are more mobile and often visit widely separated leks in a single breeding season (Lill 1976). In sexually dichromatic genera (e.g., *Chiroxiphia*, *Pipra*, *Manacus*), individuals in immature male plumage often cannot be sexed morphologically and perhaps not behaviorally in the field (Graves 1981); the home range movements of immature-plumaged males are unknown.

To assess differences in movement, relative abundance, and time until asymptote for accumulation curves of females and adult and immature males, two mist-net "capture-removal" experiments were conducted on local populations of manakins in the foothills of the Andes in the Department of La Paz, Bolivia (as part of a broader program of studying bird communities and geographic variation at selected sites in this region).

STUDY SITE AND METHODS

Blue-backed Manakins (*Chiroxiphia pareola boliviana*; $n = 146$) were netted daily from 11 July to 2 August 1980, in humid hilly forest with a canopy height of 15-30 m in the Serranía Bellavista, 47 km by road north of Caranavi (1350 m). Seventeen 12 m nets were set on 11 July. This total was increased to 22 on 15 July, to 25 on 16 July, 28 on 26 July, 29 on 28 July, and 32 on 29 July, for a total of 6490 net hours. Round-tailed Manakins (*Pipra chloromeros*; $n = 171$) were netted daily from 6 June to 6 July 1981, in humid hill forest with a canopy height of 20-35 m on the Rio Beni, ca. 20 km by river north of Puerto Linares (600 m). Both sites were within 2 km of expanding slash-and-burn agriculture, and it is likely that both sites will be destroyed within the next 10 years. Twenty-one nets were set on 6 June; this total was increased to 24 on 7 June and to 29 on 12 June, for a total of 11,090 net hours. In both exercises, mist-nets (30 mm mesh) were set along lanes cut through forest understory. Net lanes were not intentionally placed near known lek sites, and once set, nets were not removed until the end of each study. Cumulative net hours (12 h/net/day) and captures were

TABLE 1. Numbers of Blue-backed Manakins netted during three successive periods with sample size (n), expected Chi-square values (χ^2) and standardized residuals (SR) adjusted by an estimate of the variance (see Whittam and Siegel-Causey 1981)¹. Cells that deviate significantly from independence at the .05 level are marked by an asterisk.

<i>Chiroxiphia pareola</i>		Mist net hour periods		
		0-2000	2001-4000	>4000
Adult males	n	16	10	3
	χ^2	5.76	12.12	11.12
	SR	3.41*	-.41	-1.70
Immature males	n	5	13	6
	χ^2	4.76	10.03	9.21
	SR	-.09	.65	-.75
All females	n	8	38	47
	χ^2	18.47	38.86	35.67
	SR	-1.98*	-.06	.89

¹ $d_{ij} = \left(\frac{O_{ij} - E_{ij}}{\sqrt{E_{ij}}} \right) [(1 - ni+/n++) (1 - n+j/n++)]^{1/2}$ where cell (ij) has an expected value E_{ij} and observed value O_{ij} .

totaled at the end of each day. All manakins (Tables 1 and 2) were sexed internally and prepared as study skins or skeletons (deposited in Louisiana State University Museum of Zoology). Because all females captured had pneumatized skulls, adult and immature females could not be distinguished in all cases and were not separated for comparison in this study.

We cannot directly compare the "capture-removal" and "capture-mark-release" census methods, nor assess the impact that the removal

TABLE 2. Numbers of Round-tailed Manakins netted during 5 successive periods with sample size (n), expected Chi-square values (χ^2) and standardized residuals (SR) adjusted by an estimate of the variance (see Table 1). Cells that deviate significantly from independence at the .05 level are marked by an asterisk.

<i>Pipra chloromeros</i>		Mist net hour periods				
		0-2000	2001-4000	4001-6000	6001-8000	>8000
Adult males	n	15	7	10	11	2
	χ^2	7.37	11.05	10.53	10.00	6.05
	SR	2.22*	-.91	-.12	.24	-1.32
Immature males	n	3	18	11	12	3
	χ^2	7.70	11.54	10.99	10.44	6.32
	SR	-1.32	1.72	.00	.36	-1.05
All females	n	10	17	19	15	18
	χ^2	12.94	19.60	18.48	17.56	10.63
	SR	-.55	-.34	.08	-.39	1.53

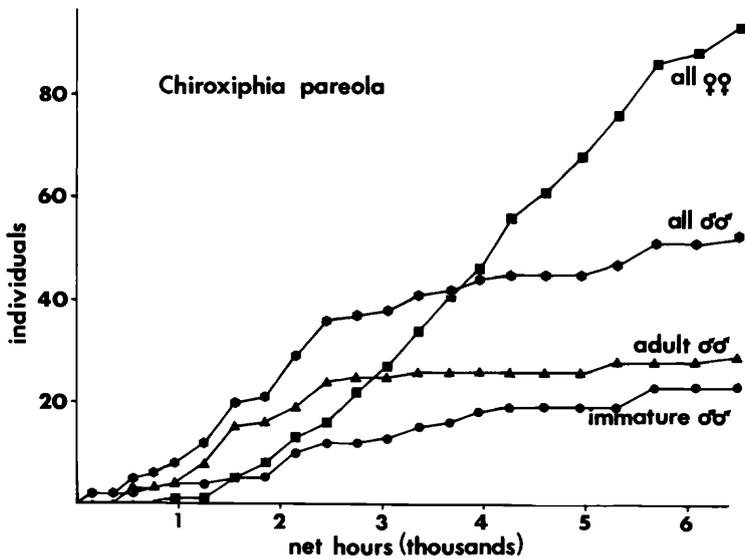


FIGURE 1. Accumulation curves of Blue-backed Manakins.

procedure had on local social organization and movement patterns beyond speculation that removal of large numbers of individuals produces more local dispersal than normal for the time of year.

RESULTS

Blue-backed Manakins are locally common inhabitants of humid forest understory of the Andean foothills. Lekks are located in open or dense understory (Gilliard 1959, G. R. Graves pers. observ.). At the time of removal, display activity and presence of enlarged ova indicated that at least some Blue-backs were breeding. Size of gonads per se is not a reliable indicator of breeding status in many tropical species, because gonad size is relatively constant through the year in many adult birds (Foster 1975 and references therein). A better indicator of breeding is the size of the largest ovum. In this study, ova >1.5 mm were used as criteria of incipient breeding or breeding condition. As defined here, at least 37% of the female Blue-backs collected were in breeding condition.

Accumulation curves (Fig. 1) suggest that local adult males were quickly netted and not replaced by other adult males. Of the total Blue-backs captured, 55% of the adult males, but only 8% of females, and 21% of immature males were netted during the first 2000 net hours (30.8% of total net hours). A Chi-square test for independence of the Blue-backs R X C table is highly significant ($\chi^2 = 36.07$, $P < .001$, Table 1). However, an examination of residuals adjusted by an estimate of the variance

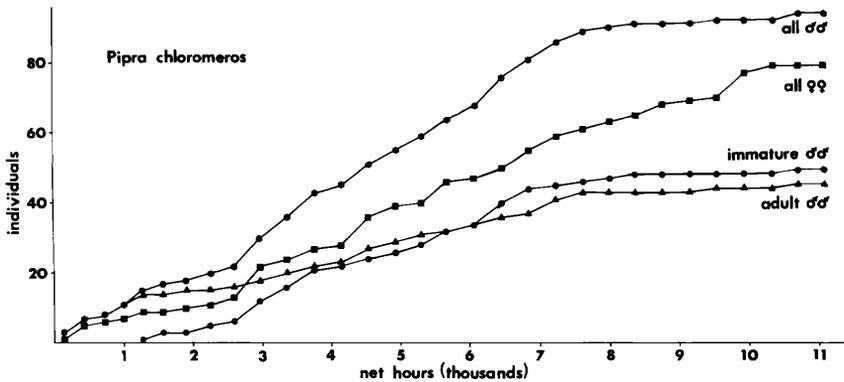


FIGURE 2. Accumulation curves of Round-tailed Manakins.

shows that only two cells deviate significantly from independence ($d_{ij} > 1.96$ or < -1.96). The number of adult males netted in the first 2000 h was much higher than expected, whereas the number of females netted during this period was lower than expected. Also, slightly fewer adult males were netted in the final period ($.10 > P > .05$). The deviations of the other cells are not significant.

The Round-tailed Manakin, a common tropical zone species in forested western Amazonia, has a lek system superficially similar to other *Pipra* (Graves and M. B. Robbins pers. observ.). No display behavior or gonadal evidence of breeding was observed during the capture period. Adult males were more quickly netted than females and immature males, although less so than in Blue-backs (Fig. 2). A Chi-square test for independence is highly significant ($\chi^2 = 27.14$, $P < .001$, Table 2) but only one cell in the $R \times C$ table deviates significantly from independence. The number of adult males netted in the first 2000 h is higher than expected; other cells do not deviate significantly at the .05 level.

Capture rates of the two species were comparable during the first 2000 net hours. The relative proportions of Blue-back and Round-tail females and males are not significantly different ($\chi^2 = .76$).

DISCUSSION

Our results support the observations of Snow (1962a, b) and Lill (1974) that adult male manakins are more sedentary than females, and the general finding that female birds disperse farther than males (Greenwood 1980). In a mist-net study in Panama, Karr (1971) found extensive, almost day-to-day, turnover in individuals of the Red-capped Manakin (*Pipra mentalis*). The most likely explanation for this was the high mobility of immatures and females, but also that few adult males were recaptured.

Although we lack data on the seasonality of dispersal for both species, in our results, we interpret the apparently non-asymptotic accumulation curves of females to indicate that females probably visit widely separated leks during the breeding season. On the other hand, adult males were netted relatively quickly and not replaced. This trend was somewhat reduced in the non-breeding Round-tails, owing possibly to the decreased attendance (or attractiveness) at local leks. Thus the observed differences in the capture curves are a result of sampling wide-ranging (females and immature males) versus local (adult males) populations. Alternative explanations for the differential capture rates, such as variable ability in avoiding the nets, are not supported by the data.

In both experiments the increase in immature males captured after the first 2000 net hours may indicate that adult males locally exclude immature males; females, however, increased dramatically also. As implied by capture rates, immature males in female-like plumage are intermediate (no highly significant cell deviations) in home range mobility between sedentary males and wider ranging females.

Of wider application, these exercises suggest that the cumulative captures of some age/sex classes of certain tropical species do not reach an asymptote within the 3–5-day period of continuous netting usually allowed in mist-net studies (Karr 1971, 1979, Wilson and Moriarty 1976).

SUMMARY

Mist-net "capture-removal" experiments on local populations of manakins (*Chiroxiphia pareola* and *Pipra chloromeros*) suggest that local adult males were more quickly netted and less likely to be replaced than females and immature males. Immature males were somewhat intermediate in home range mobility between sedentary males and wider ranging females. Both experiments suggest that cumulative captures of some tropical species do not reach an asymptote within the 3–5-day period usually allowed in mist-net studies.

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