Despite the above arguments, I believe the Red Siskin's establishment in Puerto Rico most probably coincided with the period of its heaviest importation. This probably would have been in the 1930's when the species was still relatively common in its native lands and there was an extremely high demand for it among Canary breeders. Discussions with long-term residents in the region where the Red Siskin occurs could shed additional light on this matter.

Regardless of the length of time that the Red Siskin has inhabited Puerto Rico, its continued survival will depend on protective safeguards. While the species may have been a will-o'-the-wisp for ornithologists, we cannot depend on it remaining so for pet traders.

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Received 19 August 1982, accepted 4 January 1983.

A Comparison of White-bearded Manakin (*Manacus manacus*) Populations and Lek Systems in Suriname and Trinidad

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The White-bearded Manakin (*Manacus manacus*) is a neotropical, primarily frugivorous, lek-mating passerine. The ecology and behavior of *M. m. trinitatis* in the Arima Valley, Trinidad has been described (Snow 1962; Lill 1974a, b). Snow (1962) found the Trinidad population density to be unusually high with respect to mainland populations and suggested that this was due to either a high proportion of secondary forest, caused by limited clearing and lumbering, or reduced interspecific competition on the island. Secondary forest may benefit survival and reproduction, because many of the trees abundant in secondary forest are prime food sources (Snow 1962) and there is an abundance of saplings on which the males depend for their display (Snow 1962, Lill 1974a).

There has been little research on *M. manacus* in mainland South America. In this study, a population of *M. m. manacus* in virgin rain forest in the interior of Suriname was compared to the Arima Valley population with respect to population density, morphology, reproductive behavior, male mating success, and lek characteristics. At least two resident males, with display courts near each other, constitute a lek. A display court is a circular area of forest floor, between saplings, cleared of leaf-litter by a male. A resident male successfully defends his court and a small area surrounding his court against intruding conspecific males. [See Snow (1962) and Lill (1974a) for a more complete description of the lek mating display.] The lek characteristics investigated in our study include interlek distance, lek area, intercourt distance, and the number of resident males per lek.

Male dispersion in Suriname and Trinidad was compared and related to the lek characteristics investigated. Male dispersion patterns have been described as a continuous gradient in the degree of male clustering. This gradient ranges from uniform fields

of male territories through partial clustering of males with smaller territories to highly clustered males and large intercluster distances, the classical lek dispersion (Bradbury 1981). We examined male clustering and the possible influences of habitat resources and population density on male dispersion in *M. manacus*.

The study site was in the Raleigh Falls/Voltzberg Nature Reserve (approximately 4.5°N, 56.0°W), Suriname, adjacent to the Coppename River. The primary rain forest was interspersed with unforested granite outcrops in the form of large, flat plates and domes rising to 100 m above the forest canopy. Forest characterized by thick undergrowth and a low canopy surrounded the outcrops. This apparent secondary growth may be attributed to rocky soil at the edge of the granite outcrops. These areas comprised about one-third of our study site, which was located at the base of the Voltzberg granite dome within an area of approximately 200 ha.

Data were collected at four leks from December 1980 to May 1981. The average nearest neighbor, interlek distance was determined with adjustments for topographic relief at the Voltzberg study site and compared with the average two-dimensional interlek distance, approximated from Lill (1974b), in the Arima Valley. The number of adult resident males per lek and the location of adult male display courts were determined by observation during the breeding season. The extent of the breeding season in Suriname has not been described. In Trinidad, breeding generally occurs from March to August (Snow 1962, Lill 1974a).

Snow (1962) estimated the population density of adult *M. manacus* by counting the number of active display courts at the leks to determine the number of resident adult males and then calculating the proportion of trapped nonresident males and females to trapped resident males. Population density was determined in the same manner at the Voltzberg study site from trapping data at leks.

Males and females at two leks were uniquely color banded, weighed, and measured for right-wing length. We visited a lek consisting of three color-banded resident males daily and observed it from a blind on days of high activity. The behaviors of adult males, females, and juvenile males at the lek were recorded during 158 h of observation, between 0600 and 1800. Juvenile males were identified by their use of male display patterns. Resident-male territory areas, determined by locations of agonistic encounters surrounding individual courts, and lek area in which all display activity occurred were determined for this three-male lek. The polygonal area enclosed by resident-male display-court centers was used as the minimum-lek-area (MLA) estimate for each lek at the Voltzberg site. A Zeiss MOP-3 System for Quantitative Digital Image Analysis was used to determine area.

Four *M. manacus* leks were located adjacent to granite plates and domes in dense vegetation characteristic of secondary growth. Males were not observed to display solitarily or in areas disturbed by treefalls, but the displays of several males were heard at two other possible lek locations in dense vegetation near the edge of granite outcrops; these birds were not observed. *M. manacus* dispersion may be limited to areas with vegetation characteristic of secondary forest. Secondary growth may supply adequate male display sites, food resources (Snow 1962), and nesting sites for manakins.

The comparisons of population density, interlek distance, lek area, number of males per lek, and intercourt distance between the two sites are shown in Table 1. Snow (1962) determined the population density in the Arima Valley to be 2.7 adults/ha. Lill (1974b), 10 yr later, estimated that the density had declined by 20% and attributed the decline to the reduction of secondary forest. The Voltzberg adult population density was much less than either of these Trinidad estimates, confirming Snow's (1962) observation of a lower mainland population density. The average interlek distance between the four Voltzberg leks was much greater than the average of 11 Arima Valley leks. The four Voltzberg leks consisted of 2, 3, 4, and 5 resident adult males. Lill (1974a) described the number of resident males as ranging from 6 to 50 in a typical Arima Valley lek. Snow (1962) found 205 display courts at seven leks, an average of 29 males per lek. The largest lek in Trinidad had 70 display courts within an area of approximately 18.3 by 9.2 m (Snow 1962) and was smaller than the average polygonal MLA at the Voltzberg site (which does not include the two-male lek). MLA was an extreme underestimate of the area surrounding the display courts in which resident males actively displayed. The MLA of the three-male lek was 110 m^2, whereas the area in which all territorial and mating displays occurred was approximately 548 m^2. The nearest-neighbor distance between resident male display courts at the four Voltzberg leks ranged from 6.2 to 21.5 m, with an average of 13.6 m, whereas the Arima Valley courts were, on average, 0.9–4.6 m apart (Snow 1962).

Morphological variation was found between Surinam and Trinidad. Adult male wing lengths and weights at the Voltzberg site were significantly different ($P < 0.001$) from those of the Arima Valley population (Table 1).

We observed breeding activity from the onset of our study in mid-December until March. Breeding activity was most intense in December and January, at the start of the short dry season, during which we logged 114 h of observation time between 0700 and 1700. Most of the female visits and copulations were recorded between 1200 and 1600, during 75 h of observation.

The behavior patterns of birds at the Voltzberg site

TABLE 1. Lek characteristics, population density estimates, and adult male wing lengths and weights from the Trinidad and Suriname study sites.

	Arima Valley	Voltzberg
Average interlek distance (m)	371[a]	706
Number of resident males/lek	6–50[b]	2–5
Lek area (m^2)	167[c]	266 (MLA)
Intercourt distance (m)	0.9–4.6[c]	6.2–21.5
Population density (adults/ha)	2.19[a]	0.17
Adult male weight (g)		
Mean	18.20[c]	17.05[d]
SD	1.24	0.46
n	185	9
Adult male wing lengths (mm)		
Mean	52.47[c]	50.55[d]
SD	1.07	1.67
n	55	9

[a] Approximated from Lill (1974b).
[b] Lill (1974a).
[c] Snow (1962).
[d] $P < 0.001$; Student's *t*-test (Snedecor and Cochran 1980: 96).

during the breeding season were similar to those described by Snow (1962) and Lill (1974a, b). Stereotyped male and female courtship displays, juvenile displays, male-male aggression, and male-male dominant-subordinate relations were observed at the Voltzberg leks. Lill (1974a) found a nonrandom mating distribution among males at the leks in Trinidad: a small proportion of resident males received the majority of copulations. Nonrandom male mating success has been recorded in other lek species [Sage Grouse (*Centrocercus urophasianus*), Wiley 1973; hammerheaded bat (*Hypsignathus monstrosus*), Bradbury 1977; Guianan Cock-of-the-Rock (*Rupicola rupicola*), P. W. Trail, pers. comm.]. Behavioral observations of three males (A, B, C) made at one Voltzberg lek during the breeding season also indicated skewed male mating success. Male A received 29 (88%) female visits and 11 (92%) copulations, male B received 4 (12%) female visits and 1 (8%) copulation, and male C was unvisited. Lill (1974a) found a relationship between male mating success and territory defense in the Arima Valley. At the Voltzberg site, male A was most successful in defending his territory, which surrounded his display court, contiguous with the territories of males B and C. Male A always displaced intruding males during encounters within his territory. A displacement was recorded when a male left his perch upon the approach of another. Males A and B equally displaced each other during encounters at the boundary between their territories. Male B did not always displace one of the banded nonresident males from his territory. Male A always displaced male C during boundary encounters and often displaced male C within C's territory. Male C maintained resident male status because he displaced nonresident intruding males from his territory and remained at the lek throughout the breeding season. There was no observed interaction between males B and C. Male A maintained the largest territory, 202 m^2, B's territory was 189 m^2, and C's was 36 m^2. Male territory defense and territory size seem to be related to male mating success at this Voltzberg lek.

Male clustering at leks may be assessed by examining the number of resident males per lek, intercourt distance, and lek area. The largest number of resident males in a Voltzberg lek did not reach the smallest number observed in the Arima Valley. Intercourt distance, an indicator of male territory size, and lek area were greater in Suriname. The degree in male clustering at leks was less and interlek distances were larger in Suriname, but a classical lek dispersion was maintained.

Although a higher population density coincided with greater clustering of males at leks at the Arima Valley, this is not an expected result. An increase in population density need not change male clustering, as determined by lek areas, numbers of males per lek, or male territory sizes. For example, an increase in male density might result in an increase in the number of nonresident, "floater" males or in the formation of new leks in the area, neither of which need alter resident male clustering at existing leks. Because we found less male clustering and a lower population density in Suriname, however, a relation between these factors is suggested. Bradbury (1981) proposed that male clustering arises from a preference for clusters by females. If females are attracted to larger clusters then male clustering may increase with population density.

Patchily distributed resources may limit lek size, the number of leks per area, or population density, any of which could subsequently affect male clustering at leks. Secondary forest may be a resource limiting *M. manacus* populations. Although the distribution, abundance, and composition of secondary forest at the Arima Valley and Voltzberg study sites

have not been determined and, consequently, a direct comparison between the sites cannot be made, the Voltzberg site probably contains a much smaller proportion of secondary growth. The abundance of secondary growth may limit manakin display sites, food resources, or nesting sites, which, in turn, might influence male dispersion patterns. These and other factors that may affect *M. manacus* dispersion and population density, such as interspecific competition and predation, should be investigated.

Correlations among indicators of male clustering and population density or habitat resources have been reported in few other lek species. Few studies provide sufficient information to examine these specific relationships. The number of males per lek increased with an increase in population density in the Lesser Prairie Chicken (*Tympanuchus pallidicinctus*, Hoffman 1963), and the Sage Grouse (Patterson 1952), but data from these studies concerning male territory sizes or lek areas are not sufficient to assess male clustering fully. Bradbury (1981) found no relation between the degree of male clustering and density when interspecific comparisons were made of several grouse species. A relationship among population density, male clustering, and habitat resources, has been shown for two lekking mammals. Clustering of male territories increased with increasing population density and food-resource availability in the topi (*Damaliscus korrigum*, Monfort-Braham 1975). In the Uganda kob (*Adenota kob thomasi*), single large territories were prevalent in marginal habitat, while small clustered territories were more common in optimal habitat, and seemed to develop in large populations with high population densities (Leuthold 1966). In the topi and Uganda kob, the degree of male clustering varied along the whole gradient of dispersion patterns, from a uniform field of male territories to a classical lek. It is interesting to note that, although *M. manacus* male clustering was different in Suriname, the classical lek dispersion was maintained. A more detailed examination of lek characteristics in other lek species may reveal a similar pattern of intraspecific variation in male clustering coincident with changes in population density and habitat resources. Such information would further the understanding of the evolution of male dispersion patterns and the adaptive significance of leks.

We wish to thank K. Fristrup and P. W. Trail for their support in all aspects of our fieldwork. We are grateful to STINASU, the Suriname Nature Conservation Foundation, for their assistance and the use of their research facilities at the Raleigh Falls/Voltzberg Nature Reserve. We thank K. Fristrup, P. W. Trail, S. I. Rothstein, and especially A. R. Blaustein for critically reading this manuscript. We are indebted to R. P. Hard for the use of the Zeiss MOP-3 System for Quantitative digital Image Analysis and to C. Flack and S. Sargent for typing the manuscript.

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Received 19 August 1982, accepted 28 January 1983.