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A BREEDING BIRD CENSUS AND NESTING SUCCESS IN CENTRAL AMERICA

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INTRODUCTION

In the North Temperate Zone numerous studies of the nesting success of birds have been made, and the results of some of the more important of these studies have been summarised in convenient form by Lack (1954) and Nice (1957). For tropical America, few studies of this sort have been published, these chiefly in recent years by Marchant (1960), Snow (1962 a), and Snow & Snow (1963). For lack of more adequate information, a passing remark on the poor success of nests in tropical forests, made by me long ago (1945), has been frequently quoted. My work in tropical America for the last 35 years has been largely directed to learning the patterns of life of representative species of birds rather than the collection of statistics; for statistics about things of which scarcely anything is known are empty numbers. However, in the course of this work, thousands of nests have been found, and the outcome of many of them was recorded. From these records, it is possible to obtain an indication of the reproductive success of various species, and to compare the hazards of nesting of the avian populations of diverse regions. The present paper is devoted to the presentation of such pertinent information as I have been able to extract from a large accumulation of nest records, gathered during more than three decades.

Most of my effort has been directed to the study of selected nests which were often widely scattered rather than to finding, and learning the outcome of, all the nests in a circumscribed area, which is the proper procedure for determining the reproductive success of a whole population. But during four years I tried to find, and to learn the result of, all the nests in a small area of dooryard and shady pasture surrounding my house. This census of breeding birds in a park-like area in a region which not long ago was covered by heavy rain forest is not of paramount interest. It would be far more valuable to know how many birds nest per acre in the neighbouring primary forest, or in the thickets which densely cover areas from which the forest has been cleared, when such lands have been allowed to rest after bearing one or more crops; but for too many years I have searched fruitlessly for the nests of species which evidently breed in this forest to have any confidence in my ability to discover all or even most of the nests in even a small part of it. And the secondary vegetation which soon takes possession of neglected clearings in the forest is, especially in the early successional stages, so impenetrable to man that to make a thorough search for nests would necessitate cutting trails so close together that the character of the habitat would be significantly altered. Accordingly, in view of the dearth of information on the breeding density of tropical birds, I shall begin this paper by giving the results of my census in the small area where some of my more important data on breeding success were gathered.

A CENSUS OF BREEDING BIRDS

Issuing from a lake near the summit of Cerro Chirripó (12,580 ft.), the Río Peña Blanca, collecting the water of many tributary streams, flows southward to join the Río General. The union of these two rivers and several others forms the Río Grande

de Térraba, which enters the Pacific Ocean northwest of the Golfo Dulce. Our farm lies along the right or western bank of the Río Peña Blanca, just below the hamlet of El Quizarrá, at about 2,500 ft. (762 m.) above sea level. The house stands on a high terrace overlooking the river and some distance back from it. The area where the census was made, about 3·75 acres (1·5 hectares) in extent, includes the level terrace surrounding the house and the rocky pasture between its foot and the broad, clamorous mountain torrent to the east. This area is shaded by scattered trees, more crowded in the dooryard than in the pasture, including many orange trees and guavas *Psidium Guajava*, a few avocado and rose-apple trees *Eugenia Jambos*, and a variety of the spontaneously springing trees of the region. Especially around the house, there is a good deal of planted and native shrubbery that provides sites for nests. The guava trees and some of the shrubs offer fruit for the birds, and beside the house is a feeding shelf where bananas and plantains have been placed for them almost daily since the first census was started. On the south and in part on the west, the area is bordered by an extensive tract of the original forest, which at one point is separated from the pasture by a narrow strip of second-growth woods that has become very tall. Behind the house, also on the west, is a hillside pasture with scattered trees, not included in the census area. To the north and northeast, the area is bounded by a creek which enters the Río Peña Blanca in front of the house. These waterways are fringed by trees and bushes in which certain birds nest. Beyond the creek and river are second-growth woods and thickets, and fields which are alternately planted and permitted to become overgrown with dense weedy vegetation. Between the dooryard and the hillside pasture to the west there was, in the 1940's, about 100 yards of dense *Stachytarpheta* hedge, whose tiny purple flowers attracted many hummingbirds; but by the time the last census was made, in 1961, this untidy hedge had been replaced by neater privet, which offers little to nectar-drinking birds.

In the breeding season of 1943, I found so many nests in this area that I was stimulated to try to find all that would be built there in the course of a year. The first census was started on 1 September 1943 and continued to 31 August 1944, and the second census occupied the following year, 1 September 1944 to 31 August 1945. Then, after a long interval, I began on 1 September 1960 to make a census which continued for the next twelve months. In each census period, by far the greater number of the nests was found from March to July, so that the first census was essentially a record of the breeding season of 1944, and correspondingly for the others. I believe that each year I found nearly all the nests that were built in the area, although a few, especially those hidden amid the dense foliage of orange trees, and very small ones such as those of hummingbirds, probably escaped detection. Only nests in which at least one egg was laid were counted. In a few cases, a bird, after starting a nest, abandoned it before laying and apparently went beyond the area to build another.

Table 1 gives the number of nests found in each of the three years, and the probable number of pairs that attended them. The number of breeding pairs in the area is less certain than the number of nests, for in some cases, when several nests of the same species were occupied successively rather than simultaneously, I was not sure how many pairs were involved. Among the resident birds I have included a few species that were rather constantly present in the area while the census was being made but whose nests escaped detection then, although they were found here in other years. In a few species, such as the hummingbirds and the flycatcher known as the Eye-ringed Flatbill *Rhynchocyclus brevirostris*, the female attends the nest without a mate; this is indicated by a "$\frac{1}{2}$" in the columns giving the number of pairs in the census area.

In 1943–44 the census area contained 83 nests representing 25 species. These nests were, as far as I could tell, attended by 49 pairs and two single females. In addition, six male Rufous-tailed Hummingbirds *Amazilia tzacatl* had established their singing

TABLE 1. *Birds nesting in 3·75 acres of shady dooryard and pasture in El General, Costa Rica.*

	1943–44		1944–45		1960–61	
	nests	pairs	nests	pairs	nests	pairs
Ruddy Ground-Dove *Columbigallina talpacoti*	2	2				
Blue-chested Hummingbird *Amazilia amabilis*					1	½
Rufous-tailed Hummingbird *Amazilia tzacatl*					1	½
Scaly-breasted Hummingbird *Phaeochroa cuvierii*	3	2×½	3	½	1	½
Amazon Kingfisher *Chloroceryle amazona*	1	1				
Blue-diademed Motmot *Momotus momota*					1	1
Olivaceous Piculet *Picumnus olivaceus*			1	1		
White-winged Becard *Pachyramphus polychopterus*	1	1	1	1		
Tropical Kingbird *Tyrannus melancholicus*	1	1	1	1		
Piratic Flycatcher *Legatus leucophaius*	1	1	3	1		
Vermilion-crowned Flycatcher *Myiozetetes similis*	4	3	4	4		
Grey-capped Flycatcher *Myiozetetes granadensis*	6	5	5	3		
Sulphury Flatbill *Tolmomyias sulphurescens*	1	1	2	1	1	1
Eye-ringed Flatbill *Rhynchocyclus brevirostris*					1	½
Black-fronted Tody-Flycatcher *Todirostrum cinereum*	1	1				
Yellow-bellied Elaenia *Elaenia flavogaster*	2	1	1	1		
Bellicose Elaenia *Elaenia chiriquensis*	1	1	1	1	1	1
Paltry Tyranniscus *Tyranniscus vilissimus*		1		1	3	2
Rough-winged Swallow *Stelgidopteryx ruficollis*	1	1				
Blue-and-white Swallow *Pygochelidon cyanoleuca*	1	1			1	1
Southern House Wren *Troglodytes musculus*	3	1	3	1		
Gray's Thrush *Turdus grayi*	5	2	2	1	3	2
Tropical Gnatcatcher *Polioptila plumbea*			1	1		
Yellow-green Vireo *Vireo flavoviridis*		1				
Green Honeycreeper *Chlorophanes spiza*			1	1		
Blue Honeycreeper *Cyanerpes cyaneus*	1	1				
Bananaquit *Coereba flaveola*	1	1	2	1	2	2
Golden-masked Tanager *Tangara larvata*	6	2	4	2	3	2
Silver-throated Tanager *Tangara icterocephala*	1	1	2	1	5	2
Bay-headed Tanager *Tangara gyrola*					2	1
Speckled Tanager *Tangara chrysophrys*		1	1	1		
Scarlet-rumped Black Tanager *Ramphocelus passerinii*	23	6	17	7	8	4
Blue Tanager *Thraupis episcopus*	4	2	3	2		
Buff-throated Saltator *Saltator maximus*					2	1
Yellow-faced Grassquit *Tiaris olivacea*	4	3	1	1	1	1
Variable Seedeater *Sporophila aurita*	8	5	8	5	6	3
Black-striped Sparrow *Arremonops conirostris*		1			2	1
Grey-striped Brush-finch *Atlapetes assimilis*	1	1				
TOTALS	**83**	**49+2♀**	**67**	**39+1♀**	**45**	**25+4♀**
BREEDING BIRDS PER ACRE IN 1943–1944	**28·2**					

posts here and sang every morning before sunrise, except at the height of the dry season. In the following year, the corresponding figures were: 67 nests, 22 species, 39 pairs plus one female. I attribute the diminution of the breeding population to the severe, prolonged dry season of 1945, which delayed the onset of breeding of a number of species and reduced the number of nesting attempts they had time to make. Fifteen years later, in the 1960–61 period, the number of nests in the area had fallen to 45, representing 19 species, of which 25 pairs and four single females were present. In addition, five male Blue-chested Hummingbirds *Amazilia amabilis* and two male Rufous-tailed Hummingbirds had their courtship stations in the area. In the long interval between the second and third census, the chosen area and its immediate surroundings had changed little; and I believe that the shrinkage in the breeding population reflects the deterioration of the wide surrounding region as a habitat for birds, in consequence of the rapid increase in the human population, the destruction of the forests and sterilization of the soil by cropping and burning, and direct persecution of the birds by boys with rubber catapults and stones. During this interval of 15 years, poachers and their dogs had exterminated

a number of the larger birds in the neighbouring forest, including the Chestnut-mandibled Toucan *Ramphastos swainsonii*, the Crested Guan *Penelope purpurascens*, the Marbled Wood Quail *Odontophorus gujanensis*, and the snake-eating Laughing Falcon *Herpetotheres cachinnans*; while a number of other species were drastically reduced in numbers.

In 1944, when 49 pairs, two single female and six courting male hummingbirds were present, the breeding population in the census area of 3·75 acres consisted of 106 individuals, giving a density of 28·2 breeding birds per acre, or at the rate of 2,820 per 100 acres. Many of these birds found part of their food beyond the chosen area, either in the neighbouring forest or in the thickets or pastures on the east, north, and west. On the other hand, numerous birds which nested beyond the census area entered it occasionally or regularly to forage. Few censuses in other parts of the world have revealed a concentration of breeding birds greater than that found here. Bird sanctuaries in England and Germany have supported birds at the rate of 5,800 and 5,600 adults, respectively, per 100 acres; gardens in England may have 3,000 adult birds per 100 acres; and in Tanganyika, Africa, tropical grassland has been credited with a population of 4,000 per 100 acres; but most censuses have shown far lower densities (see Welty 1962 : 348, Table 18.2).

In addition to the 38 species of birds listed in Table 1, the following species have been found nesting in this area since 1942: Blue Ground-Dove *Claravis pretiosa*, White-fronted Dove *Leptotila verreauxi*, Groove-billed Ani *Crotophaga sulcirostris*, Blue-throated Goldentail Hummingbird *Hylocharis eliciae*, Violet-headed Hummingbird *Klais guimeti*, White-crested Coquette Hummingbird *Paphosia adorabilis*, White-tailed Trogon *Trogon viridis*, Red-crowned Woodpecker *Centurus rubricapillus*, Tawny-winged Dendrocincla *Dendrocincla anabatina*, Buff-throated Automolus *Automolus ochrolaemus*, Plain Xenops *Xenops minutus*, Orange-collared Manakin *Manacus aurantiacus*, Oleaginous Pipromorpha *Pipromorpha oleaginea*, Boat-billed Flycatcher *Megarhynchus pitangua*, Sulphur-rumped Myiobius *Myiobius sulphureipygius*, Torrent Flycatcher *Serpophaga cinerea*, Northern Royal Flycatcher *Onychorhynchus mexicanus*, Southern Beardless Flycatcher *Camptostoma obsoletum*, Rufous-breasted Wren *Thryothorus rutilus*, Grey-headed Greenlet *Hylophilus decurtatus*, Turquoise Dacnis *Dacnis cayana*, Buff-rumped Warbler *Basileuterus fulvicauda*, Yellow-crowned Euphonia *Tanagra luteicapilla*, Tawny-bellied Euphonia *Tanagra imitans*, Blue-black Grosbeak *Cyanocompsa cyanoides*, and Streaked Saltator *Saltator albicollis*.

This brings the total number of species found nesting in these 3·75 acres up to 64, which seems unusually large for so small an area. After a succession of ornithologists had been studying the birds on the approximately 3,609 acres of Barro Colorado Island in the Panamá Canal Zone for a quarter of a century, Eisenmann (1952: 3) wrote that direct evidence of breeding (in the form of nests or fledglings) was available for fewer than 100 species, although it is probable that twice that number breed more or less regularly on the island. On a quarter square mile of lowland "jungle" at Kartabo, British Guiana, Beebe (1925 : 153) gathered breeding records of 205 species of birds, but he failed to reveal how many of these records were based on the actual discovery of nests and how many on the far quicker but less satisfactory method of collecting and dissecting the birds.

NESTING SUCCESS

PRELIMINARY CONSIDERATIONS

Ideally, a study of the breeding success of a population of birds should be based on nests found for this purpose alone. Each nest included in the calculation of the percentage of success should be found before the first egg is laid, and thenceforth it should be visited, as briefly as possible and with the utmost caution to disturb nothing in the surroundings, only at the critical periods of laying, hatching, and departure of the nestlings, to learn how many eggs are deposited, how many hatch, and how many young are fledged. Previous knowledge of the size of the set for the species under study, and of the length of the incubation and nestling periods, would obviate numerous visits. Other human activities at the nest, such as measuring eggs, observing incubation and the care

of the nestlings, following their development, and, above all, photography, may, by reducing its concealment, by exciting the parents to forms of protest or distraction displays that may attract hostile eyes or ears, by leaving tell-tale human scent, or by other subtle ways difficult to recognize, increase to an inassessable degree the incidence of predation.

Obviously, these ideal conditions can seldom be realised, except possibly with common birds that can be induced to nest in specially prepared sites, such as nest boxes. Many kinds of nests, especially in the tropics, are so hard to find that the student would feel that he was wasting his opportunities if he did not attempt to learn far more from each of them than just how many fledglings it produced. Another difficulty is that a large proportion of all nests are not noticed until after incubation has begun, or after the young have hatched. Since losses from various causes, such as instability of the nest-site, weather, and predation, begin with the laying of the first egg, it is evident that nests found after several days of incubation have already escaped certain perils, and those discovered after the young have hatched have survived while others in the vicinity have succumbed. Nests found late in the incubation period, and even more those with well-grown nestlings, represent a favoured class; and the inclusion of many such nests in the sample used for the estimate of nesting success may make it appear to be substantially higher than it really is. On the other hand, nests so well hidden that they are not found until the more frequent parental visits that follow the hatching of the nestlings call attention to them are just those that were from the beginning most likely to be successful, so that their exclusion from the sample would make the nesting success appear too low. Moreover, the exclusion of nests not seen until after incubation was in progress might, for many species, leave too small a sample on which to base conclusions.

Another source of error is that it is easier to learn that a nest has failed than that it has been successful. A single visit at any time between the laying of the eggs and the earliest date that the young could leave may, by revealing that the nest is empty, place it among the number of failures; but if one is unable to visit a successful nest at the critical time of fledging, it may have to be excluded from the sample because its outcome is uncertain. These are some of the seemingly insoluble perplexities that beset one who attempts to assess the breeding success of birds in woodland and thicket where widely scattered nests are difficult to find.

Recently Mayfield (1961) proposed a method of escape from the disturbing necessity of rejecting nests that were found late when we come to calculate the rate of nesting success. Indeed, this method permits us to draw conclusions about the success of nests for which we know neither when the eggs were laid nor whether the young survived to the age of fledging. The essence of the method consists in reducing the observational data to units of exposure, the suggested unit being the nest-day, equivalent to one nest whose history is known for one day. If we assume that losses tend to be randomly distributed throughout a given stage in the nesting cycle, and know for a sufficiently large number of nests how many succumb in 24-hour intervals, we can calculate the rate of success, perhaps with an accuracy greater than the conventional procedure ordinarily gives us. Although the mathematical theory underlying Mayfield's method seems to be unassailable, it fails to give due consideration to a serious practical difficulty. The daily visits to the nests that would provide the most complete data for the subsequent calculations would probably wear trails to them or otherwise increase their exposure, especially in the case of low nests, with resulting increase in predation. I suspect that, for many species of birds, Mayfield's procedure would give far too low an index of nesting success.

What we wish to know is the success of nests under natural conditions, wholly unaffected by the activities of the observer. Obviously, except perhaps for nests that can be viewed from afar, we cannot be certain how they would have fared if we had paid

no attention to them; and without knowing the rate of success of nests that are completely undisturbed, we cannot measure the effects, unfavourable or otherwise, of our visits of inspection. We must content ourselves with the closest approximations we can make.

THE DATA

With the foregoing admission of its imperfections, I offer the information on nesting success which I have collected in various parts of Central America over an interval of more than 30 years. Probably the soundest records are those gathered in the census area around my house in the years 1943–1945 and 1961 (Table 2). Wherever possible, high nests were inspected by raising a mirror above them, with a minimum of disturbance; but in certain cases clustering foliage made this method of examination unsatisfactory, and the outcome of the nest could not be ascertained. This area was not " managed " in any way (other than the usual cleaning of pastures, pruning of trees when birds were not nesting, and the like), except that intruding snakes known to be nest robbers, no less than venomous kinds, were whenever possible removed. For the first three years, the proportion of the nests in which at least one egg was laid that produced at least one fledgling was surprisingly uniform, 38, 39 and 38% of the nests of known outcome. Fifteen years later, the success of a smaller sample of nests had, inexplicably, risen to 53%. Taking the four years together, 208 nests of 37 species showed a nest-success of 41%.

TABLE 2. *Nesting success in 3·75 acres of census area in El General, Costa Rica.*

Year	Species	Nests of known outcome	Successful nests	% successful
1942–43	20	45	17	38
1943–44	20	76	30	39
1944–45	21	55	21	38
1960–61	16	32	17	53
4 years total	**37**	**208**	**85**	**41**

Table 3 presents data on 23 species of altricial birds which nearly always nest in gardens, plantations, pastures, thickets, and other secondary vegetation, but not in primary forest. Only two of these species, the Little Hermit Hummingbird *Phaethornis longuemareus* and the Orange-collared Manakin *Manacus aurantiacus*, breed in the forest with any frequency, and their nests are then usually found near its edges. All 23 species build their nests amid vegetation rather than in holes. Their structures are open or roofed (oven-shaped or pensile); the Little Hermit attaches its nest beneath the tip of a palm leaf, and the Buff-rumped Warbler *Basileuterus fulvicauda* builds its oven-shaped nest on a bank. The records which enter into Table 3 were gathered over many years, nearly all of them in the valley of El General between 2,000 and 3,000 ft. above sea level. Some of the nests in this table were found in the census area and accordingly are also included in Table 2.

In part A of Table 3 I have included every nest of known outcome in which at least one egg was laid, at whatever stage it was found. Part B is restricted to nests found before the last egg was laid. Since, as previously explained, nests found at an advanced stage of incubation, or with nestlings, have already survived some of the perils to which nests are exposed, one would expect class A to show a substantially higher rate of success than class B; assuming that the nests in class A were found randomly at all stages between laying and the departure of the young, the average stage of the nests in this group when found would be about halfway through the period of occupancy, and observed losses

TABLE 3. *Nesting success of 23 species of Central American altricial birds with open or roofed nests in clearings and second-growth.*

SPECIES	A. ALL NESTS			B. NESTS FOUND BEFORE LAST EGG WAS LAID							
	No. of nests	Nests successful	Nest-success %	No. of nests	Nests successful	Nest-success %	Eggs laid	Eggs hatched	% hatched	Young fledged	Egg-success %
Ruddy Ground-Dove *Columbigallina talpacoti*	22	5	23	9	3	33	17	7	41	5	29
White-fronted Dove *Leptotila verreauxi*	13	5	38	4	2	50	7	4	57	4	57
Little Hermit Hummingbird *Phaethornis longuemareus*	14	4	29	7	2	29	14	12	86	3	21
Scaly-breasted Hummingbird *Phaeochroa cuvierii*	14	6	43	5	1	20	9	3	33	1	11
Orange-collared Manakin *Manacus aurantiacus*	54	11	20	23	3	13	46	17	37	6	13
Tropical Kingbird *Tyrannus melancholicus*	18	5	28	9	1	11	18	8	44	1	6
Boat-billed Flycatcher *Megarhynchus pitangua*	17	7	41	8	3	38					
Vermilion-crowned Flycatcher *Myiozetetes similis*	16	4	25	10	3	30	29	12	41	6	21
Grey-capped Flycatcher *Myiozetetes granadensis*	38	17	45	30	13	43	76	47	62	31	41
Yellow-bellied Elaenia *Elaenia flavogaster*	32	13	41	20	4	20	36	13	36	6	17
Bellicose Elaenia *Elaenia chiriquensis*	39	11	28	21	7	33	37	13	35	8	22
Gray's Thrush *Turdus grayi*	44	14	32	24	6	25	62	19	31	10	16
Orange-billed Nightingale-Thrush *Catharus aurantiirostris*	15	10	67	8	5	63	15	10	67	10	67
Yellow-green Vireo *Vireo flavoviridis*	12	7	58	6	2	33	14	8	57	4	29
Buff-rumped Warbler *Basileuterus fulvicauda*	24	8	33	15	5	33	30	19	63	9	30
Golden-masked Tanager *Tangara larvata*	31	9	29	20	5	25	38	23	61	8	21
Silver-throated Tanager *Tangara icterocephala*	18	8	44	11	3	27	22	8	36	5	23
Scarlet-rumped Black Tanager *Ramphocelus passerinii*	133	50	38	80	35	44	156	96	62	66	42
Blue Tanager *Thraupis episcopus*	42	20	48	27	12	44	50	34	68	22	44
Buff-throated Saltator *Saltator maximus*	35	13	37	23	9	39	44	18	41	14	32
Yellow-faced Grassquit *Tiaris olivacea*	65	20	31	44	13	30	105	47	45	27	26
Variable Seedeater *Sporophila aurita*	31	17	55	16	6	38	31	14	45	11	35
Black-striped Sparrow *Arremonops conirostris*	29	13	45	14	7	50	27	19	70	12	44
TOTALS, 23 SPECIES	**756**	**277**	**37**	**434**	**150**	**35**	**883**	**451**	**51**	**269**	**30**

should be only about half as great as in the group under observation throughout the period of occupancy. The actual difference between the two classes, 37% against 35% (Table 3, columns 4 and 7) is surprisingly small. The explanation of this unexpectedly close agreement seems to be that when many of these nests were found I was more interested in learning incubation and nestling periods than in nesting success; hence I tended to neglect nests of common birds discovered after the eggs hatched, as they could not yield the information that I was most eager to gather. Yet these advanced nests were just those most likely to be successful.

Columns 4 and 7 of Table 3 give what might be called " nest-success ", as every nest which yielded at least one living fledgling was counted as successful. The final column gives what may be designated " egg-success ", as it gives the percentage of all the eggs laid which produced young that survived to leave the nest by their own power. As is to be expected, egg-success is somewhat lower than nest-success, 30% as opposed to 35% for the class B nests, since some eggs fail to hatch, and some nestlings are lost, even in nests which are (at least partly) successful.

It is of interest to compare the nesting success of certain species in Table 3 with the success of related species in other regions. On the island of Trinidad, the nest-success of 227 class B nests of the Black-and-white Manakin *Manacus manacus*, largely a forest-dweller, was 19% (Snow 1962 a), in contrast to 13% for the much smaller number of class B nests of the Orange-collared Manakin of Costa Rica, a species that prefers light secondary woods and forest edges to the interior of forests and often nests in gardens and coffee plantations that are near such habitats. Two Trinidad thrushes that nest wholly or in part outside the forest, *Turdus fumigatus* and *T. nudigenis*, may be compared with the Central American *T. grayi*. Class B nests of these two Trinidad thrushes showed a nest-success of 33% (Snow & Snow 1963), *T. grayi* only 25% for class B nests. Perhaps predators are more numerous on the mainland than on the island of Trinidad.

Table 4 contains data on the nesting success of 30 species of birds that build open or roofed nests in the primary forest of El General, between 2,000 and 3,500 ft. above sea level. Because of the small number of records available, I have included in this table two species of ground-nesting nidifugous birds (a tinamou and a quail) and also the Black-throated Trogon *Trogon rufus*, whose niche in a trunk is open and exposed. These records are the harvest of many years of searching through these wet forests; the paucity of nests of all the species reflects the difficulty of finding them; the meagre proportion that were successful suggests the hazards that the birds face when they attempt to rear their families and the disappointments which confront the ornithologist who tries to complete the story of their lives. The nest-success of 23·5% for class A nests and 23% for class B nests is substantially lower than the corresponding figures, 37% and 35%, for nests in the adjoining clearings. It is understandable why many forest birds venture into these clearings to build their nests, while the reverse tendency, that of open-country birds to enter the high forest for breeding, is very rare. In this table, as in Table 3, the difference in the success of class A and class B nests is far less than theory leads us to expect.

Table 5 gives the success of 16 species of birds that nest in holes and burrows of various types, all in El General between 2,000 and 3,500 ft. above sea level. Since the number of records is small, I have lumped together birds of the forest and those of the clearings; several of the included species nest in both situations. The two trogons carve deep, well-enclosed chambers in rotting trunks or termitaries, both in the forest and beyond it. The Rufous-tailed Jacamar *Galbula ruficauda* breeds in short burrows in banks in the high forest and amid lighter vegetation, and the same is true of the Buff-throated Automolus *Automolus ochrolaemus*. The White-whiskered Puffbird *Malacoptila panamensis* is confined to the forest, where it digs short descending tunnels in sloping or nearly level ground. The Scaly-throated Leaf-tosser *Sclerurus guatemalensis* digs tunnels

TABLE 4. *Nesting success of 30 species of birds with open or roofed nests in the forests of El General, Costa Rica, 2,000–3,500 feet a.s.l.*

SPECIES	A. ALL NESTS		B. NESTS FOUND BEFORE LAST EGG WAS LAID				
	No.	Successful	No. of nests	Eggs laid	Eggs hatched	Young left	No. of successful nests
Great Tinamou *Tinamus major*	3	0	1	3	0	0	0
Marbled Wood-Quail *Odontophorus gujanensis*	4	1	2	9	4	4	1
Ruddy Quail-Dove *Geotrygon montana*	11	4	2	4	4	2	1
Long-tailed Hermit Hummingbird *Phaethornis superciliosus*	7	1	3	6	2	2	1
Little Hermit Hummingbird *Phaethornis longuemareus*	3	1	2	4	4	1	1
Violet-headed Hummingbird *Klais guimeti*	1	0	1	2	0	0	0
Blue-crowned Woodnymph Hummingbird *Thalurania colombica*	2	0					
Black-throated Trogon *Trogon rufus*	6	2	2	4	1	0	0
Black-hooded Antshrike *Thamnophilus bridgesi*	2	1	2	4	4	2	1
Plain Antvireo *Dysithamnus mentalis*	6	3	2	4	4	3	2
Slaty Antwren *Myrmotherula schisticolor*	4	1	1	2	1	0	0
Tyrannine Antbird *Cercomacra tyrannina*	2	1	1	2	0	0	0
Chestnut-backed Antbird *Myrmeciza exsul*	3	1					
Streaked-chested Antpitta *Grallaria perspicillata*	3	0					
Blue-crowned Manakin *Pipra coronata*	10	1	4	8	2	0	0
Yellow-thighed Manakin *Pipra mentalis*	3	0	3	6	2	0	0
Orange-collared Manakin *Manacus aurantiacus*	14	1	3	6	0	0	0
Thrush-like Manakin *Schiffornis turdinus*	3	0	3	5	1	0	0
Rufous Piha *Lipaugus unirufus*	1	1					
Golden-crowned Spadebill *Platyrinchus coronatus*	11	6	5	10	4	4	2
Sulphur-rumped Myiobius *Myiobius sulphureipygius*	5	2	5	9	6	3	2
Northern Bentbill *Oncostoma cinereigulare*	1	0					
Lowland Wood-Wren *Henicorhina leucosticta*	3	0	1	2	2	0	0
Long-billed Gnatwren *Ramphocaenus rufiventris*	1	1	1	2	2	2	1
Tawny-crowned Greenlet *Hylophilus ochraceiceps*	2	1	1	2	0	0	0
Tawny-bellied Euphonia *Tanagra imitans*	2	0					
Red-crowned Ant-Tanager *Habia rubica*	6	0	2	2	0	0	0
Grey-headed Tanager *Eucometis penicillata*	3	1	2	5	1	0	0
Blue-black Grosbeak *Cyanocompsa cyanoides*	4	1					
Orange-billed Sparrow *Arremon aurantiirostris*	10	1	3	6	5	0	0
TOTAL 30 SPECIES	**136**	**32**	**52**	**107**	**49**	**23**	**12**

Success of Class A nests 23·5%

Success of Class B nests 23·0%

Eggs hatched 46%

Eggs producing fledglings 21·5%

in banks or in the mass of clay raised up on the roots of an uprooted tree, always in the forest, as far as I have seen. The Black-faced Ant-thrush *Formicarius analis* nests in low hollow trunks, often in cavities open to rain at the top, and the Bicoloured Antbird *Gymnopithys leucaspis* chooses still lower cavities, often in the centre of decaying palm stumps, open above. The Southern House Wren *Troglodytes musculus* hides its nest in an amazing variety of holes and niches, always in clearings and frequently in or near human habitations (Skutch 1953). The other birds in this table all breed in holes in trees, usually carved by themselves in the cases of the two woodpeckers, the piculet, and the xenops; caused by decay or made by other birds in the cases of the araçari, the dendrocincla, and the Streaked-headed Woodcreeper *Lepidocolaptes souleyetii*. Practically all the nests of the last three species were near rather than in the forest. The Golden-naped Woodpecker *Tripsurus chrysauchen* prefers to carve its nest cavity deep into fairly sound wood, high in a dying or dead tree standing near the forest where it often forages.

TABLE 5. *Nesting success of* 16 *species of hole-nesting birds in El General, Costa Rica.*

SPECIES	A. ALL NESTS		B. NESTS FOUND BEFORE LAST EGG WAS LAID				
	No.	Successful	No. of nests	Eggs laid	Eggs hatched	Young left	No. of successful nests
Massena Trogon *Trogon massena*	3	0					
White-tailed Trogon *Trogon viridis*	5	1	4	8	2	0	0
Rufous-tailed Jacamar *Galbula ruficauda*	8	4	6	14	12	7	3
White-whiskered Puffbird *Malacoptila panamensis*	10	6					
Fiery-billed Araçari *Pteroglossus frantzii*	3	1					
Golden-naped Woodpecker *Tripsurus chrysauchen*	22	14	14	?	?	22	9
Red-crowned Woodpecker *Centurus rubricapillus*	8	5					
Olivaceous Piculet *Picumnus olivaceus*	7	4	2	5	4	0	0
Tawny-winged Dendrocincla *Dendrocincla anabatina*	7	4	3	6	2	2	1
Streaked-headed Woodcreeper *Lepidocolaptes souleyetii*	2	1					
Buff-throated Automolus *Automolus ochrolaemus*	7	3	4	9	6	5	3
Plain Xenops *Xenops minutus*	2	2	1	2	2	2	1
Scaly-throated Leaf-tosser *Sclerurus guatemalensis*	3	2	3	6	6	4	2
Black-faced Ant-thrush *Formicarius analis*	10	6	6	12	8	7	4
Bicoloured Antbird *Gymnopithys leucaspis*	3	2					
Southern House Wren *Troglodytes musculus*	45	33	25	90	68	56	18
TOTAL 16 SPECIES	145	88	68				41
Success of Class A nests			60·6%				
Success of Class B nests			60·3%				

Taken together, these varied hole-nesters were almost three times as successful as the birds with open nests in the same forests where many of them lived, and about 60% more successful than the birds that built open or roofed nests amid the vegetation of the clearings. The Southern House Wren, with a record of 33 productive nests out of 45, shows a nest-success of 73%, almost twice as high as that of the open-nesters amid which it lives.

The data for each of the localities in Table 6 were gathered in a single season, by the writer alone, or with the help of a boy in El General in 1939 and with less help at Vara Blanca in 1938 and Los Cartagos in 1963. The six localities which appear in this table may be characterized as follows:—

Barro Colorado Island. A forested island of about 3,600 acres in Gatún Lake, Panamá. Nests were found within the forest, in a narrow clearing where the buildings stood, and along the shore of the lake.

Motagua Valley, Guatemala. "Alsacia" plantation, where the breeding season's work was done, lies at the foot of the Sierra de Merendón, opposite Quiriguá. Nests were found in scrubby pastures, banana plantations, second-growth woods and thickets, and along the shores of the Río Morjá, a tributary of the Motagua. Primary forest was too distant to have much effect on the bird life.

El General, Costa Rica. The season's work was done by the Quebrada de las Vueltas, below San Isidro, in plantations, shady pastures, second-growth, and a considerable tract of heavy forest.

Vara Blanca, Costa Rica. Studies were made at " Montaña Azul ", on the exceedingly wet northern or Caribbean side of the Cordillera Central, largely in clearings at the very edge of a vast extent of practically undisturbed, heavy, subtropical forest.

Los Cartagos, Costa Rica. " La Giralda " dairy farm, where the season's work was done, lies near the western end of the massif of Volcán Barba, a few miles from the hamlet of Los Cartagos, Province of Heredia, and not over 5–6 miles in an air-line from the preceding locality, but on the opposite or Pacific side of the continental divide. Extensive pastures with scattered trees were separated by wooded ravines, one of which contained over 100 acres of heavy subtropical forest.

Sierra de Tecpán, Guatemala. A range in the Department of Chimaltenango, above the town of Tecpán (or Tecpam) in west-central Guatemala. Observations were made on the estates of " Chichavac " and " Santa Elena ", amid temperate-zone woods of pine, oaks and other broad-leafed trees interrupted by extensive bushy pastures. Above 9,000 ft. were forests of huge cypress trees *Cupressus Benthamii*, but few nests were found in this zone.

TABLE 6. *Nesting success in six Central American localities.*

Locality	Altitude in feet	Period	Nests found	Species represented	Nests of known outcome	Nests successful	% successful
Barro Colorado Island, Canal Zone	85–500	Feb.–June, 1935	83	38	62	13	21
Motagua Valley, Guatemala	200–800	Feb.–June, 1932	96	41	68	29	43
El General, Costa Rica	2,000–2,300	Jan.–June, 1939	136	61	85	28	33
Vara Blanca, Costa Rica	5,000–6,000	July, 1937–Aug., 1938	123	47	80	42	53
Los Cartagos, Costa Rica	6,500–7,500	Feb.–July, 1963	81	27	41	18	44
Sierra de Tecpán, Guatemala	8,000–10,000	Jan.–Dec., 1933	82	28	67	37	55

In compiling Table 6 I have excluded colonial nesters, of which one species was observed on Barro Colorado, one at Vara Blanca, two in the Motagua Valley, and none in the other localities. A single fortunate or ill-fated colony may greatly alter the percentage of success for the whole locality. In view of the small number of pertinent records, I have lumped hole-nesters, everywhere a minority, along with birds that build in the open.

Table 6 shows that nesting success increases as one rises from the tropical lowlands into the subtropical and temperate altitudinal zones. The effect is complicated by the character of the vegetation, and doubtless by other factors which we cannot analyse without far more data than are available. Low as was the success of all the nests found on wooded Barro Colorado in 1935, that of those actually in the forest was still lower: here, of 35 nests of known outcome, only 5 (14%) produced at least one living fledgling. Such poor success is evidently widespread in the lowland forests of Central America. In Belize or British Honduras, Willis (1961 : 499) studied 53 nests of the ant-tanagers *Habia rubica* and *H. gutturalis*, of which only 8 (15%) were successful. From at least

147 eggs laid in these nests, only 16 young were fledged, an egg-success of 11%. All but two of the nests which failed were emptied by predators.

Although the locality where I worked in El General in 1939 was higher than that in the Motagua Valley, the nesting success was 10% less, probably due to the influence of the forest and the predators it supported. The poor success at Los Cartagos, compared with Vara Blanca, seemed to be caused by high predation, by White-tipped Brown Jays *Psilorhinus mexicanus*, Blue-throated Toucanets *Aulacorhynchus caeruleogularis* and probably also by squirrels, on the breeding species to which I devoted most attention. Amid the far more varied and concentrated bird life at Vara Blanca a quarter of a century earlier, it was possible to follow the nests of a greater and more representative variety of species in a single season. Here and on the Sierra de Tecpán the nesting success was almost as high as in northern localities where studies of this subject have been made.

DISCUSSION

Snow & Snow (1963) have pointed out that thrushes of the genus *Turdus* breeding in the tropical forests of Trinidad are about as successful as their congeners in English woodlands, and also that in both Trinidad and England thrushes that live in plantations, gardens, parkland, and other man-made habitats on the other hand show much higher nesting success. They suggested that further studies may demonstrate that the low success observed in tropical forests is typical of forests as a whole, whether in or beyond the tropics, and that the real contrast may be " not between the tropics and temperate regions, but between relatively unaltered habitats, where predators abound, and man-made habitats, where predation is much reduced ".

The present study supports the Snows' conclusion that losses of nests are substantially more frequent in tropical forests than in neighbouring clearings where the vegetation has been thinned and altered in character by human activities. In these habitats altered by man, the birds' chances of hatching their eggs and rearing their young may be from 50–100% greater; and many forest birds take advantage of this situation by entering adjoining clearings to build their nests, even when they regularly return to the forest to forage (as is true, for example, of the Gray-headed Tanager *Eucometis penicillata*). Whether or not nest losses in temperate-zone woodlands are consistently as high as those cited by Snow & Snow for *Turdus* is a question which must await further studies for decision; practically all the studies of nesting success (especially of birds with open nests) summarised by Lack (1954 : 78–79) and by Nice (1957) are of species that breed outside the forest. Evidently nests are difficult to find in dense woodland everywhere, and this discourages studies of nesting success.

It seems evident, however, that Central American birds breeding outside the forests, especially lowland birds, are considerably less successful than birds nesting outside the forest in northern countries. Twenty-four studies summarised by Nice (1957 : 307) show a nest-success of 49·3%, and 29 studies (largely overlapping the foregoing) show an egg-success (fledging success) of 45·9%. This is substantially higher than the success for the population as a whole that I found in any lowland area in Central America; only a few of the species listed in Table 3 equal or surpass it, and unfortunately the number of records available for these species is relatively small. Perhaps, however, the difference between my results and those tabulated by Lack and Nice may reflect differences in the degree of human alteration of the areas in which the studies were made rather than a true contrast between tropical and temperate-zone conditions. Although I regard forest diversified by clearings as more favourable for life-history studies than a large expanse of unbroken forest, I have always tried to work in localities where human disturbance was relatively slight. Evidently many of the studies of breeding success in northern lands were made in areas far more drastically altered by man, with a resulting diminution of " natural " predators.

Nesting success may be substantially higher in the drier parts of tropical America than in the humid regions and compares favourably with that in northern countries. On the Santa Elena Peninsula of western Ecuador, a region of far less rainfall and far lighter and more open vegetation than any part of Central America where I have spent more than a few weeks, the great mass of data published by Marchant (1960) shows that few open-nesting species for which he gathered more than 20 adequate records had a nest-success of less than 50%: of 283 nests of the dove *Eupelia cruziana*, 57% were successful; of 188 nests of the flycatcher *Pyrocephalus rubinus*, 50% were successful; of 184 nests of the mockingbird *Mimus longicaudus*, 51% were successful; of 264 nests of the finch *Neorhynchus peruvianus*, 50% were successful. One of the poorest showings was made by the seedeater *Sporophila telasco*, with 37% success for 254 nests. In this species, 24 of the failures were due to desertion. For the 14 open-nesting species for which Marchant gathered the most complete data, he knew the outcome of 1,538 nests, of which 771 (50·1%) were successful. These nests contained 3,618 eggs, of which 1,640 (45·3%) produced fledglings. These percentages are surprisingly close to those given by Nice for birds of the North Temperate Zone. A factor contributing to the high rate of success in Marchant's study was evidently the short incubation and nestling periods of some of the birds, compared with related species in the humid tropics. The shorter period of occupancy of nests may decrease the incidence of predation.

In the tropics, as beyond them, hole-nesting birds are, on the average, far more successful than those which build in the open, doubtless because their nests are harder to find and to reach. Unfortunately for our present purposes, the tabulated studies of the breeding success of northern hole-nesting birds are mostly in the form of egg-success rather than of nest-success. For the Golden-naped Woodpecker, one of the hole-nesters for which I have most data, I could nearly always tell whether a nest was successful, and how many young were reared, by counting them as they returned to their nest to sleep, but I could rarely reach the high hole to count the eggs. The nest-success of 64% found for this woodpecker compares favourably with the egg-success of 77% for two species of woodpeckers in Finland (Pynnönen, *in* Lack 1954 : 76); but it should be remembered that, in any species, nest-success is nearly always higher than egg-success. The egg-success of the Southern House Wren, 62%, was higher than that of the Northern House Wren *Troglodytes aëdon* of the United States in two of the studies summarised by Nice (1957 : 308) but lower than that in another two studies.

Published information on the success of hole-nesting birds in the tropics is difficult to find. At Amani, 5° S. in Tanzania, East Africa, White-rumped Swifts *Micropus caffer*, breeding in nests built by swallows at the top of a smooth, white-washed wall, reared 74 young from 97 eggs, giving an egg-success of 76% (Moreau 1942). In the Chestnut-collared Swift *Cypseloides rutilus* in Trinidad, 15 of 24 nests produced fledglings, giving a nest-success of 63% (Snow 1962 b : 137).

What are the causes of the high mortality of nests in the tropics? A few nests are lost from mechanical causes, such as tilting over or falling because built on an inadequate support, or being struck by a falling branch; but in none of the localities where I have worked has wind caused any considerable destruction. Some eggs fail to hatch because of infertility or death of the embryo; and in late nests at high altitudes, when cold rains may become frequent and long-continued, eggs may become chilled or nestlings perish while their parents seek food.

By far the most important cause of nest losses is predation. Usually it is impossible to tell what has emptied the nest between successive visits of inspection, but over the years a good deal of evidence has accumulated. In tropical American lowlands, snakes appear to destroy more nests than any other class of animals. In the clearing in the forest on Barro Colorado Island, two nestlings of the Crimson-backed Tanager *Ramphocelus dimidiatus* were successively taken from the same nest by snakes of different

kinds in the course of 18 hours. In the same locality, all but two nests in a colony of 15 nests of the Yellow-rumped Cacique *Cacicus vitellinus* were pillaged by a Mica *Spilotes pullatus*, which evidently hid in one of the long pensile pouches by day and at night emerged to plunder neighbouring nests. The destruction of the colony would doubtless have been complete but for my intervention (Skutch 1954). Below a nest of the Yellow-green Vireo *Vireo flavoviridis* beside the Río Pacuar in El General, I found a green tree snake with a nestling in its mouth; and nearby lurked a larger snake of a different colour, apparently awaiting its opportunity. It would be tedious to relate all the instances of predation by snakes that have come to my attention; it is evidently largely because they become rarer as one ascends into the Central American highlands—and above 6,000 or 7,000 feet one may pass a whole season afield without seeing one—that nesting success increases with altitude. The Mica, one of the chief nest-robbers, occurs as high as 4,000 ft. in Costa Rica, but above this it soon disappears.

In the semi-arid no less than in the humid parts of tropical America at low altitudes, snakes are apparently the most devastating predators on birds' nests. Marchant (1960 : 354) found them the most formidable predators in southwestern Ecuador, at least in certain years. Statistical analysis by Lloyd (1960) supports the view that the fluctuations in breeding success which Marchant found from year to year " can most reasonably be attributed to changes in the abundance of snakes ".

The behaviour of the parent birds themselves often suggests that snakes are the predators they most fear. Some species approach their eggs or young with the utmost circumspection; yet, while they hesitate to go to the nest, they all the while utter loud calls which would seem to cancel all their caution. If their hesitancy has reference to sharp-eared mammals or predatory birds, this seems ridiculous; if, however, their chief concern is snakes with poor hearing, the great caution and loud calls may not be incongruous.

Of mammalian predators, I have seen squirrels and White-faced Monkeys *Cebus capucinus* and Tayras *Tayra barbara* in the act of pillaging nests. Undoubtedly numerous other quadrupeds do so; but many of them, such as the abundant opossums of several species, are active chiefly at night, when their depredations are likely to escape observation.

Among the nest-robbing birds, the chief culprits are toucans (both the big *Ramphastos* and *Pteroglossus* of the lowlands and the little toucanets *Aulacorhynchus* of the cool mountains), jays, and Swallow-tailed Kites *Elanoides forficatus*, which snatch the young from exposed nests that they can reach while they hover in the air. The only other falconiform bird that I have seen rob a nest was an immature Black Hawk-Eagle *Spizaetus tyrannus* which carried off two feathered nestlings of the Vermilion-crowned Flycatcher, crushed in its talons together with the straws that roofed their domed nest. Other diurnal birds of prey, such as the Barred Forest-Falcon *Micrastur ruficollis*, prey inveterately upon fledglings, but I have not surprised one of them attacking a nest. Still others, such as the Laughing Falcon or Guaco *Herpetotheres cachinnans*, are among the best friends of nesting birds, as they feed almost wholly on snakes.

If a nest has been torn apart, one may suspect a mammalian or an avian rather than a reptilian predator, for the latter usually swallow eggs or nestlings without damaging the structure that sheltered them. If one is uncertain of the fate of nestlings barely old enough to leave the nest that have disappeared between visits of inspection, an examination of the lining may afford a clue. If the lining lies flat, the young birds probably left by their own power; if it has been pulled up, this was probably done by the young clinging to the bottom of the nest in a vain attempt to save themselves from being carried off by a predator. Sometimes, however, the lining of a newly abandoned nest is pulled up by a bird gathering building materials.

In lowland forests, I have sometimes found a roofed or pensile nest, such as are constructed by numerous wrens, American flycatchers and other birds, empty and with a

neat round hole in the roof or rear wall. Evidently some predator made this opening to extract the eggs or young, instead of removing them through the doorway provided by the nest's builder. I do not know what animal does this, but suspicion falls upon bats. In the tropics of both hemispheres, there are species of these flying mammals known to prey on birds (Allen 1939); but because of their nocturnal habits, the role of these exceedingly numerous animals as nest robbers is difficult to assess.

Many nests are destroyed by ants. Fire ants (*Solenopsis*), which prefer open places and avoid deep shade, seem more destructive than army ants (*Eciton*), whose mobile hordes operate chiefly in and near woodland. Once I watched a bird as tiny as a Variable Seedeater continue to incubate her eggs while a column of army ants crawled over her nest, from which they soon withdrew without having done any apparent damage to her or the eggs. I have also known army ants to pass over unattended eggs without injuring them; and once a swarm of small army ants flowed over the mouth of a White-whiskered Puffbird's short burrow in the forest floor, without harming the feathered nestlings. Fire ants are more persistent, sometimes continuing to molest a nest until the incubating parent, fidgeting under their persecution, cracks an egg shell, which gives the insects access to the contents and seals the nest's doom. Nests in holes in trees and burrows in the ground are no more immune from their attacks than are open structures. I have known fire ants to ruin the nests of birds so diverse as kingfishers, trogons, woodpeckers, goatsuckers, and hummingbirds. If they find nestlings too young to escape, they leave only the fleshless bones in the nest.

One reason for the higher proportion of failures among the nests of tropical birds may be their longer exposure to predation. Small passerines in the tropics may have incubation periods 25–50% longer than those of temperate-zone birds of about the same size, with nests of the same type. Even in a single family, such as the wood warblers or wrens, the tropical species may have longer incubation and nestling periods than northern species. It does not follow, however, that more rapid development, especially of nestlings, would decrease losses from predation. More rapid development would necessitate more rapid feeding, with more frequent parental visits to the nest. If, as I suppose, predators, especially snakes, find nests by seeing the parents approach and leave them, the more frequent passage of the birds through the predator's field of vision might result in the more effective summation of stimuli, with the consequent discovery of nests that might escape detection if parental visits were more widely spaced. More rapid development might be attained only at the price of heavier predation.

These are some of the causes of the high losses of birds' nests in humid tropical lowlands. Although in my limited experience with araçari toucans *Pteroglossus* I have not known them to make a second nesting attempt in the same year if their first attempt fails, most birds try again and again until they succeed in rearing a family or the breeding season ends. The broods of tropical birds, however, tend to be small and the season of reproduction of most species is of limited duration, so that, with the prevailingly low rate of success, relatively few young can be reared to independence in the course of a year. From these considerations, I long ago concluded that, if they escape the perils of infancy, tropical birds must, on the whole, enjoy fairly long lives; for otherwise their populations could not be maintained (Skutch 1940). Recently Snow (1962a) has provided supporting evidence by his outstanding statistical study of the Black-and-white Manakin in Trinidad. Only 19% of 227 class B nests produced fledglings. By means of two to four nesting attempts in a season, each female reared on average one fledgling a year; and with about one-third of the fledglings surviving to adulthood, she may contribute 0·33 individuals to the adult population of the following year. This low rate of increase is sufficient to maintain the population, because the annual survival rate of adult males (and presumably also of adult females, since the sex ratio is about 1 : 1) was 89%. Although by their courtship antics these manakins make themselves most conspicuous

in the undergrowth of tropical forest with its many predators, no other small bird whose survival rate is known lives so long.

SUMMARY

In a park-like area of 3·75 acres adjoining primary forest in Costa Rica, at an altitude of 2,500 ft., 83 nests, made by about 49 pairs of birds and two single females, were found in one year. Over a period of 20 years, 64 species were recorded as nesting in this same area.

The difficulties of learning the actual rate of success of nesting birds are discussed, and it is concluded that, in view of the impossibility of assessing the effects of visits of inspection to nests in natural habitats, statements of breeding success are at best rough approximations of what happens in the absence of an observer.

In the area of the census, nest-success (the proportion of nests in which at least one egg was laid that produced at least one living fledgling) was 38–53% in four different years. During the four years 41% of 208 nests were successful.

Of 756 nests of 23 species of altricial birds of the Central American lowlands that build open or roofed nests in clearings and second-growth, 37% were successful. When the computation is restricted to nests found before the last egg was laid (class B nests), 35% of 434 nests were successful, and 30% of 883 eggs produced living fledglings.

In the neighbouring forests, nesting success was much lower, only 23·5% of 136 open or roofed nests producing at least one fledgling. Many forest birds increase their chances of success by entering neighbouring clearings to breed, but few open-country birds build their nests in the forest.

In both forest and clearings, hole-nesting birds in Central America are much more successful than open-nesters, as has been found also in the North Temperate Zone.

A comparison of the results of a single season's observations in each of six Central American localities shows an increase of nesting success with altitude. In lowland Panamá, the nest-success was only 21%, in the Subtropical Zone of Costa Rica 53%, and in the altitudinal Temperate Zone of Guatemala 55%. The effect of altitude is complicated by differences in the amount of forest in the localities chosen for study, as well as by other factors difficult to assess.

In both the tropics and the North Temperate Zone, nest losses are substantially higher in woodland than in man-made habitats, evidently because there are fewer predators in the latter; but, even in clearings in Central America, nesting success was considerably lower than it was found to be in numerous studies in the North Temperate Zone. The difference may, however, reflect the greater " wildness " of the localities where the writer's studies were made, rather than a true contrast between tropical and temperate zone conditions.

Snakes appear to be of the greatest single cause of nest losses in tropical America, but mammals, a few predatory birds, ants, and possibly even bats, destroy many eggs and young.

Since small broods and heavy predation permit only a small annual contribution to the adult population, it is evident that, in order to maintain the species, adults must enjoy fairly long lives. Recent statistical studies support this theoretical conclusion.

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