LONGEVITY RECORDS FOR SOME NEOTROPICAL LAND BIRDS

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The small family size and low nesting success of many tropical land birds must mean that adult survival rates are high, at least by comparison with land birds of temperate latitudes; but not much direct information is available on survival rates in the tropics. Snow (1962a) found that male White-bearded Manakins (*Manacus manacus*) in Trinidad had an annual survival rate of at least 89%. This was based on a group of established adult males holding courts at a lek, which were followed over a 3-year period. An indirect estimate for the Golden-headed Manakin (*Pipra erythrocephala*), another lek-forming species, based on the proportions of males, females, and young birds in a trapped population, gave a similar figure (Snow 1962b). Fogden (1972) calculated a minimum annual survival rate of 86% for a sample of birds of many different species trapped in a forest in Sarawak, Borneo.

These percentages are far higher than those recorded for European and North American passerines, for which annual survival rates of adults are predominantly in the 30–50% range (Lack 1954, Table 21). They are in fact much closer to the very high survival rates of the larger seabirds.

Fogden's figure was based on one year only, during which conditions might have been either better or less good than usual. Snow's data for the manakins were based on 3 years, but these data could also have been influenced by a period that was unusually favorable or unfavorable. This paper reports on the subsequent survival, over a further 10 years, of the same population of manakins and some other species in the Trinidad study area. Although the data are incomplete, so that annual survival rates can be calculated for only one species and are almost certainly too low, they show that ages of 10 years and more are normal in the two manakin species and probably are attained regularly in a number of other forest species.

STUDY AREA AND METHODS

The study area lies about 500 ft above sea level in lower Arima Valley of the northern mountain range of Trinidad (10–11° N, 61–62° W). The natural vegetation of the area is transitional between lower montane rain forest and deciduous seasonal forest (Beard 1946), but it has been disturbed by a limited amount of cultivation. There is one main dry season (January to May) and one main wet season; the mean annual rainfall is about 100 inches. Temperatures in the shade range from about 75 to 88°F and nightly minimal temperatures vary between 65–75°F. Relative humidity is close to saturation on most nights. The climate and vegetation of the area have been described more fully by Beebe (1952) and Snow (1962a).

Between 1957 and 1961 Snow conducted a mist-netting and banding program in one of the narrow side-valleys through which streams run to their confluence with the Arima River, which flows southward through the valley. This side-valley is an area of secondary forest abutting onto primary forest. Though some large trees remain, most are in various stages of growth, up to a height of about 75 ft. Snow netted regularly at four sites in the lower reaches of this side-valley, three of which were shallow places on the stream used by many forest birds for bathing. He banded all trapped birds with numbered aluminum bands and/or, in a few species, colored plastic bands. He also recorded data on weight, wing-length, and molt. From 1967 to 1971, Lill netted regularly at the same sites and a few others between them, using similar netting techniques. The species, sex, and recapture site of all birds originally banded by Snow were recorded. From late 1968, weight and wing-length measurements were taken on most recaptures by methods similar to those used by Snow. Lill also obtained sight records for some other species banded by Snow, particularly color-banded manakins. He also collected breeding and mating records for banded birds of four species. Four marked birds, two of which had been banded in the main trapping area, were recaptured at infrequently used netting sites elsewhere in the valley.

RESULTS

LONGEVITY

Seventy-one banded birds belonging to 15 species in 8 families were recaptured or ob-

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TABLE 1. Longevity records for two species of manakins in Trinidad.

		Minimal or exact age (yrs)[a] when last recorded
Pipra erythrocephala	males	8.5(2); 9(E); 10(2); 11(3); 11.5(1)
	females	6.5(1); 8(2); 9.5(1); 10(1); 10.5(3); 11(2); 12(3)
Manacus manacus	males	7(2,1E)[b]; 7.5(2); 8(2,1E)[b]; 9(1); 9.5(1); 10(E); 12(E); 14(1)
	females	7(2); 7.5(5); 8(4); 8.5(3); 9(1); 9.5(1); 11(1); 11.5(1); 12.5(1)

[a] The number of recaptured birds of each recorded minimal age is indicated in parentheses. Exact ages are indicated by E.
[b] Two recaptured, one of which was of exactly known age.

served between 1967 and 1971. Fifty-two of these were White-bearded and Golden-headed Manakins. These are the two most common species in the forest avifauna of the study area; Snow trapped more individuals of these two than of any other species (Snow and Snow 1963). The *exact* age at recapture was known for only six of the recaptured birds which had been banded as juveniles; minimal ages at recapture, to the nearest half-year, were determined for the others. Minimal longevity at recapture was calculated as the interval between

TABLE 2. Longevity records for 13 species of Trinidad land birds.

Species	Sex	Minimal or exact* age at recapture (to nearest 0.5 yr)	% wt change	% wing-length change	Distance between capture and recapture sites (meters)
Momotidae:					
Momotus momota[a] (Blue-crowned Motmot)		10.5			
Dendrocolaptidae:					
Dendrocincla fuliginosa		10.5	0		0
(Plain-brown Woodcreeper)		8.5	+1.4		200–300
		8.0	−1.3		0
Formicariidae:					
Dysithamnus mentalis	♂	7.0			1–100
(Plain Antvireo)	♀	10.5	+12[b]	+2[b]	0
Tyrannidae:					
Platyrynchus mystaceus (White-throated Spadebill)		9.0	−5	0	1–100
Myiopagis gaimardii (Forest Elaenia)		10.0	+8	0	1–100
Pipromorpha oleaginea	[c]p ♂	8.5			100–200
(Ochre-bellied Flycatcher)	♀	6.0			300–400
	p♀	8.5			0
Turdidae:					
Turdus albicollis (White-necked Thrush)		11.0			1–100
Turdus fumigatus (Cocoa Thrush)		10.5			1–100
Thraupidae:					
Tangara gyrola (Bay-headed Tanager)		5.0			0
Thraupis episcopus (Blue-gray Tanager)		7.0			0
Thraupis palmarum (Palm Tanager)		9.0	+28	+2	0
Ramphocelus carbo	♂	9.5*	+8	+4	700–800
(Silver-beaked Tanager)	♂	8.0			200–300
Fringillidae:					
Tiaris fuliginosa (Sooty Grassquit)	♂	6.0			c. 6,500

[a] A sight record only.
[b] Changes measured over minimal age minus 1 year.
[c] p adjacent to sex symbols indicates the probable sex of a bird based on winglength for species exhibiting sexual dimorphism in this character but not in plumage color.

banding and (last) recapture plus, in some cases, an additional minimal period during which the bird must have been alive prior to banding, as judged from its plumage-type. Tables 1 and 2 summarize the minimal ages at recapture of manakins and other species separately.

Manakins. Recaptured males and females of both species (*M. manacus* and *P. erythrocephala*) were extremely long-lived compared with most similarly sized passerines of temperate zones. The greatest minimal age at recapture observed in *M. manacus* was for a male at least 14 years old that was still resident at a lek in the study area when Lill's trapping program terminated in 1971. By that time this male had probably been a continuous, territorial resident at the lek for 11.5 years. A comparable minimal age at recapture was recorded for a female *P. erythrocephala* (12 yrs), and 27 of the 52 recaptured manakins were at least 9 or more years old.

We obtained no exact figures for the life span of any individuals of either species. After abandoning their territories at a lek where they have resided for an extended period, old males may survive for at least a year in the general vicinity of the lek. Their disappearance from the lek cannot therefore safely be interpreted as indicating that they have died (Lill 1974a, b). However, the date of death of one male of each species could be pinpointed fairly confidently, since these birds were caught or observed regularly in the year following their reversion to nonterritorial status and then abruptly disappeared from the population. One of these males which had shown progressive loss of body plumage during its presumed final year of life (possibly a senile trait) was exactly 10 years old when he disappeared, and the other was at least 10 years old.

The recapture of 52 manakins in the same small side-valley where they had been banded many years earlier illustrates the sedentary nature of these populations. This might be expected in lek-displaying species which use a traditional mating arena. Many of the recaptured manakins probably occupied the same highly localized home ranges (within the quarter-mile stretch of side-valley forming the study area) throughout much of their lives. The distance between the original capture and subsequent recapture sites was recorded for 22 individuals of each species. At precisely the same site where they were banded, 40.9% of *M. manacus* and 50.0% of *P. erythrocephala* were recaptured; 22.7% of *M. manacus* and 36.4% of *P. erythrocephala* were retrapped within 100 m of their original capture sites.

Sight records were obtained of two additional *P. erythrocephala* females marked by Snow which could not be individually identified or aged very accurately; they visited males at a lek when at least 8.5 years old.

Other species. Minimal ages at recapture ranging from 5 to 11 years were recorded for 19 individuals of 13 other species of land birds of varying ecology and morphology. The greatest minimal ages at recapture among the forest-dwelling insectivores were 10.5 years, recorded for the Plain Antvireo (*Dysithamnus mentalis*), weighing 14 g; the Plain-brown Woodcreeper (*Dendrocincla fuliginosa*), weighing 39 g; and the Blue-crowned Motmot (*Momotus momota*), weighing 100–120 g. Comparable minimal ages at recapture were noted for two thrush species: the White-necked Thrush (*Turdus albicollis*), a forest species, weighing 55–74 g; and the Cocoa Thrush (*Turdus fumigatus*), a species of both forest and plantations, weighing 64–83 g. These are primarily insectivorous but also take small fruits. Minimal ages of 9 and 9.5 years at recapture were found for single individuals of two tanager species which occur primarily in open habitats and are mixed insectivore-frugivores. A minimal age of 8.5 years was recorded for the small, largely frugivorous forest-dwelling Ochre-bellied Flycatcher (*Pipromorpha oleaginea*). The single representative of a primarily granivorous species, the Sooty Grassquit (*Tiaris fuliginosa*), weighing 13 g, was at least 6 years old when recaptured. This species occurs at the interface between forest or second growth and grassland. The results show that some individuals of a number of species differing in habitat, size, and feeding ecology attain great longevity in northern Trinidad. Willis (1972) has recorded longevity similar to that reported here for the forest-dwelling *Dendrocincla fuliginosa* in the more seasonal forests of Barro Colorado Island in Panamá.

Some individuals banded by Snow dispersed beyond the main trapping area. Lill caught two marked birds at locations outside, but within 0.5 mile of the main trapping area, at sites where he netted only rarely. Nonetheless, many individuals were remarkably sedentary over long periods. Seven (38.9%) of 18 birds for which capture and recapture sites were recorded were retrapped at the exact site where they had been banded, and six others (33.3%), within 200 m.

Sight records of a banded Oilbird (*Steatornis caripensis*) at least 12 years old and a banded White-lined Tanager (*Tachyphonus rufus*) at least 6–7 years old indicated that individuals of these species also attain considerable age in Trinidad.

AGE OF BREEDING BIRDS

Manakins. Male White-bearded and Golden-headed Manakins display in leks and the female rears the young alone. Females breed as yearlings, but males experience deferred sexual maturity and do not molt into adult plumage until their second year (Snow 1962a, b). Most males may first breed when much more than one year old, however, since it often takes them a season or more to establish a territory at the mating arena. Also, there is a markedly nonrandom distribution of mating in the lek in which older males appear to be more successful (Lill 1974a, b).

The single nesting record obtained for a banded *P. erythrocephala* was of a female which laid an unsuccessful clutch at a minimal age of 9.5–10 years. This female also visited leks and displayed with males the following season when one year older. Another female copulated when at least 11 years old and two others displayed with males at leks when at least 12 years old. Thus some females of this species may breed for a period of at least 11 years. The single recaptured male which was resident at a lek was observed copulating at a moderate frequency when he was at least 9 years old and in his last season of residence at a lek. He was thought to have died a year later. Although the age of first breeding may be considerably delayed in male Golden-headed Manakins, this observation indicates that they may still breed for at least 7–8 years.

Nests of six female White-bearded Manakins banded by Snow were found in 1967 and 1968. These breeding females were at least 7.5, 8, 8.5 (3), and 10 years old. Four of the six breeding attempts were successful, including that of the hen with a minimal age of 10 years. Five other banded females were observed copulating at minimal ages of 7, 7.5, 8.5 (2), and 9 years, respectively. Three other females displayed with males at a lek when at least 7 and at least 8 (2) years old. Thus some female *M. manacus* may breed until at least 10 years old.

One recaptured male White-bearded Manakin copulated with a female when at least 11 years old and continued to display (and possibly copulate) with visiting females at a lek for a further 3 years. A second male was still resident at a lek and sexually responsive to visiting females when at least 12 years old. Though deferred maturity and the competitive nature of the lek system reduce the male's *effective* breeding life in this species, it seems clear that many males breed for extended periods.

Other species. A banded member of a pair of Blue-crowned Motmots, active in 1969 and 1970 at a nest tunnel whose interior could not be reached for examination, was at least 10 years old in the latter year. The behavior of this bird clearly suggested it was nesting in both years. A female Plain Antvireo was paired and occupied the same tract of forest in the study area from 1968 to 1971; Lill found four of her nests during this period (see also Lill and ffrench 1970). She was last observed nesting when at least 9.5 years old. Her behavior suggested that she also nested in the area the following year, though no nest was found. None of her nesting attempts was successful.

ANNUAL SURVIVAL RATE

Although accurate annual survival rates cannot be calculated from our data, the minimum survival rates which can be calculated for the White-bearded Manakin are of interest.

A total of 264 individuals was banded from May 1958 to September 1961. Of these, 182 were seen subsequently or trapped again at least once during this period; most of them were seen or trapped several times, and some were familiar occupants of, or visitors to, the leks which were being watched. In other words, these 182 birds can be assumed to have been settled on the study area, or at least were regular visitors. The other 82 birds that were trapped and not recorded again were mainly in female or juvenal plumage; probably most of them were unestablished young birds. Of the 182 birds which were recorded again at least once, 30 (17%) were known to be alive an average of 9 years later (table 1). This corresponds to an annual survival rate of 82%. If the calculation is based on the grand total of 264 birds banded, the percentage survival over 9 years is 11.4%, corresponding to an annual survival rate of about 79%. This latter figure is an extreme underestimate, and 82% is also almost certainly a considerable underestimate, since it is likely that a certain number of settled individuals in the study area escaped being retrapped. Furthermore, nearly half of all the birds trapped were given two color bands only (the other half being given

a combination of color bands and a metal band). It is known that some color bands were lost between the time when the birds were last recorded by Snow and retrapped by Lill 7 years or more later, and some birds probably lost both bands. The true annual survival rate over this period can hardly, therefore, have been much less than the 89% calculated for established males at leks (Snow 1962a).

DISCUSSION

Annual survival rates of 80% or more may have important effects on reproductive and other strategies. This is a consequence of the fact that the expectation of further life (derived from the formula $2 - m/2m$, where m is annual mortality expressed as a fraction) increases more and more rapidly as the rate of annual survival increases. Thus if annual survival is increased from 50 to 60% (i.e., by 20%), the expectation of further life increases by 33%, from 1.5 to 2.0 years. If annual survival increases from 70 to 80% (by 14%), the expectation of further life increases by 61%, from 2.8 to 4.5 years; another 12% increase in survival, from 80 to 90%, results in an increase in expectation of further life of 111%, from 4.5 to 9.5 years. Under these circumstances, if the effort and risk entailed by attempts to establish a territory and breed, or to raise a larger rather than a smaller family decrease the individual's chance of survival by only a little, it should be more profitable to defer the attempt or to raise a smaller family; the gain in increased life expectation should outweigh the uncertain immediate advantage. This general argument has been formulated in mathematical terms by Williams (1966), and we wish simply to draw attention to the fact that it is especially applicable to species whose mortality rates are at the level we have found for *M. manacus*.

Another, largely independent process may be involved in the evolution of low reproductive rates. If nest losses are very high (whether they involve risk to the adult or not) and approach 80–90%, any strategy which reduces the percentage loss, even by a little, will very greatly increase productivity. Thus a 10% decrease in nest mortality, from 90 to 81%, would nearly double reproductive success, other things being equal. If a reduction in family size, either by enabling the parent to make fewer visits to the nest or by allowing a smaller and less conspicuous nest, reduces nest mortality by only a little, it might be very strongly selected for. This argument has been used in discussing the single-egg clutch of the Bearded Bellbird (*Procnias averano*) (Snow 1970) and the two-egg clutch of *M. manacus* (Lill, unpubl. data).

The equable climate of tropical forests, a food supply buffered against periods of scarcity by the great diversity of prey species or plant foods, and consequent elimination of the need to migrate, must all be predisposing factors for high annual survival rates in tropical-forest passerine birds. The great variety of nest predators, some of them specialized as such, must tend to depress nesting success. For the above reasons, these factors acting together must be expected to favor all adaptations which further reduce annual adult mortality and those which increase nest safety at the expense of family size. Such a result is to be expected whatever may be the ecological circumstances of particular species. A low annual mortality has been interpreted as a necessary consequence of a low reproductive rate (e.g., Lack 1954). Taking the opposite view, Skutch (1949) has interpreted the low reproductive rate of tropical birds living in stable environments as an adaptive response to their low mortality rates. Whatever the outcome of this long-standing controversy, it seems that both a low adult mortality and a low reproductive rate are promoted, at least in tropical forests, by factors that are not directly involved in the regulation of population levels.

SUMMARY

Records are presented of longevity in two species of manakins and some other tropical-forest birds in Trinidad, based on a trapping program extending over 13 years and on behavioral field study of the manakins.

The greatest minimal age at recapture was 14 years for a male *Manacus manacus* and 12 years for a female *Pipra erythrocephala*. The 14-year-old *M. manacus* had probably been a continuous territorial resident at a lek for at least 11.5 years. Minimal ages at recapture ranging up to 11 years were recorded for a number of other species.

Female *P. erythrocephala* were recorded breeding up to ages of at least 11 years, and female *M. manacus*, up to ages of at least 10 years.

The minimal annual survival rate for *M. manacus* over a 9-year period was calculated from recaptures as 79% (an extreme minimum) or 82% (almost certainly too low).

The true survival rate is thought to have been nearer 89%.

The factors promoting longevity in tropical-forest birds, and some evolutionary consequences of longevity, are briefly discussed.

ACKNOWLEDGMENTS

It is a pleasure to thank all those who facilitated or helped in this study. Barbara Snow, Pooran Ramdass, and John Hernandez assisted in the netting programs. Richard ffrench, Charles T. Collins, Marc Buchanan, C. Brooke Worth, and the Trinidad Regional Virus Laboratory kindly supplied additional information on some banded birds from their netting records. Chris Lill helped with data processing. The work was generously supported by grants from the U.S. Air Force Office of Scientific Research (AF-AFOSR 1254-67) and National Science Foundation (GB 4385, G21007, GB 8313, GB 23824, and GB 16606). Additional support was provided by the New York Zoological Society and Rockefeller University. We wish to acknowledge our indebtedness to the late William Beebe, Bill Conway, Donald and Jocelyn Griffin, and Peter Marler for making this work possible.

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Accepted for publication 20 August 1973.