THE RED-WINGED BLACKBIRD IN TROPICAL MARSHES

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In temperate zone marshes the emergence of aquatic insects during the spring and summer provides a rich and rapidly renewed food supply which is exploited by a number of species of birds for food for their offspring. The breeding cycles of these birds and many of the features of their ecologies and social systems are related to this abundant and synchronized food supply (Orians 1966; Willson and Orians 1963; Willson 1966; Orians and Horn 1969). Some of these species of birds, or close relatives, also occur in the tropics, but little work has been done on the food-producing properties of tropical marshes or the adaptations of breeding passerine birds to them. Of the common marsh-breeding passerines of North America, the Red-winged Blackbird (*Agelaius phoeniceus*) ranges as a resident, breeding species in the lowlands of México and Central America south to northern Costa Rica. In Costa Rica, where I carried out my studies, Redwings breed on both the Atlantic and Pacific slopes of the northern part of the country, and there is an isolated population on a large, shallow lake on the continental divide (Arnold 1966).

My investigations in Costa Rica were designed to answer the following questions. (a) How does the availability of food in tropical marshes compare with that in temperate marshes? In particular, does food ever become as abundant in tropical marshes as in temperate marshes during the peak emergence of aquatic insects in late spring? (b) How does the Redwing respond to the annual cycle of events in tropical marshes? Does it utilize different foods when breeding? How have its mating and spacing patterns responded to tropical conditions? (c) Why do tropical Redwings lay fewer eggs than temperate Redwings?

THE STUDY AREAS

TABOGA, GUANACASTE PROVINCE

The major study area was located on the Estación Experimental Jiménez Nuñez (hereafter referred to as Taboga), operated by the Costa Rican government, located 11 km SW of the town of Cañas. In this area the dry season is long and severe, with very little rain falling from early November until late April (fig. 1). The months of heaviest rainfall, May–June and September–October, are separated by 2 months of reduced precipitation, the "short dry season." Of the 2 years of this study, 1966 was a "typical" year with approximately normal amounts and distribution of rainfall. In contrast, 1967 was a relatively dry year. Significant rains did not fall until early June, and the June rains were followed by an unusually dry July and August. In addition, ditching and diking activities in the area had altered drainage patterns enough that water drained more rapidly from the marshes during the drier intervals. Therefore, water levels were neither as high nor as constant in 1967 as they were in 1966.

In 1966, the marshes were full in early July when I began field work, and they remained so with only minor variations in level until late September when, due to heavier rains, levels in all rivers and marshes rose. Water levels reached a peak during the heavy rains of late October when the rivers overflowed their banks and spread out over much of the low-lying ground that had not previously been flooded. Levels returned to normal by the third week of November but again rose during December on the main study marsh. All marshes in the area were virtually dry by mid-February 1967.

At Taboga I concentrated my efforts at five different marshes, all located within a mile of the station headquarters. Their characteristics were as follows. The major plants in the marshes are listed in Appendix 1.

West Marsh. Large, with relatively stable water levels. Bounded by pasture to the south and a drainage ditch and a scrubby forest to the north. About one-third of the marsh was occupied by a large bed of cattail. The area close to the drainage ditch was occupied primarily by a dense stand of a tall, coarse grass (Job's Tears, *Coix lacryma-jobi*) reaching heights up to 9 ft. Most of the rest of the marsh was covered with beds of grass interspersed, especially in the shallower areas, by *Alisma* sp. and *Limnocharis*. Part of one Redwing territory was covered with a bed of *Eleocharis* sp. and parts of another with a tall (8–9 ft) stand of *Thalia geniculata*. There were almost no shrubs growing in this marsh. To aid direct observations of the birds I erected a 10-ft tower at the edge of the marsh and built a platform in a small tree in the pasture.

Mid Marsh. Part of the same marsh system but shallower than the West Marsh and subject to more extreme fluctuations in water levels. There was no *Typha* or *Thalia* in this marsh and the grasses were primarily coarse bunch grasses (*Coix* and *Paspalum*). The marsh was bounded on the south by pasture and on the north by the drainage ditch and brush. There were quite a few shrubs (mostly *Mimosa*) and scattered large *Tabebuia* and *Enterolobium* trees in the marsh, and several dead *Enterolobium* which were regularly used as song perches by the Redwings.

East Marsh. Also part of the same marsh system and bounded by brushy pasture, drainage ditch, and

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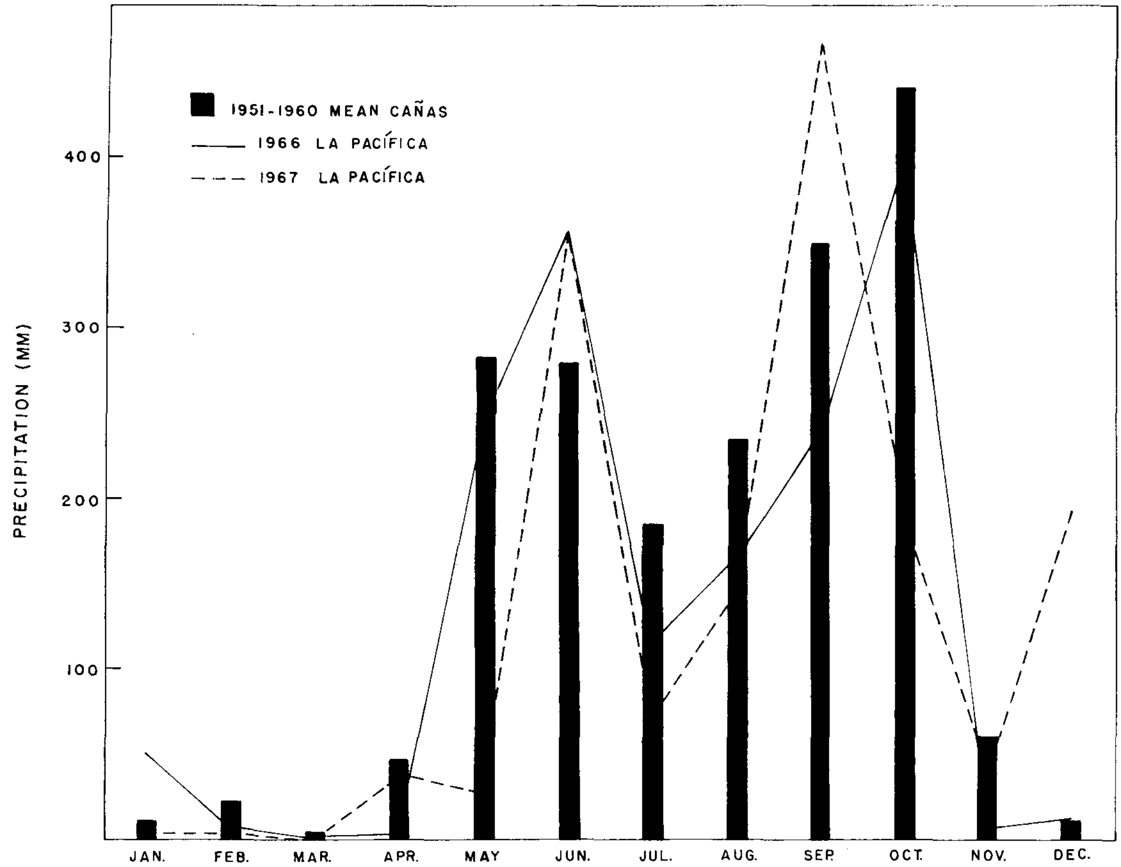

FIGURE 1. Seasonal pattern of precipitation in the Taboga area. The station at La Pacífica is located 3 km NW of Cañas.

rice fields. Most of this marsh was covered with a large stand of *Typha* in 1966, bordered by beds of low grasses mixed with *Alisma* and *Limnocharis* and quite a few *Mimosa* bushes. The cattails were completely burned during the dry season, and because of the better drainage ditches, the marsh was slow to refill in 1967 and water levels fluctuated irregularly depending upon the rainfall.

Masked Duck Marsh. A small pond surrounded by agricultural land. There was no *Typha* or *Coix*, but there were beds of a very tall (up to 2 m) sedge (*Cyperus*) around most of the pond. Most of the rest of the emergent vegetation consisted of various tall grasses and *Polygonum*. This marsh was very slow to fill in 1967 and had not reached capacity by 20 August.

Iguana Marsh. A pond surrounded by rice fields but with a brushy border. The emergent vegetation was almost entirely *Typha*, but there were many small dead trees and logs lying in the water. About one-third of the marsh consisted of open water. Water levels in this marsh were very stable, and some water was retained through the dry season, though there was no more than a mud hole when the rains finally came. The pond filled rapidly in 1967.

In addition, Redwings nested in other similar marshes in the area and a few bred along drainage ditches. I also visited a marsh (the River Marsh) along the Rio Higuerón vegetated primarily by two large sedges, one of them the same as the large *Cyperus* at the Masked Duck Marsh, and *Polygonum*. Redwings seldom foraged at the marsh, and I never found any signs of breeding there. The beds of sedges were conspicuous by the scarcity of grasshoppers, and the only lepidopteran larvae I found were of the "hairy" types never utilized by Redwings.

ANNUAL CYCLE OF REDWINGS IN COSTA RICA

During the nonbreeding (dry) season, Redwings at Taboga traveled in flocks as they do in other areas. Birds roosted in dense, herbaceous vegetation, over water if possible, and spread out into the surrounding agricultural land to feed. At this time they were pests in the rice and sorghum fields and consumed primarily vegetable matter. In 1966, the adult birds began to molt the second week of September and by the end of the month all birds that I observed were in full molt. Large flocks of molting birds were seen in October but by 16 November nearly the whole population appeared to have completed molting.

During the molt period, territorial behavior was reduced to a minimum, but as soon as individual males completed their molt, first observed in late October, they engaged in increased territorial behavior including sexual chasing (Nero 1956). At this time the marshes were still full of water. The birds did not roost on their territories at night but returned early in the morning from their unknown roosting areas and engaged in vigorous territorial activity until about 08:00. They began returning for evening territorial activity at about 15:30.

Territorial behavior increased during December, with males remaining on their territories all day even though activity declined during the middle part of the day. Many females visited the marsh; some of them gave territorial calls, and there was much sexual chasing. Activity was so intensive that I fully expected breeding to begin again but it did not. Nevertheless, considerable territorial behavior persisted until early February, by which time the marsh was nearly dry. During March, most of the marshes in the area were burned, but some early morning and late evening territorial activity nevertheless continued, though at a much reduced level, until the advent of heavy rains at the end of May.

By 6 July 1966 when the field observations began, there were already fledged young, indicating that the first eggs were laid no later than the first few days of June. However, since young from earlier nests could already have left the marshes, nests might have been started in May. Breeding that year extended until mid-September. In 1967 the first rain fell in the general area, though not at Taboga, on 17 and 18 May. A brief (½ hr) shower fell at Taboga on 21 May, but there was no further rain until a heavy downpour on 30 May. Thereafter, rains were regular and heavy for most of June. As indicated previously, birds were very active following the first heavy rains and nest construction began 12 June. There were still a few nests under construction and some with eggs on my last visit to the marsh 20 August 1967.

LOS CHILES, ALAJUELA PROVINCE

Redwings breed in large numbers in marshes along the Rio Frío and its tributaries in northern Costa Rica, near the Nicaraguan border. This area receives more rainfall than Taboga, and the dry season is short (January–April) and not so dry. The marshes there are formed primarily as a result of overflow of rivers during the wet season. The most readily accessible marsh where Redwings bred was characterized by extreme fluctuations in water level. Originally, this area had been chosen to represent a less seasonal environment to be compared with Taboga. It quickly became apparent, however, that conditions in the marshes at Los Chiles were more variable than at Taboga. Therefore, this study area was abandoned after a few months of work.

On 20–21 July 1966, 36 nests of Redwings were found at Los Chiles, all but one of which contained eggs. One nest contained three young 3 days old, and I found two recently fledged young. Between that time and the next visit on 29 July many of the nests were destroyed by rising water, but the six that were still active all contained young 3–5 days old, suggesting strong synchrony in the original nesting at the beginning of July.

Even during the peak breeding time in July, there were many nonbreeding individuals traveling in flocks and feeding in the wet pastures near the marsh. These pastures were infested with a noctuid larva upon which the birds were feeding. The stomachs of nine birds collected 20 July contained 137 noctuid larvae, 3 adult Coleoptera, 3 dipteran larvae, 1 adult Hemiptera, and 1 teneral dragonfly.

On 29 August, the marsh was almost completely dry, and there were no active Redwing nests. The youngest fledglings had been out of the nest at least a week, and I saw no territorial activity. All birds were traveling in large flocks. On 12 October, the marsh was again flooded, but there were no indications of Redwing breeding. All birds were molting and I heard no singing. During the last visit to this area, 23–24 November, some birds were again defending territories. The females on the marsh were mostly in small flocks, and in the evening there were movements of large flocks of Redwings over the nesting areas. A search of part of the main study marsh revealed the presence of three fresh nests, two still under construction, but all of them were empty. This suggests that some birds may breed during December and January, which at Los Chiles, unlike at Taboga, are relatively wet months.

In the vicinity of Los Chiles, there are also large llanos along some of the smaller rivers. Local informants claimed that these llanos were dry from late January until May, the driest period of the year in that area, but that Redwings were common in the marshes during the wet season. They reported finding many nests. Thus, the scant information I obtained at Los Chiles suggests a pattern not too different from that found at Taboga with a main breeding period from May or June to August, followed by the annual molt. There is some breeding following the molt in late November and December, but its extent needs to be documented.

AVAILABLE FOOD IN THE MARSHES AT TABOGA

The food available to Redwings at Taboga was measured in two ways. Preliminary investigations at the Masked Duck Marsh revealed the presence of many dragon fly exuviae on the sedges near the shore. Thereafter, regular collections of exuviae were made from about 5 m^2 of *Cyperus* clumps on one side of the pond. The sedges were cleared of exuviae during the afternoon, and the overnight emergence was determined by collecting exuviae the following morning. Because damselfly exuviae were too small and fragile to be sampled accurately in this manner, the data pertain only to dragonflies. However, unlike temperate marshes, where damselflies constitute the vast majority of emerging odonates, dragonflies greatly outnumbered damselflies at Taboga.

The data (table 1), though meager, suggest a sustained emergence of dragonflies during most of the wet season. The number of dragonflies emerging per square meter was much greater than we have captured with emergence traps at productive lakes in Washington. At the Columbia National Wildlife Refuge near Othello, six traps on a productive lake yielded only 0.057 dragonflies per square meter per day from 1 May to 15 July, the period of peak emergence, while on the lake with the largest emergence of odonates at Turnbull National Wildlife Refuge near Spokane, five traps yielded 0.035 dragonflies per square meter per day between 1 May and 30 July. In contrast, during these intervals the same traps yielded 6.5 damselflies per square meter per day at Columbia and 6.6 damselflies per square meter per day at Turnbull. This rate of emergence, though double the number of individuals at the Masked Duck Marsh, represents fewer calories per unit area because the damselflies are much smaller than the dragonflies. However, in Washington, during the peak emergence periods, the rate was several times greater than the average, and some traps did consistently better than others.

TABLE 1. Dragonfly exuviae collected from 5 m^2 of *Cyperus* clumps at the Masked Duck Marsh, Taboga, Costa Rica, 1966.

Date	Number of exuviae collected	#/m^2
11 August	26	5.2
25 August	33	6.6
26 August	29	5.8
4 September	11	2.2
5 September	12	2.4
14 September	9	1.8
15 September	12	2.4
29 September	17	3.4
25 October	7	1.4
26 October	14	2.8
18 November	2	0.4
	172	3.1

Note: By December the water had receded sufficiently that the clumps were on dry land.

Even though considerable numbers of dragonflies did emerge at the Masked Duck Marsh, all of them did so at night and were largely unavailable to the birds. Only at dawn, before they have attempted their maiden flights, are newly emerged dragonflies available to Redwings at Taboga.

Insects on the vegetation in the West Marsh and adjacent pasture were sampled with a standard (50.5-cm rim diameter) sweep net. At weekly intervals during the breeding season of 1967 and approximately at three-weekly intervals during the nonbreeding season, 25 sweeps each were taken in the middle of the aquatic grass, the edge of the marsh, and the adjacent pasture (fig. 2). No samples were taken in February because the marsh burned at that time.

Most of the common large insects present on the marsh are active at night, but the orthopterans rest on the stems and blades of the grass and *Alisma* during the day where they are vulnerable to predation by Redwings. The most common grasshoppers were members of the genus *Stenacris*, green katydid-like acridids. The lepidopteran larvae are relatively scarce in the sweep samples primarily because they move down to the bases of the vegetation during the day where, though they can still be found by Redwings, they are not taken by the net. Compared to the marsh and edge, the adjacent pasture was very poor in insects that could be sampled with a net.

Most of the common large insects fed on emergent vegetation, particularly the grasses. Aquatic insects were insignificant in the sweep samples. The acridids and tettigoniids, the most abundant insects present and the most common prey of the blackbirds, apparently "overwinter" as adults away from the marsh area during the long dry season. Immediately following the first rains, they appeared in large numbers in the marshes, at which time there were more adults at the marsh than any other time of year. Our data suggest, but do not prove, that these insects

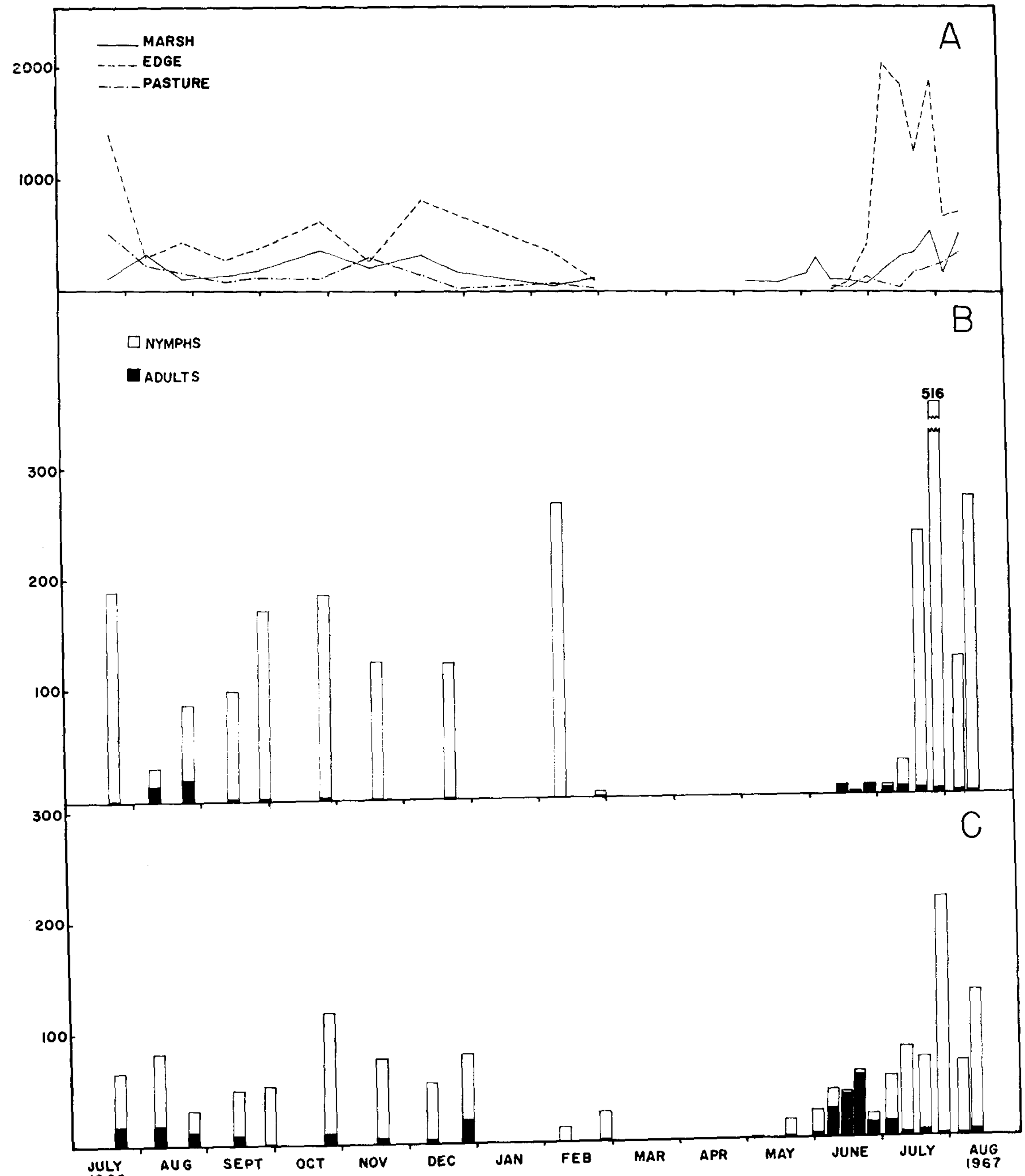

FIGURE 2. Abundance of arthropods at the West Marsh, Taboga, as assessed with a standard sweep net. A. Total number of insects and spiders obtained in 25 sweeps in the middle of the aquatic grass, the edge of the marsh, and the adjacent pasture. B. Numbers of adult and nymphal orthopterans obtained at the edge of the marsh. C. Numbers of adult and nymphal orthopterans obtained in the center of the aquatic grass.

had a single generation per year at the study area (figs. 2 and 3). Orthopterans were present in abundance in the study marsh for about 2 months after the cessation of breeding by the blackbirds. Thus during the molt period and the postfledging period of the young, food supplies were as abundant as at any time during the breeding period. During 1966, the Groove-billed Ani (*Crotophaga sulcirostris*), the other common insectivorous species on the study marsh, continued to breed during this period, the last young fledging in mid-December.

Of the types of insects present in the study marsh, the net sampling program was probably effective for orthopterans and hemipterans but not for lepidopterans or spiders, the other important prey in the diets of the blackbirds. Spiders were either on the surface of the water in the marsh or on the ground in the pasture; in neither place were they likely to be taken by the net. Nevertheless, the abundances of these other two groups probably changed in parallel with those of the orthopterans, as juvenile insects are very scarce during the dry season in tropical areas (Janzen and Schoener 1968).

The grasses in tropical marshes are taller, coarser, and more dense than temperate species. They often form dense mats on or just below the surface. They grow very rapidly when the rains come and rapidly change the nature of the marshes. Despite massive egg-laying by dragonflies at the beginning of the rains, there was no emergence at all of many of the species in the West Marsh because of the rapid growth of the vegetation (D. R. Paulson, pers. comm.). Aquatic dipterans (Tendipedidae and Chaoborinae) are abundant in some tropical lakes (Beauchamp 1964), but were scarce at my study marshes. In contrast, however, they supported much larger populations of herbivorous insects, particularly Orthoptera and Lepidoptera, than I have found in temperate marshes.

TABLE 2. Redwing territories at Iguana Marsh, Taboga, Costa Rica, 1967.

Territory number	Size in m²	Number of nests laid in	Minimum number of females
1	628	0	0
2	1,423	4	2
3	1,498	0	0
4	1,932	1	1
5	892	4	3
6	847	4	3
7	487	0	0
Average	1,101	1.9	1.3

TERRITORIAL AND MATING PATTERNS

With the exception of December 1966, the males occupied their territories only in the early morning and late evening during the nonbreeding season. At Taboga the transition to all-day occupancy of territories was more sudden than in the temperate areas I have observed (Orians 1961). Immediately following the first heavy rains at the end of May, the males remained on their territories all day except for brief foraging trips either to the adjacent pastures or rice fields some distance to the northwest. The displays of both males and females were as described for Redwings of the temperate zone (Orians and Christman 1968).

Field maps were made of two of the study areas at Taboga, the West Marsh and the Iguana Marsh, and territories were plotted at both localities in 1967. At the Iguana Marsh the seven territories ranged in size from 487–1932 m², the average being 1101 m² (table 2). At the West Marsh the nine territories ranged from 1022–4343, with an average of 2361 m² (table 3). These territories are about two to

TABLE 3. Redwing territories at West Marsh, Taboga, Costa Rica, 1967.

Territory number	Size in m²	Number of nests laid in	Minimum # of ♀♀	Number of young prob. fledged	Mean no. of days between success. nests	Minimum interval (days)
1	1,022	1	1	0	–	–
2	2,508	5	3	0	?	–
3	2,206	6	4	0	10.4	6
4	2,113	5	4	0	15.5	1
5[a]	1,510	4	3	0	6.5	5
6[a]	1,974	0	0	0	–	–
7	3,298	6	6	5 (2 nests)	5.2	2
8	4,343	11	9	3 (2 nests)	7.8	0
9	2,276	4	3	3 (1 nest)	5	2
Total	21,250	42	33	11		
Averages/Territory	2,361	4.7	3.7	1.2		

[a] Interior territories.

four times the sizes of territories recorded in marshes in the United States (Nero 1956; Orians 1961; Case and Hewitt 1963; Goddard and Board 1967). At the West Marsh in 1967, my visits were frequent enough for me to find all the nests (with the possible exception of a few that might have been abandoned during construction and subsequently pulled apart), to determine the minimum number of females that could be responsible for the nests, and to estimate nesting success (table 3).

In the West Marsh there is a correlation between the size of the territory and the number of females that settled to breed in it when tested by the Spearman Rank Correlation test ($r_s = 0.816$ for nests laid in and $r_s = 0.748$ for minimum number of females). A stronger correlation would probably have been obtained if territories had been more uniform with respect to vegetation. As in temperate marshes, stands of cattails in the tropics have few insects in them. Moreover, because of the scarcity of emerging aquatic insects, foraging for these insects in cattails would not be as profitable as it is at higher latitudes. Female Redwings at Taboga spent very little time foraging in the cattails. Therefore, it is likely that territories consisting entirely or primarily of cattails are less desirable than territories containing significant beds of grass. Cattails comprised about 90% of both territories 5 and 6 which attracted only three and zero females, respectively. They were also interior territories, that is, territories with another territory intervening between themselves and the nearest areas of grass or marsh edge.

On six of the territories where there were at least three females, the mean intervals between the starting dates of successive nests on the same territory ranged from 5.2 to 15.5 days. On four of the six territories, the minimum interval between the starting of different nests was 2 days or less, and on one territory two nests were begun the same day. These data strongly suggest that female territoriality was not of major importance in determining the temporal pattern of female settling.

This is surprising because in 1967, possibly as a result of the drought and draining operations, the amount of available marsh for nesting was much reduced over what it had been in 1966, and there were large flocks of apparently nonbreeding females flying over the study marshes during the entire breeding season. I also observed much territorial behavior by resident females on the marshes and gained the distinct impression that more females would have settled on the study area had they been able to insert themselves. The data do not support this impression, but it cannot be excluded that though the first females to settle were not deterred by the prior presence of others, later females encountered stronger resistance without which they might have settled. Carefully controlled decimation experiments would be necessary to clarify this point.

NEST SITES, CLUTCH SIZE, AND INCUBATION

At Taboga, Redwing nests were built almost exclusively over water in herbaceous vegetation. Because of the cutting and burning of the marsh during the dry season, there was a considerable time in many areas after the arrival of the rains before there was vegetation strong enough to support nests. At the West Marsh, however, cattails had reached a height of 6 ft in one part of the marsh by the time the rains came and were already suitable for nests. In parts of the East Marsh early nests were attached to burned and charred stumps of large cattails. As vegetation growth proceeded, however, a wider variety of nesting sites became available, and the sites chosen by the birds were different (table 4). Since the amount of available cattail also increased during this period, the change is at least in part due to a preference for nesting in tall grass. At Taboga, small shrubs, mostly *Mimosa*, were widely scattered in the marshes but were not favored as nesting sites. At Los Chiles, however, where the common *Mimosa* bushes were the only available nesting sites over most of the study marsh, all nests were placed in them.

Following the trend shown by most passerine birds, Redwing clutches are smaller in Costa Rica than at higher latitudes. In 1966, I obtained reliable information on clutch size on 46 nests at Taboga. There were 4 clutches of two, 40 clutches of three, and 2 clutches of

TABLE 4. Seasonal change in Redwing nest sites at Taboga, Costa Rica, 1967.

Nest site	Nest construction initiated 10 June–14 July #	%	15 July–20 August #	%
Cattail (*Typha*)	21	38.2	11	29.7
Alisma	16	29.1	7	18.9
"Sawgrass"	6	10.9	0	0
Job's Tears	5	9.9	2	5.4
Sedges	6	10.9	4	10.8
Tall Grasses	1	1.8	13	35.1
	55		37	

TABLE 5. Clutch size in the Redwing, Taboga, Costa Rica, 1967.

Marsh	Clutch size				Average
	1	2	3	4	
West Marsh	2	11	26	0	2.61
Mid Marsh	1	8	15	0	2.58
East Marsh	1	3	16	1	2.81
Masked Duck Marsh	0	1	9	0	2.90
Iguana Marsh	1	2	7	0	2.60
Total	5	25	73	1	2.67

four, giving a mean of 2.96 eggs per clutch. In 1967, I obtained reliable estimates of clutch sizes of 104 nests at five different marshes (table 5). The mean clutch of 2.67 is significantly lower than in 1966, and since my visits to the nests were more frequent in 1967, my estimates are probably more accurate for that year. Therefore, since clutch size tends to be underestimated with less frequent checking, the difference in clutch size between the 2 years may have been even greater. It is tempting to correlate the lower clutch size in 1967 with the lateness of the rains and poorer conditions in the marshes, but I do not know if foraging conditions were poorer for adults in 1967 than they were in 1966. The sweep sample data (figs. 2 and 3) do not indicate that there were fewer insects on the marshes in 1967 during the peak of the breeding season, but conditions may have been poorer when the females were forming their eggs.

The delay between completion of the nest and deposition of the first egg, measured at 18 nests in 1967, may be indicative of poorer foraging conditions for the females than in temperate areas. At three nests in 1967 the interval was as long as 9 days. Nest construction itself was about as rapid as in Washington, but nests commonly were not laid in for 2–4 days after completion, whereas in temperate areas there is seldom a delay of over one day.

Eggs were laid one a day early in the morning. The average weight of 73 eggs from Taboga was 3.6 g, about 0.5 g lighter than Redwing eggs in central Washington. However, since Costa Rican Redwings are smaller than Washington Redwings, the eggs are about the same proportion of adult weight (9% and 6% of female and male weights, respectively). Incubation began with the penultimate egg as elsewhere.

In 1966, my visits were not regular enough to allow me to determine the incubation periods at any of the nests at Taboga, but in 1967 I was able to determine the times of egg-laying and hatching at seven nests. Only those nests were used in which I visited the nest at least twice during the egg-laying period, once during incubation, and again before the young were 2 days old. The incubation period was 11 days at three of the nests, 12 days at two of the nests, and 13 days at the remaining two. This incubation period is the same as in Washington where 12 is the most common incubation period, but some eggs hatch in 11 or 13 days.

NESTLING FOOD, GROWTH, AND SURVIVAL

Foods delivered to the nestlings were sampled by the pipe-cleaner, neck-collar technique (Orians 1966; Willson 1966). By this method 50 samples totaling 62.5 nest-hours were obtained in 1966, and 78 samples totaling 84.75 nest-hours were obtained in 1967. The food collected is summarized in table 6 which shows that insects with aquatic stages in their life histories are insignificant in the diet. Instead, spiders, orthopterans, and lepidopteran larvae together comprised 89.9% of the food items in 1966 and 86.1% of the food items in 1967. Food delivery to the nestlings was almost entirely by the females, but at one nest in 1966 I observed the male delivering food to the nestlings three times.

Because of the great diurnal variations in the availability of prey and the prey actually captured by Redwings in temperate marshes (Willson and Orians 1963; Orians and Horn 1969), I collected food samples at all hours of the day both years. However, at Taboga there was no evidence of any diurnal pattern in the foods delivered to the nestlings. Since the diet consists primarily of spiders, which are apparently active all day, and the nocturnal orthopterans and lepidopteran larvae, which are resting and equally susceptible to capture all day long, this result is not surprising.

Seasonal differences in the foods delivered to the young also were insignificant. In 1966, during which my food samples cover a longer time interval, spiders and lepidopteran larvae were important at all times. The acridids declined in importance in the nestling diets later in the season, but the tettgoniids increased so that the proportion of Orthoptera did not change significantly.

The sweep net samples contain many small insects and provide an estimate of the numbers and kinds of small insects present in the marshes and probably encountered by the foraging female Redwings. For the most part,

TABLE 6. Food samples from nestling Redwings, Taboga, Costa Rica.

Group	1966	Order total	Proportion	1967	Order total	Proportion	Total	Proportion
Araneae	52	52	0.26	46	46	0.14	98	0.19
Odonata		1	0.01		12	0.04	13	0.03
Libellulidae larvae	0			9				
Libellulidae tenerals	1			0				
Libellulidae adults	0			1				
Lestidae tenerals	0			2				
Orthoptera		82	0.41		86	0.27	168	0.32
Mantidae nymphs	1			0				
Mantidae adults	1			0				
Tettigoniidae nymphs	18			30				
Tettigoniidae adults	25			12				
Tettigoniidae ?	1			3				
Acrididae nymphs	15			20				
Acrididae adults	15			19				
Acrididae ?	1			1				
Family ? larvae	0			1				
Family ? adults	3			0				
Family ? ?	1			1				
Isoptera	0	0		2	2	0.01	2	0.00
Hemiptera		2	0.01		6	0.02	8	0.02
Belostomatidae nymphs	1			4				
Belostomatidae adults	0			2				
Family ? adults	1			0				
Homoptera		4	0.02		3	0.01	7	0.01
Cercopidae adults	2			3				
Family ? adults	2			0				
Lepidoptera		41	0.21		141	0.44	182	0.35
Family ? larvae	28			116				
Family ? pupae	12			18				
Family ? adults	1			7				
Diptera		4	0.02		2	0.01	6	0.01
Family ? larvae	4			1				
Family ? pupae	0			1				
Coleoptera		5	0.03		4	0.01	9	0.02
Curculionidae adults	0			1				
Chrysomelidae adults	3			0				
Family ? larvae	1			3				
Family ? pupae	1			0				
Gastropoda	4	4	0.02	15	15	0.05	19	0.04
Order ?		4	0.02		4	0.01	8	0.02
Family ? larvae	1			2				
Family ? pupae	0			1				
?	3			1				
Total	199			321			520	

the smaller insects were not delivered to the nestlings at Taboga. The most interesting case was the Orthoptera which were present in the marsh in many different instars, some of which were smaller than the insects normally delivered to the nestling Redwings. In figure 3, the size distributions of orthopterans obtained in the sweep samples and those obtained from the nestling Redwings are compared. Though individuals smaller than 13 mm in length were

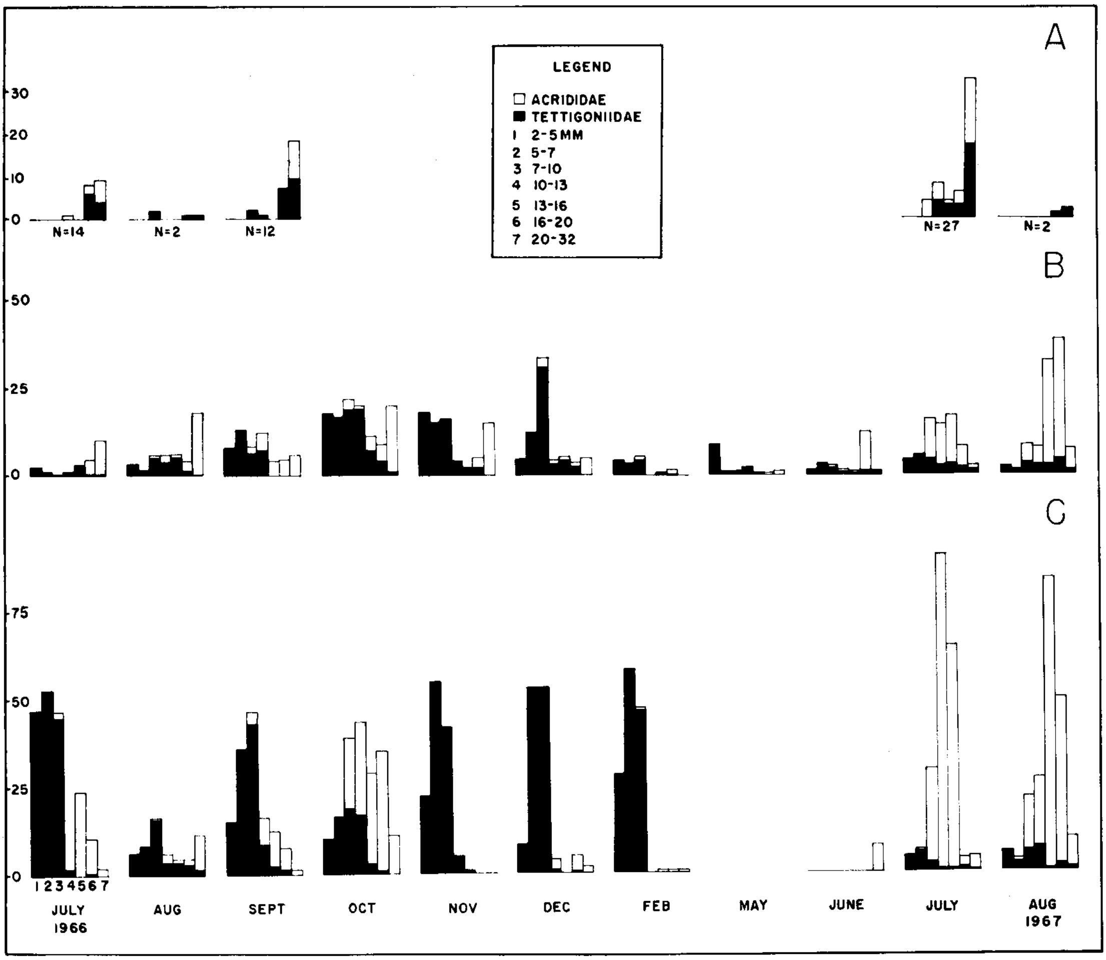

FIGURE 3. Size distributions of orthopterans from the food samples of Redwings and the sweep net samples. A. Sizes of orthopterans in the food samples of Redwings. N = the number of food samples. B. Size of orthopterans in the sweep net samples from the middle of the aquatic grass. C. Size of orthopterans in the sweep net samples from the edge of the marsh.

usually more abundant than large ones, they constituted only a small fraction of the individuals delivered to the nestlings.

A 13-mm grasshopper contains about 50 calories, the same number yielded by a damselfly, the most common food of nestlings in Washington. Smaller insects are regularly rejected both places. However, the pattern of food delivery at Taboga was different. All females scolding me when I was near the nests and all females seen delivering food to the nestlings while I watched from a distance had only a single prey item in the bill. In contrast, 25–30 moderate-sized insects are regularly brought to the nest each trip in Washington.

Correlated with this, I recovered fewer items per food sample from nestlings at Taboga than from nestlings in Washington. In 1966, there were 3.4 items/nest/hour or 1.7 items/nestling/hour. In 1967, I obtained 4.1 items/nest/hour or 2.2 items/nestling/hour. In central Washington over several years, I have obtained about 22 food items/nest/hour (about 7 items/nestling/hour), a rate four times as great as at Taboga. The neck-collar technique does not retain all the food delivered and, hence, is not an accurate measure of the rate of food delivery. Nonetheless, the differences in the number of prey recovered are doubtless indicative of a real difference in the rate of delivery of food to the nestlings because there is no reason to believe that sampling efficiency is not comparable. This interpretation is supported by the differences in rate of growth of nestlings at Taboga.

A major difference between temperate and tropical Redwings is in the amount of time the female spends brooding young. In Washington, female Redwings brood young 3–10 days old only at night or during heavy rain. In contrast, I found females brooding young of that age range on 19 of 56 cases (33.9%) in 1966 and 24 out of 100 cases (24.0%) in 1967 at Taboga. During my direct observations of nests in 1967, females brooded young 27.9% of the time, a figure in good agreement with the estimate obtained from spot visits to the nests. Also, Redwings at Taboga permitted closer approach to the nest before flushing. I was regularly able to approach to within 5 ft of incubating or brooding females, and several females performed distraction displays when leaving the nest, a behavior I have not observed elsewhere.

Since more food was present in the marshes in the immediate vicinity of the nests than in the adjacent upland pasture, it was to be expected that most of the foraging for food for the young would be made on the marsh itself. Of 48 visits to the nests by several different females for which I observed the foraging location, 34 came from the marsh, 10 from the edge, and 4 from the pasture. This foraging pattern should be favored both by energy saved as a result of reduced travel and greater abundance of food there. For the same reasons, the placement of nests in these locations is also desirable.

During the breeding season, adult Redwings fed themselves mostly on insects but ate more Lepidoptera and fewer Orthoptera than they delivered to the nestlings. The stomachs of 14 individuals (6 males, 8 females) collected 8 August 1967 at the East Marsh contained 1 adult, 19 pupal and 13 larval Lepidoptera, 2 tettigoniids, 11 adult Coleoptera, 1 tipulid larva, 2 stratiomyid larvae, 2 insect egg cases, and some grass seeds.

There is suggestive evidence that young Redwings at Taboga were sometimes short of food. Young older than 6 days, if they are well fed, normally crouch in the nest and remain very quiet when a human approaches. Hungry young, however, beg vigorously at this age, and, in Washington at least, they are likely to die of starvation prior to fledging. At Taboga, I also regularly encountered young which begged when older than 6 days and showed other signs that I associate with undernourishment. The nestling growth rate varied greatly; some young grew much more slowly than others but this was not correlated with the number of young in the nest.

Normally, a predator takes all of the young in a nest at one time. Therefore, partial (within brood) losses of young usually indicate mortality due to disease and/or starvation. I have estimated this loss at Taboga, using data for all nests in which young were observed for a minimum of 3 days. When a nest was not visited for a number of days, a nestling which disappeared during that interval was assumed to have survived one-half of the time. By these criteria in 1966, eight nestlings disappeared during 293 potential nestling days (0.027 nestlings/nestling day). In 1967, ten nestlings disappeared during 401 potential nestling days (0.025 nestlings/nestling day). This rate of loss is considerably less than the rate of total loss of nestlings. During 1967, when my records of predation (total loss) are better, 47 young were taken during 524 potential nestling days (0.090 nestlings/nestling day). Those passerine birds of the wet tropics that have been studied have almost no within brood losses (Ricklefs 1969), but partial losses are characteristic of species breeding in arid tropical region (Marchant 1960). The highest partial losses of nestlings have been found in temperate marsh-nesting passerines (Ricklefs 1969), presumably because of the temporal variability of the food supply, but this would not appear to be the case with the food supply of the Redwings at Taboga.

At Los Chiles, nestling starvation was prevalent during the short time of my study. The period of 29 July through 1 August was characterized by almost constant overcast and heavy rains. During this time, I weighed young at several nests. Most of them either did not gain weight or actually lost it, and several died of starvation. One nestling, judged to be 6 days old on the basis of feather growth, weighed only 10 g (normal 23 g), and another died when 7 days old weighing 20.7 g (normal 27 g).

Because of the high predation rates, it was also difficult to determine the average number of young fledged from clutches of different sizes. At Taboga in 1967, I was able to determine the number of young fledging from 18 nests—13 nests with a clutch of three, 3 nests with a clutch of two, and 2 nests with a clutch of one. An average of 2.2 young were fledged per successful nest from clutches of three, and four of the nests fledged all three young. Only 1.3 young were fledged per successful nest from clutches of two. Thus, of the clutches of three, all young were fledged in about one-third of the nests which escaped predation, indicating that many females were able to find sufficient food for this number of young.

If predators are able to locate nests as a result of cues provided by the visits of the adults, it should be true that a nest has a higher probability of being destroyed by predators if it has more young in it. My data, though limited, do not provide any evidence of such differential predation. Of nests known to have escaped predation until after hatching, three out of six (50.0%) broods of two and 14 out of 27 (51.8%) broods of three were destroyed.

Predation was, nevertheless, the most important cause of egg and nestling mortality at all marshes at Taboga. At the West Marsh in 1967, only 20 out of 93 nests (21.5%) fledged any young. Of these nests, 55 (59.1%) were destroyed while they contained nestlings. In most cases the actual predation was not observed, and nests were simply found empty the next visit. This is characteristic of snake predation, and since I observed a *Boa constrictor* actually taking young from one nest and Indigo Snakes (*Drymarchon corais*) predating two others, most nests were probably taken by snakes. *Drymarchon* in particular was very common in the marshes and may have been the chief predator.

At the Masked Duck Marsh, a major source of nest loss was Rice Rats (*Oryzomys*), which were very common and appropriated Redwing nests for their own use by doming them over. Many Redwing nests at this marsh showed unmistakable signs of mammal predation, i.e., they were ripped down on one side. In 1966, only one out of 16 nests fledged young, and most losses appeared to be due to mammals. In 1967, when the marsh filled with water very slowly, four out of nine nests were successful, and only one was taken over and domed by *Oryzomys*.

The positioning of nests, which often gave them no concealment from above, strongly suggests that avian predators are a minor cause of nest loss. I never saw a potential avian nest robber in or around the marshes, and I never observed Redwings mobbing or showing other signs of fear of such predators.

Other sources of nest loss included flooding, vegetation growth, and cattle and human disturbance. Of these, flooding was the most important during my study especially at Los Chiles in 1966 and Taboga in 1967. At Los Chiles high water in late July destroyed an estimated 30 out of 36 nests, and a few of those still active were within a few inches of the water level.

The major loss of nests due to flooding at Taboga occurred in the East Marsh in 1967. Water levels were very unstable, and as a result of cutting and burning during the dry season, there was almost no tall vegetation on the marsh. Consequently, many of the Redwings were nesting in very short grass which only projected about 1 ft above the usual water level. Heavy rains on 7 July caused a sudden rise in water level in the marsh and 9 out of the 14 active nests were inundated. At Taboga, however, under less disturbed conditions, losses due to flooding would probably be minor. Normally, there is more tall vegetation available in which to place nests, and Redwings usually build their nests as high as is consistent with strong support. Moreover, water levels fluctuate less when ditching and diking are not underway. At Taboga seven nests were destroyed by being tipped by unequal growth of the stalks supporting the nest, and a cow destroyed one nest by rubbing against it.

DISCUSSION

From the viewpoint of a terrestrial insectivorous bird, the major differences between the temperate and tropical marshes I have studied are as follows. Most aquatic insects, which form the major food in many temperate areas (Orians 1966; Willson and Orians 1963; Orians and Horn 1969), emerge at night in the tropics and are unavailable as food for birds. Tropical damselflies do emerge during the day, but they were relatively scarce in my study marshes and were insignificant as food for the blackbirds. These insects are abundant in temperate marshes and are the main food of breeding Redwings. Other groups of aquatic insects that are abundant in temperate marshes, such as Trichoptera, Ephemeroptera, and Diptera, were scarce at Taboga though they are abundant in some tropical lakes and marshes and are regular components of stream faunas in the tropics. The dense growth of grasses in the marshes at Taboga supported large populations of herbivorous insects, especially Lepidoptera and Orthoptera. These insects were also nocturnal but unlike odonates were available to the birds during the day. By contrast, herbivorous insects are scarce on emergent vegetation in temperate marshes during the Redwing breeding season.

These differences make it difficult to compare the marshes at Taboga with those in Washington with respect to their food-producing properties. The grasshoppers at Taboga could be effectively sampled with an insect net, but measuring the emergence rates of aquatic insects requires the use of emergence traps. The data from these two techniques are not readily compared. In particular, I do not know what densities would permit equivalent rates of capture by a foraging blackbird. However, I doubt that a foraging Redwing at Taboga could capture food at the rate possible in central Washington where a female can easily capture as many as 10–15 damselflies per minute during the peak morning hours of emergence (Orians, unpubl. data). In this sense, food is probably never as available at Taboga.

Redwings at Taboga, unlike birds in temperate areas, did not prefer marshes which produced more emerging aquatic insects. Instead, the birds concentrated in those areas with large populations of herbivorous insects on aquatic vegetation, especially grasses. The River Marsh, though it was a large marsh with good emergences of dragonflies, never had any breeding Redwings. The vegetation there was primarily sedges and *Polygonum* which supported almost no herbivorous insects. Similarly, the Iguana Marsh, which had mostly cattails and very little grass, was not attractive to female Redwings though males did settle there and hold territories. In 1967, there were only 1.3 females per male at the Iguana Marsh as compared to 3.7 females per male at the West Marsh; only two nests fledged young and several were apparently deserted.

The same foraging movements were used by Redwings at Taboga as in temperate areas where I have observed them. In particular, gaping was very prominent, especially around the stalks of *Alisma* and at the bases of the grasses, and was effective in exposing resting nocturnal insects. However, this method of foraging, which requires that the bill be forcibly opened for the capture of each prey item, may be incompatible with gathering more than one prey per visit to the nest. Orthopterans resting in more exposed places, though they can be captured without gaping, are nonetheless active insects which may have to be pursued. Their capture may be difficult if there are already insects in the bill. The combination of these factors may explain why tropical Redwings, unlike their temperate counterparts, bring but a single prey item to the nest each visit.

In both temperate and tropical areas the food upon which the young Redwings are fed is abundant only for parts of the year. In Washington, large damselfly emergences occur from early May until late July. At Taboga, orthopterans were common in the marshes from late June to November. In both areas breeding of Redwings stops long before the food supply begins to decline, and renesting attempts actually cease when food is most abundant. Therefore food cannot be a proximate factor in the termination of breeding at either area though ultimately it may be involved. It is not possible at present to choose clearly between two alternative explanations for this phenomenon. First, young from later nests might become independent at a time of deteriorating food supplies when both they and the adults would have to undergo the rigors of the molt. Alternatively, predation rates might be high enough on later nests to make further attempts unprofitable, but there is little evidence of this at Taboga. Predation rates in 1967, the year for which I have the best data on nesting success, were high throughout the season. Among nests for which I have good data, young fledged from only one of 17 nests in which the first egg was laid on or after 15 July, and from 19 out of 83 nests started earlier; the difference is not statistically significant ($\chi^2 = 0.005$, $P > 0.95$).

The small clutches of tropical birds have attracted considerable interest for many years, and several alternative explanations of the phenomenon have been suggested and hotly debated. Assuming that clutch size has been molded by natural selection to result in the maximum number of surviving young, as postulated by Lack (1954), lower clutches in the tropics could result from any one or a combination of the following factors. (a) Day lengths are shorter during the breeding season than at higher latitudes so that the adults have a shorter foraging period each day. (b) Food may be more difficult to capture so that less can be delivered per hour to the nestlings. (c) High temperatures may inhibit foraging activities during the middle of the day. (d) Competitive interactions such as territory defense, general agonistic encounters, etc., may consume more time in stable tropical areas where territorial invasion is likely at all times of the year, and there is a richer fauna of potentially competing species. (e) High predation rates may select against more frequent visits to the nest so that the number of young actually fledging is, on the average, greater from nests starting with fewer (Skutch 1949). The model of Cody (1966) is the most comprehensive one which attempts to integrate all of these factors.

Day length at Taboga is shorter than during the breeding season of all Redwings at higher latitudes, and this may well be a factor influencing the amount of food that can be delievered in a single day. However, it cannot be the only factor since there are significant trends in Redwing clutch size within the United States which are primarily east-west rather than north-south and, hence, are not associated with day length. Average productivity of marshes is a more likely factor (Orians, in prep.), and this may also be important for tropical Redwings.

As indicated previously, I have evidence that foraging blackbirds may not be able to capture prey as rapidly at Taboga as in the productive marshes of eastern Washington. Only one food item is delivered per visit to the nest. If prey must be exposed by gaping, capture rates are likely to be lower. There is no sharp peak of insect abundance, either seasonal or diurnal, that compares with that present in temperate marshes. There are significant partial losses of nestlings, a form of mortality associated with starvation.

Evidence for predation as a selective factor influencing clutch size of tropical Redwings is equivocal. Predation rates were very high, but the females were not cautious in their visits to the nests, approaching and leaving by direct flights and often calling as they left. Nevertheless, the attentive behavior of females may have been influenced by predators in the tropics. At Taboga, female Redwings permitted much closer approach to the nests without flushing; some of them gave distraction displays, a behavior I have never noted in the United States; and they spent much more time brooding young. These facts would be consistent with the view that a significant source of nest predation comes from predators small enough to be repulsed by the female if she is at the nest when they arrive. This might be true for small snakes and small mammals. The possibility that brooding has also been selected for because of high temperatures and the fact that the sun shines directly down on the nests at mid-day cannot be excluded, but since brooding was also prevalent during the early morning and late afternoon this seems less likely.

Evidence that competition and its demands upon time were factors selecting for smaller clutches in the Redwings at Taboga is all negative. The only species with which the Redwings interacted behaviorally were the Groove-billed Anis, and these encounters were infrequent and involved primarily male Redwings. There was no interspecific territoriality, and females were entirely nonterritorial at the time they were feeding young. No other passerines fed on insects in the study marshes.

Taken together, my data suggest but by no means prove that the major factor that has favored smaller clutches of the Redwings at Taboga is the rate at which food can be delivered to the nestlings. A secondary factor is probably predation, but this needs to be checked further. However, since nestlings in broods of three grew just as rapidly as nestlings in broods of one and two, it may be that predators are a more important factor than suggested by the data I was able to gather.

SUMMARY

A resident population of Red-winged Blackbirds was studied during the breeding seasons of 1966 and 1967 in northwestern Costa Rica, the southern limits of the range of the species. Redwings breed from the start of the rainy season in late May or early June until early September, 2 months prior to the ends of the rains. Emerging aquatic insects, except for dragonflies which emerge strictly at night, are relatively scarce in these marshes, while herbivorous insects are very common on the emergent vegetation. Adult orthopterans move into the marshes at the initiation of the rainy season, and their single annual generation grows during the rainy season, reaching a peak in September or October. Tropical Redwings are territorial and polygynous, but territories are about four times as large as those reported from temperate areas. Nests were built almost exclusively over water in herbaceous vegetation, but shrubs in the marshes were also utilized. Clutch size was smaller than reported in any other population, being 2.96 (46 nests) in 1966 and 2.67 (104 nests) in 1967. Females delivered only one prey item per trip to the nest and spent about one-third of the daylight hours brooding young over 3 days of age. The young were fed primarily orthopterans, lepidopteran larvae, and spiders. Aquatic insects were insignificant in the diet. Nest losses were very high, only 21.5% of nests fledging one or more young in 1967. Predation losses, probably mostly to snakes, were the major source of egg and nestling mortality, but there were also partial nestling losses, indicative of starvation. There was no evidence that competitive interactions with other species had led to a reduction in the energy devoted to reproduction. Redwings were not interspecifically territorial and had few agonistic interactions with other species. A lower capture rate of prey items was suggested for Costa Rica as compared to temperate marshes by the smaller number of prey items per nestling per hour in the food samples, fewer visits per hour to the nest, and by the fact that only one prey item is delivered per trip to the nest. However,

the high nestling losses to predators, the independence of nestling growth rates and the number of young in the nest, the higher fledging success of nests with more young, and the greater percentage of time spent brooding by the females, all indicate that predation has been an important factor influencing foraging behavior in tropical Redwings.

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APPENDIX A. Important plants in the marshes at Taboga, Costa Rica.

Family	Genus and species
Typhaceae	*Typha angustifolia*
Alismaceae	*Alisma* sp.
Butomaceae	*Limnocharis flava*
Gramineae	*Coix lachryma-jobi*
	Panicum sp.
	Paspalum sp.
Cyperaceae	*Cyperus* sp.
	Eleocharis sp.
Marantaceae	*Thalia geniculata*
Polygonaceae	*Polygonum* sp.
Leguminosae	*Mimosa* sp.