

BREEDING AND THE ANNUAL CYCLE IN THREE TRINIDAD THRUSHES

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FIVE species of the Turdidae breed in Trinidad. One species of *Catharus* and one of *Platycichla* are highland birds, breeding in montane forest mainly above 2,000 feet. The other three are typical members of the genus *Turdus*, they are widely distributed over the island and all occur from sea level to 2,000 feet, where the habitat is suitable. It is with the three *Turdus* species that this paper is concerned.

Their habitat preferences are different but overlapping. *T. albicollis* is rather strictly confined to forest. *T. fumigatus* occurs in forest, well-timbered plantations, and even in gardens if they have large trees and are close to forest. *T. nudigenis* occurs in more open habitats: orchards, gardens, and park-like savanna. Outside the breeding season it also feeds to some extent in secondary forest. Thus in the breeding season *T. albicollis* and *T. nudigenis* are completely isolated from each other by habitat, and *T. fumigatus* overlaps both of them. All three species feed on invertebrates obtained from the ground and on fruit, and no important differences were noted in their feeding habits, though the differences in their habitats must ensure that to some extent they take different foods.

They are medium-sized thrushes, all of much the same build. *T. albicollis*, the forest thrush, is the smallest (weighs mostly 50–60 grams); *T. fumigatus* and *T. nudigenis* are about the same size (weigh mostly 65–80 grams and 60–75 grams, respectively). All are plain-colored above, and their colors seem to some extent to be related to their habitats. Thus *T. albicollis* is dark olive-brown above, a similar color to some of the ground-living antbirds and furnariids, while *T. fumigatus* is a rich cinnamon color above, very like the woodhewers found in the same habitats. By contrast, *T. nudigenis*, inhabiting semi-open country, is a paler, greyer olive-brown, similar to the color of several other birds inhabiting this kind of country. *T. albicollis* is the only one with any contrasting feature in its plumage: it has a white throat patch which shows up conspicuously in the poor light of the forest. *T. nudigenis* has a broad ring of bare golden-yellow skin around the eye, lacking in the other two.

The quality of their songs too seems related to their habitats. The leisurely, rather simple and measured phrases of *T. albicollis*, and the vigorous, more varied and quickly repeated phrases of *T. fumigatus* are both far-carrying and suitable for the forest, where visibility may be only a few yards and sounds are muffled by the thick vegetation. They are much finer performances than the halting, feeble phrases of *T. nudigenis*, which probably relies more on visual contact than on song in intraspecific relations. All three species sing

from cover, not from the exposed song-perches favored by northern thrushes.

Little information was obtained on territory, pair-formation, and the function of song in these species. In *T. fumigatus* at least, the only one whose behavior could regularly be observed, territorial behavior seemed to be weakly developed: birds were occasionally seen foraging close to the nest of another pair, and none of the displays associated with defense of territory in northern *Turdus* species was ever seen. Individual birds were, however, sedentary, and in two cases color-banded pairs remained together for successive years.

All three species build nests of typical thrush type, comparatively bulky cups strengthened with mud and with an inner lining of dry fibers. The two forest thrushes use much moss in the outer part of the nest: *T. nudigenis*, nesting in drier places, uses various plant materials, but usually not moss. *T. fumigatus* and *T. albicollis* usually place their nests on substantial supports such as crotches and recesses in tree trunks, stumps, tops of tree ferns and niches in banks. Many of the nests of *T. fumigatus* were found along roads and paths in cocoa plantations. As a consequence, more nests of this species were found in roadside banks than in any other site, but in forest, too, *T. fumigatus* was found to use banks more often than *T. albicollis*. *T. nudigenis* usually places its nest in a fork of the branches of a tree or large shrub: none was found in a crotch or recess in a tree trunk, on a stump, or in a niche in a bank, nest-sites which seem properly to belong to the forest habitat, though many such are now available in places where *T. nudigenis* breeds.

The data presented here were collected during 4½ years in the Northern Range of Trinidad, the range of forested mountains that runs along the north side of the island, at latitude 10° 45' N, while one of us (D.W.S.) was Resident Naturalist at Simla, the New York Zoological Society's tropical field station. We are grateful to the following persons for help in the field work: Dr. W. G. Downs and Dr. T. H. G. Aitken of the Rockefeller Foundation, for nesting and trapping data obtained during the field studies of the Trinidad Regional Virus Laboratory; and Commander C. S. Bushe, Mr. John Dunston, and Dr. V. C. Quesnel, for nest records of *T. nudigenis*. H. Mayer-Gross and B. Nelson have kindly allowed us to quote unpublished information on the breeding success of *Turdus* species in England. This work, part of a wider program of studies on the biology of neotropical birds, was generously supported by National Science Foundation Grants G 4385 and G 21007.

BREEDING SEASONS

Information on the breeding seasons came from regular searching for nests in all months of the year. Altogether, 200 breeding records were obtained for *T. fumigatus*, 74 for *T. albicollis*, and 151 for *T. nudigenis*. Four hundred six of the total of 425 records were based on nests found, the remaining 19 on observations of recently fledged young birds.

Figure 1 shows the breeding seasons of the three species based on these records (see also Table 1). It will be seen that the breeding seasons of *T.*

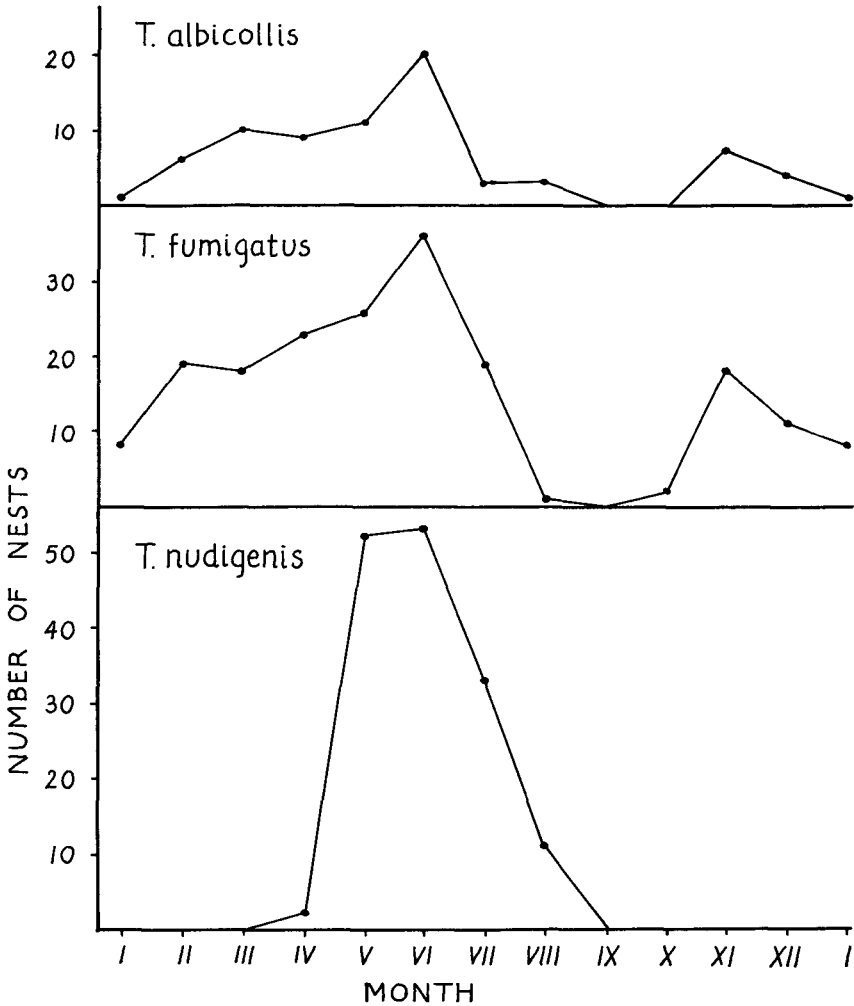


FIG. 1. Breeding seasons of *Turdus albicollis*, *Turdus fumigatus*, and *Turdus nudigenis* in Trinidad.

fumigatus and *T. albicollis* (the two species inhabiting forest) are long and very similar to each other, while that of the open-country *T. nudigenis* is far shorter. In the first two species, breeding starts usually in late October or early November; after a peak in November activity declines in December and January, and then rises again to a second, main peak in May and June. It continues until July or early August and then ceases. Only in September was there no record of breeding.

TABLE 1
BREEDING SEASONS, IN HALF-MONTHLY PERIODS
(number of nests started)

Dates	<i>T. fumigatus</i>	<i>T. albicollis</i>	<i>T. nudigenis</i>	Dates	<i>T. fumigatus</i>	<i>T. albicollis</i>	<i>T. nudigenis</i>
October				April			
1	1			1	13	5	
2	1			2	10	4	2
November				May			
1	10	3		1	13	4	18
2	8	4		2	13	7	34
December				June			
1	4	2		1	26	11	35
2	7	2		2	10	9	18
January				July			
1	2			1	14	2	24
2	6	1		2	5	1	9
February				August			
1	9	3		1	1	2	9
2	9	3		2		1	2
March							
1	9	3					
2	9	7					

In *T. nudigenis* breeding does not begin until late April. It quickly rises to a peak and ends at about the same time as in the other two species. It may be noted that only for this species is Belcher and Smooker's statement of the breeding season correct (Belcher and Smooker, 1937). For the other two they give far too short a season.

January–May are the dry months of the year. The wet season begins variably, usually in May, and continues until the end of the year, often with a minor interruption in September or October. The effect of the dry season is more severely felt in open country than in the forest, and this may be the environmental factor ultimately responsible for the short breeding season of *T. nudigenis*, which does not start to breed until the wet weather begins, compared with the other two, which breed right through the dry season.

Breeding activity is reduced in the two forest thrushes at the beginning of the dry season, but this decline is not directly related to weather. It seems to be inherent in the birds' physiological cycle. Thus breeding declines in December, before the dry season has begun, and increases again in February or March, while the dry season is at its height. This was especially clear in *T. fumigatus* in the 1960–61 breeding season. There was, as far as could be ascertained, no breeding in December and January, although the weather was

rather wet. Breeding started again in February, when the weather was very dry, and continued through March, which was also dry. Song, which is very closely related to breeding, fluctuated in the same way. But if the weather is exceptionally dry in the latter half of the dry season breeding is eventually inhibited. In 1959, March and the first half of April were very dry, and there was an unusual gap in breeding in this period. In 1961, the drought was severe at the end of the dry season, and wet weather did not begin until 22 May. No nests were started from 9 April to 31 May, an exceptional gap not recorded in any other year. After the wet weather began there was a great outburst of breeding and more nests were recorded in the first half of June than in any other half-monthly period in the whole course of the study. It is probable that in other years, too, the varying numbers of nests recorded in the months March–May were correlated with the severity of the dry weather, but the numbers are too small for statistical significance.

The main song-period of each species coincides very closely with its breeding season. It was especially striking how in *T. albicollis* and *T. fumigatus* the reduction in breeding activity from December to March was exactly matched by the incidence of song, which varied in the different years as the breeding season varied. In *T. nudigenis* the period of regular, sustained song is short, like the breeding season, lasting from April to August, but a little song was heard in each year from February or March onwards; and in each year occasional song, which was usually subdued, was heard in November or early December.

NUMBER OF BROODS

Nests of *T. fumigatus* in sheltered sites, especially in roadside banks, are regularly reused. Usually they are reused only if the previous brood was successful. Of the 26 instances of reuse of a nest, the previous nesting was known or presumed to have been successful in 18 instances. In seven of the cases where the previous nesting had been unsuccessful, the nest was not reused until several months later; in only one case was a nest reused soon after a previous failure.

Two records were obtained of the same nest being used four times, and one of a nest being used three times, at intervals which suggested successive nestings by the same bird, and a record was obtained of four nestings, probably successive, by a color-banded bird. Nine other records were obtained of a nest being used twice at intervals suggesting successive nestings. The first-egg dates for the series of three or four successive nestings were as follows:

- (1) 12 May, 8 July, 6 August (molt), 9 November;
- (2) 17 May (molt), 14 November, 19 January, 21 April;
- (3) 1 June (molt), 23 November, 1 May (molt), 11 November;
- (4) 23 April, 7 June (molt), 14 October.

TABLE 2
INTERVALS BETWEEN SUCCESSIVE BROODS IN *TURDUS FUMIGATUS*

Month in which previous nesting attempt ended	Number of days before laying of first egg of next clutch
December	20, 33, 38, 52, (132)
January-February	9, 20, 33, 52, 63
April-May	13, 16, 18, 199
June-July	6, 10, 11, 27, 113, 152, 154
August	95

The presumed times of molt are based on trapping records (see below). It will be apparent from these records that three or four broods may be reared in the year.

Table 2 gives all the intervals between successive nesting attempts recorded for *T. fumigatus*. It will be seen that re-laying followed rather soon after the ending of a previous nesting attempt in the months April-July, or else there was a very long interval, doubtless due to the fact that the molt intervened. In December-February the intervals were mostly rather long, but variable, corresponding to the erratic and low incidence of breeding during these months.

For *T. albicollis* comparable data could not be collected, as the nests, being usually in more exposed positions, are rarely reused. There were only three cases of successive nestings in the same nest, the intervals being long (June, 38 days; December, 77 days; January, 87 days).

For *T. nudigenis* there were two records of successive nestings in the same nest, the intervals being 10 and 15 days. Thus two broods may be reared in their short breeding season, but only exceptionally could three be reared, if a pair started early and continued late.

CLUTCH SIZE

Clutch sizes of the three species are given in Tables 3-5, and family sizes in Table 6. Mean clutch size is highest in *T. nudigenis*, lowest in *T. albicollis*,

TABLE 3
CLUTCH SIZES OF *T. FUMIGATUS*, *T. ALBICOLLIS*, AND *T. NUDIGENIS*

	Numbers of clutches of			Mean clutch size
	2	3	4	
<i>T. fumigatus</i>	19	66	2	2.80
<i>T. albicollis</i>	47	2	1	2.08
<i>T. nudigenis</i>	9	41	7	2.96

TABLE 4
CLUTCH SIZE OF *T. FUMIGATUS*

Month	Numbers of clutches of		
	2	3	4
October		1	
November	3	5	
December	1	5	
January	1	3	
February	2	5	2
March	2	8	
April	3	6	
May	2	10	
June	4	14	
July	1	9	
All months	19	66	2

and intermediate in *T. fumigatus*. In view of their habitat distributions, this might suggest that food for young thrushes is more abundant in semi-open country than in the forest. There is no evidence on this point, but in open country, where the effect of the dry season is more severe, there may well be a greater flush of insect and other invertebrate life in the ground at the beginning of the wet season than in the more equable conditions of the forest. On the other hand, in *T. nudigenis*, with its short breeding season, selection for a large family may have an overriding effect, whereas in the two species with long breeding seasons there might be a greater selective advantage in the reduced strain entailed in feeding and attending a smaller family. Another factor could be suggested: the high rate of nest predation in forest might, as suggested by Skutch (1949), result in a reduction of clutch size in the two forest species. All, or none, of these factors may be operating, but as yet there is no information enabling them to be tested critically.

There was no evidence of any seasonal change in clutch size in *T. fumigatus* (Table 4) or *T. albicollis*, but in *T. nudigenis* (Table 5) there was a slight,

TABLE 5
CLUTCH SIZE OF *T. NUDIGENIS*

Month	Number of clutches of			Mean clutch size
	2	3	4	
May	1	19	3	3.1
June	6	13	4	2.9
July	2	9		2.8

TABLE 6
FAMILY SIZE
(Number of young in nests at 8 days or older)

	Numbers of families of				Mean family size
	1	2	3	4	
<i>T. fumigatus</i>	11	21	12		2.02
<i>T. albicollis</i>	4	10			1.72
<i>T. nudigenis</i>	2	18	20	2	2.52

but statistically insignificant, decrease in mean clutch size as the season advanced.

INCUBATION AND FLEDGING PERIODS

In all three species the eggs are laid daily. In *T. fumigatus* and *T. albicollis* the time of laying was ascertained for seven eggs, as follows:

<i>T. fumigatus</i>	0900-1215 (probably about 1100, when the bird was seen on the nest)
	0715-0940
	0945-1445 first and second eggs of the same clutch
	0700-1100
	before 1130 (probably about 1030, when the bird was sitting)
<i>T. albicollis</i>	1100-1215
	0720-1145

In working out incubation periods (taken as the time from the laying of the last egg to the hatching of the last young), it has therefore been assumed that the last eggs were laid in the latter half of the morning.

According to the frequency of visits of inspection there was usually a period of from several hours to a day within which the last nestling might have hatched. This accounts for the varying accuracy of the incubation periods which follow. Two were found with almost complete accuracy:

<i>T. fumigatus</i>	12½ (±½), 13, 13 (±1), 13 (±1), 13½ (±¼), 14½ (±¼), 17
<i>T. albicollis</i>	12½ (±¼), 12½ (±½)

In the nest with a 14½-day incubation period, one of the three eggs did not hatch. In the nest with a 17-day incubation period, one of the three did not hatch, and of the other two one hatched two days after the other. In the seven other nests all the eggs hatched. The two long incubation periods were

therefore probably caused by the inefficient incubation behavior of the female.

Fledging periods were obtained only for *T. fumigatus*. At one nest, two young flew at 13 or 14 days; at another, two young flew at 14 days, and at the third, two young flew at 15 days. These latter were the two young mentioned above, which hatched at an interval of two days, and they left the nest at the same interval.

In *T. fumigatus*, information on the length of time the young are attended by the parents after leaving the nest was obtained for three families. In one case, a single young bird was seen to be attended by a parent up to 32 days after fledging; in another, a young bird was seen to be fed by the male (color-banded) 28 days after fledging; and in the third case the young bird was still being attended by the male (color-banded) 22 days after leaving the nest. This last young bird was trapped and was found to have started its post-juvenile body molt.

BREEDING SUCCESS

In calculating breeding success, only those nests have been used that were found before the clutch was complete. If nests found during incubation are included, the sample is biased, as the nests found during incubation should be balanced by those that failed at an early stage and so were not found (Snow, 1955*b*). This is especially important when the rate of nest loss is high in the early stages, as in these tropical thrushes. Unfortunately for the present purpose, the majority of the nests of *T. nudigenis* were used by the Trinidad Regional Virus Laboratory for obtaining blood samples from nestlings, so their success cannot be analyzed.

For *T. fumigatus*, 57 nests can be used in the analysis of breeding success; 33 of them, and perhaps 4 more, reached the hatching stage, and young birds fledged from 19 of them (33%). Nests by roadsides and in plantations and gardens were more successful than those in forest: 14 (40%) of the 35 nests in the former habitats were successful, compared with only 5 (23%) of the 22 nests in forest. For *T. albicollis*, 35 nests can be used for analysis; 17 of them, and possibly 6 more, reached the hatching stage, and young fledged from 7 of them (20%). Only 21 nests of *T. nudigenis* can be used, and 7 of them (33%) resulted in fledged young. Predators appeared to be responsible for nearly all the nest losses, but in not a single case was the identity of the predator definitely known.

It is possible to make only a rough calculation of the annual reproductive rate of the three species, taken as the product of the number of nests started per pair per year, the percentages of nests that succeed, and the average family size at the time of fledging. This gives the average number of young reaching the fledging stage per pair per year; the effective reproductive rate—the number surviving to maturity—is of course unknown. The average number

TABLE 7
MOLTING SEASONS
(Numbers of individuals trapped in the three main molt-categories)

Month	<i>T. fumigatus</i>			<i>T. albicollis</i>			<i>T. nudigenis</i>		
	None	Body only	Wing	None	Body only	Wing	None	Body only	Wing
January	14		1	8			6		
February	8			1			3		
March	3			1			3		
April	4			2			5		
May	11						7		
June	15	1		1		2	10		
July	4	2	2	1			13		
August	3		4	3			11	2	5
September	2	1	2	4	2				3
October	2	3	3	3			1	1	1
November	8			6			3	2	3
December	11			9			20	1	

of nests started per pair per year is the least accurately known of these quantities, but it may be taken as three for *T. albicollis* and *T. fumigatus* and two for *T. nudigenis*. We may then make the following rough calculation of the reproductive rates:

T. albicollis 3 broods, 20% success, family size 1.72; reproductive rate 1.0.

T. fumigatus 3 broods, 33% success, family size 2.02; reproductive rate 2.0.

T. nudigenis 2 broods, 33% success, family size 2.52; reproductive rate 1.7.

These figures suggest that in spite of its short breeding season *T. nudigenis* may reproduce more efficiently than *T. albicollis* and not much less well than *T. fumigatus*.

THE MOLT

Data on the molt were obtained by examining birds caught in mist-nets. Each individual caught was noted as showing no molt, body molt (including head and coverts), or wing and tail molt. Several individuals were caught more than once. If they were caught more than once in the same month their state of molt at first trapping was used for analysis; if they were recaptured in a later month their state of molt could again be used. In this way, 131 records of molt were obtained for *T. fumigatus*, 106 for *T. nudigenis*, and 51 for *T. albicollis*, distributed in all months of the year (except May for *T. albicollis*). The results are tabulated in Table 7. For *T. fumigatus* the molting period was found to be July–October, and for *T. nudigenis* August–November. Only two specimens of *T. albicollis* were caught in wing molt, both in June, at the same time and in the same place. None of the 13 adults caught in July–

October were molting the wing. But the numbers for this species are rather few, and it may be that when molting they tend to skulk in the forest undergrowth and fly little. It would be surprising if, with its essentially similar breeding season, *T. albicollis* did not molt at the same season as *T. fumigatus*.

For *T. fumigatus*, limited information was obtained on the duration of molt in the individual. Three individuals were caught twice during the same molt. One which was just beginning to molt when first caught had very nearly finished 90 days later, the wing and tail being complete and the body still molting a little. Another bird accomplished about half of its molt in 50 days, and another was caught at too short an interval for calculation of the total period of molt. Table 2 shows that two of the five intervals between successive nestings that spanned the molt were as short as 95 and 113 days. These birds must have started to molt very soon after they had finished nesting and started to nest again very soon after their molt was finished.

The restricted molting season of a bird like *T. fumigatus*, which has a very long breeding season, raises a general problem. The young may hatch in any month from November to August; their postjuvinal molt probably normally follows soon after they leave the nest (as found in one juvenile banded as a nestling and trapped 22 days after leaving the nest), but their next, full molt comes in the same three months of the year for all of them. Clearly the timing of the annual physiological cycle must be regulated by some external factor, and it must be the action of this external factor in inducing the first full molt at the appropriate time that brings each individual in step with the population as a whole.

COMPARISON WITH NORTH-TEMPERATE *TURDUS* SPECIES

Annual cycle.—Except that its breeding season is a bit later, the annual cycle of *T. nudigenis* is very similar to that of a north-temperate thrush: it nests from late April to August, and molts from August to November. In *T. fumigatus*, and probably also in *T. albicollis*, the molt takes place at about the same time, but immediately after the molt they begin to breed, and breeding continues, at varying intensity, until July. The annual cycle of Trinidad birds is being dealt with in more detail in another paper. With respect to the thrushes, it is sufficient here to point out that the late October and November peak of breeding in *T. fumigatus* and *T. albicollis* seems at first sight to be homologous with the autumn recrudescence of gonads in resident northern thrushes, which in exceptionally mild autumns may culminate in breeding (Snow, 1955a). Such an interpretation, however, is questionable. For any sure conclusion one would need a series of observations on the breeding seasons of these and closely related species north through Central America on the one hand, and south across the Equator on the other hand; and supporting data on the season of molt would also be desirable. So far only Skutch's data

(Skutch, 1960) for *Turdus grayi* and *T. assimilis* at 10° N in Costa Rica provide a link with the north-temperate region, and they show no autumn breeding.

An alternative explanation is that the October–November peak is the homologue of the main October peak of breeding south of the Equator. This peak is very marked at Cantagalo, 4° 30' S, still prominent at Belem, 1° 18' S (Pinto, 1953), and probably persists as far north as coastal British Guiana, 6° N, where there is a secondary peak of breeding in September (Davis, 1953). There is not enough information on the breeding season of *Turdus* species in British Guiana for comparison with Trinidad, but in Surinam, also at 6° N, the breeding season of *Turdus leucomelas* begins in November and lasts until June (Haverschmidt, 1959), thus closely resembling that of *T. fumigatus* and *T. albicollis* in Trinidad.

Clutch size.—The Trinidad thrushes have smaller clutches than north-temperate species. This is part of a well-known phenomenon, that tropical birds lay smaller clutches than birds of temperate regions, but there is not yet general agreement as to its significance (Lack, 1949; Skutch, 1949). It is of interest that the two species with very long breeding seasons show no evidence of seasonal changes in clutch size, as are found in north-temperate thrushes. There is strong evidence that seasonal variation in clutch size is correlated with seasonal changes in the amount of food which the parents can collect for the young, which depends partly on the length of time for which they can search for it (day length) and partly on its abundance. At 10° N day length varies little, and no seasonal variation in clutch size would be expected for this reason. But there is a great contrast between conditions in the dry season and in the wet, in both of which *T. fumigatus* and *T. albicollis* breed. In the dry season the ground, even in the forest, is usually dry and more or less hard except immediately after rain; while in the wet season it usually remains moist. For thrushes, which obtain their animal food from the ground, such a difference would be expected to have a considerable effect on their ability to feed nestlings. If food for the young were the critical factor determining the upper limit of clutch size, it would be expected that clutch size would be adjusted according to the conditions, as is found in British thrushes (Snow, 1958). These considerations, while not conclusive, suggest that some other factors may be involved in determining clutch size.

Tempo of breeding.—The rate of development of Trinidad thrushes, as measured by their incubation and fledging periods, does not seem to be significantly different from that of their north-temperate congeners (e.g., Snow, 1958; Young, 1955). But in the rate at which successive broods follow one another, *T. fumigatus*, and probably also *T. albicollis*, differs markedly from the north-temperate species; while in *T. nudigenis*, with its short breeding

TABLE 8
NESTING SUCCESS OF TRINIDAD AND SOME NORTH-TEMPERATE THRUSHES

Species	Country	Habitat	Number of nests	Number successful	% successful	Source
<i>T. albicollis</i>	Trinidad	Forest	35	7	20	This study
<i>T. fumigatus</i>	"	"	22	5	23	"
"	"	Plantation	35	14	40	"
<i>T. nudigenis</i>	"	"	21	7	33	"
<i>T. merula</i>	England	Woodland	107	15	14	Snow (1958)
"	"	"	63	14	22	Nelson (unpublished)
"	"	"	59	12	20	Mayer-Gross (unpublished)
<i>T. ericetorum</i>	"	"	32	4	13	"
"	"	Copses	73	22	30	"
<i>T. merula</i>	"	Gardens	169	84	50	Snow (1958)
<i>T. migratorius</i>	U.S.A.	Parkland	45	25	55	Howell (1942)
"	"	Parkland and cemetery	176	86	49	Young (1955)

season, the intervals between broods appear to be much as in the north. With their very long breeding seasons, very quick successions of broods would not be expected in *T. fumigatus* and *T. albicollis*; but the selective factors favoring long intervals are not altogether obvious. It may be that too quick a succession of nesting attempts would impose a strain on the parents that would offset the advantage gained from the higher reproductive rate, but we have no evidence that nesting activities in tropical conditions impose a sufficient strain for this effect to operate. When a nest has been successful, there might be a selective advantage in tending the fledged young for a longer period than in the north, and so increasing their chances of survival. Although we have little information on this point, two of the three periods for which fledged young of *T. fumigatus* were found to be attended by a parent (28 and 32 days) were longer than any of the 33 periods recorded for *T. merula* in England (Snow, 1958). Finally, it may be that a quicker succession of nests might result in an increase in the already high rate of nest predation, since it would be advantageous for predators to continue to hunt in an area where they had recently found a nest. With the data available the problem can only be raised, not answered.

Breeding success.—Information on breeding success for some northern thrushes is summarized in Table 8, together with the data for the three Trinidad species. It is evident that breeding success varies widely in the same species according to habitat, nests in man-made habitats being more successful than those in woodland. It is noteworthy that breeding success in forests

in Trinidad is much the same as in temperate woodland. If further studies confirm that this is so (and comparisons must be limited to related species with similar nesting habits), it may be necessary to re-examine the generalization, often made, that nesting success in tropical forest is exceptionally low. It certainly is low, but this may be the rule rather than the exception. The real distinction 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.

SUMMARY

Observations on the breeding of *Turdus albicollis*, *T. fumigatus*, and *T. nudigenis* were made in Trinidad over a period of 4½ years. *T. albicollis* breeds only in forests, *T. nudigenis* in semi-open country, and *T. fumigatus* overlaps them both, breeding both in forests and well-timbered plantations and gardens.

The two forest thrushes have very long breeding seasons lasting for nearly nine months, in contrast to *T. nudigenis*, which breeds at the beginning of the wet season, from late April to August. It is suggested that this difference is ultimately due to the more severe effect of the dry season outside the forest. The two forest thrushes breed right through the dry season, but breeding is inhibited if the drought is very severe at the end of the dry season.

T. fumigatus and probably also *T. albicollis* make three or four nesting attempts in the course of the breeding season; *T. nudigenis* not usually more than two.

Clutch size is highest in *T. nudigenis* (mean 2.96), lowest in *T. albicollis* (mean 2.08), and intermediate in *T. fumigatus* (mean 2.80). There was some evidence of a slight seasonal decline in clutch size in *T. nudigenis*, but no evidence of any seasonal variation in the two species with long breeding seasons.

Incubation periods of *T. fumigatus* ranged from 12½ to 13½ days, with two long periods of 14½ and 17 days which were probably due to inefficient attentive behavior by the female. Fledging periods were 13–15 days. Two incubation periods of *T. albicollis* were both 12½ days.

Nesting success (percentage of nests started which resulted in fledged young) was 33 per cent in *T. fumigatus*, 20 per cent in *T. albicollis*, and 33 per cent in *T. nudigenis*. In *T. fumigatus*, nests in forests were less successful than those in other habitats. It is shown that in spite of its short breeding season the reproductive rate of *T. nudigenis* is probably higher than that of *T. albicollis* and not much less than that of *T. fumigatus*. Data are presented on the season of molt in the three species. In *T. fumigatus* the duration of molt in the individual was found to be about 90 days.

On the basis of these data, a comparison is made between the breeding of Trinidad and north-temperate thrushes.

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