THE AUK

A QUARTERLY JOURNAL OF

ORNITHOLOGY

. 4

Vol. 70	October, 1953	No

CONTRIBUTION TO THE LIFE HISTORY OF THE SWALLOW-TANAGER

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THIS paper is intended to fill some of the gaps in our knowledge of one of the most fascinating South American birds, the Swallow-Tanager or Azulejo Golondrina (*Tersina viridis*).

The stimulus to deal with Tersina viridis I thankfully owe to Dr. Frederick Test of the University of Michigan. He and Mrs. Test were the first visiting scientists from the United States to the newly founded Estación Biológica de Rancho Grande in the state of Aragua, northern Venezuela. I wish especially to express my most cordial thanks to Dr. Armando Tamayo, Ministro de Agricultura y Cria (MAC), who made my work in Venezuela possible, and to Dr. Tobias Lasser, Director Forestal, who, as one of the most active promoters of modern science in Venezuela, is the actual founder of the Estación I am also very much indebted to Dr. William Phelps and Biológica. Mr. William Phelps, Jr., of Caracas, who have at all times extended to me their most generous help and encouragement; and to Mr. Guido Steinvorth and Miss Nadine Huang for facilitating the writing of this manuscript. Furthermore, I am indebted to Dr. Guillermo Zuloaga of the Creole Petroleum Corporation. Last but not least, I owe much to my co-workers, especially to my young Venezuelan friend Julio Moreno, who with great devotion, skill, and patience, has been my most helpful associate in the field during our three months of almost continuous observations from daybreak to dusk; and also to Willy Tille, Wolfram Bleuel, and José Perez, who have given their valuable assistance. The meteorological data were compiled by José García, and many of the photographs reproduced in this paper were taken by Konrad Koch.

The Parque Nacional de Rancho Grande, where these studies were made, extends from the inland basin of Lake Valencia at an elevation of 450 meters, across the peaks of the Cordillera de la Costa (2,400



SWALLOW-TANAGERS (*Tersina viridis*). (*Top*) FEMALE THREE INCUBATING, TWO METERS INSIDE NESTING HOLE. (*Bottom*) FEMALE TWO. PHOTOGRAPHS BY K. KOCH. meters high) to the rocky coast of the Caribbean Sea. Biodynamically and ecologically it can be divided into three main belts: the Tropical (0 to 800 meters), the Subtropical (800 to 1,800 meters), and the "Subtropical-temperate" (1,800 to 2,400 m.), each with its own very characteristic flora and fauna (Schäfer, Journ. für Ornith., 93: 313–352, 1952). The region is extremely rich in bird life. During the two and one-half years since the establishment of the Estación Biológica, more than 450 species of birds have been recorded in this comparatively small area comprising only about 9,000 hectares.

The tersinas comprise a very small, monotypic, purely South American group of passerine birds, which is considerably specialized in structure and habits. The form on which the following observations were made is *Tersina viridis occidentalis* (Sclater).

Although the bird occupies a prominent position in the avifauna of Venezuela and the Parque Nacional, very little is known of its habits. This is especially true of its mode of reproduction, as its nests are always concealed in natural or artificial holes and burrows. As is the case in many species of uncertain taxonomic relationships, this purely biological study may be helpful in clarifying the systematic position of *Tersina*.

Appearance and Identification Marks.—Tersina viridis is one of the most gorgeously colored species of the entire Neotropical Region. It is characterized by a very pronounced sexual dimorphism. The main field identification marks of the male are: nearly entire body turquoise blue, if seen against the light in bright sunshine, but changing to emerald green when seen with the light. Forehead, sides of head and especially throat, deep velvet-black and center of abdomen pure white, forming a sharp wedge; sides of belly with black stripes and light edgings. The general color of the female is a bright green (not as iridescent as the male). The throat is grayish, and the abdomen is yellowish with green instead of black stripes. The plumage of the juvenile birds is much like that of the female, but duller.

There is great individual variation according to age in both sexes. The males especially show all transitional stages between juvenile green without facial masks and adult turquoise blue with deep velvetblack masks. The individual females may also be recognized in the field by careful observation as they often show different shades of green and gray on the throat. As with the males, the darker, more bluish females seem to be the older ones. Old birds of both sexes show a very distinct red reflection in the eye, missing in the younger birds which have brownish-gray irides. Males breed in their first year.

According to my observations, including "types" of individual behavior, it may well be that the fully adult male plumage is acquired

only after three or even four years. The variations in plumage lead me to postulate this sequence of plumages for the males:

One year old-mottled green and blue; no facial mask.

Two years old—bluish-gray with green feathers on abdomen; facial mask dark gray, "pepper and salt."

Three years old—blue with grayish shade; black facial mask well developed but still dull.

Four years or older—brilliant blue, strongly contrasting with white waist-coat and deep, shiny velvet-black mask. Red eye.

This great individual variation together with the already-mentioned sexual dimorphism makes it easy to recognize most individual birds without the help of color banding. Nevertheless, twelve were banded during the nesting period of 1952.

Weight.—Males and females are of nearly the same weight, varying between 29 and 35 grams, according to season and state of nutrition. Females as a rule are very fat before the breeding season. A pair collected on March 23 showed marked differences in weight: male (lean, testes enlarged), 30 gm.; female (very fat), 35 gm. Two young captive males weighed: 50 days old, 25 and 26 gm., respectively; 100 days old, 28 and 29 gm., respectively.

Anatomical Peculiarities.—The flat, broad, swallow-like bill of *Tersina*, with its sharp edges and a pronounced hook on the maxilla, together with the proximally placed cone-shaped nostrils, is an ideal instrument not only for catching flying insects and holding, cutting, and swallowing big, pulpy fruit with hard peels, but also for excavating holes.

The throat of *Tersina viridis* forms an elastic pouch of great capacity, and the whole esophagus, especially in young birds, is lined with pronounced longitudinal folds, 2 to 3 cm. long, which make it capable of sac-like extension. A crop is missing, and the stomach is very muscular but relatively small (\pm 1.5 cm. long, \pm 1 cm. broad, and \pm 0.5 cm. high).

Undoubtedly these anatomical peculiarities have a certain adaptive value in the life of the species as will be described later. It also may be noted here that in two adult males I found the right testis much larger than the left one.

Geographical Distribution.—According to Phelps, Tersina viridis occidentalis is widely distributed. It ranges from northwestern Brazil, British and French Guiana, the Isle of Trinidad, Bolivia, Peru, and Colombia, up to Panama. Its local and seasonal distribution in Venezuela in general, and the Parque Nacional in particular, is extremely interesting. Like many other passerine birds, Tersina viridis is not sedentary but semi-migratory.

Oct.]

During the breeding season (February to August), in the broadest sense of the word, *Tersina viridis* seems to be confined to hilly or mountainous areas. This seems to apply not only to the northern mountains, the main Andes (states of Táchira, Mérida, Trujillo), but also to the coast range (Cordillera de la Costa), the Perijá Mountains on the Colombian border, and the vast mountainous regions south of the Llanos and the Orinoco River.

It is remarkable that, out of the 58 specimens in the Phelps Collection, 42 were collected between February and August and only 16 during the rest of the year.

In the Parque Nacional de Rancho Grande, *Tersina viridis* arrives in February, stays till August, and is completely absent from September to February. During three years of nearly continuous observation the following dates were compiled:

	First no	First noted arrival		Last noted departure	
Year	at ± 500 m.	at $\pm 1000 m$.	at ± 1000 m.	at ±500 m.	
1950	Feb. 25	March 8	July 20	Aug. 23	
1951	Feb. 26	March 5	July 15	Aug. 22	
1952	Feb. 14	Feb. 17	July 16	July 20	

During their migration, the tersinas apparently do not follow the Cordillera de la Costa, but use the transverse valley to reach their breeding grounds. The only observation in flat tropical country was made on February 11, 1952, near Turmero (about 480 m. elevation) in the Aragua Valley, when an adult male flew northward over cultivated ground toward the Cordillera. Three days later the first birds arrived in the Parque Nacional.

Although until now it has been impossible to say anything conclusive about the migration routes of *Tersina viridis*, the material in the Phelps Collection gives us some hints. If we exclude the 42 specimens taken during the breeding season, and also eliminate three specimens which were possibly still migrating: a male and a female from Hacienda Altamira, 1,200 m. (state of Carabobo), and one male from Acarigua, 300 m. (state of Portuguesa), all collected in September, we find that the rest of the 13 tersinas were collected in the nonbreeding season between October and January, and came from the humid "pocket" between the main Andes of Táchira and Mérida and the Perijá Mountains south of Lake Maracaibo, Rio Caura (state of Bolivar), all belonging to the great "hylaea" with its rather uniform hot and humid climate. Twelve of these 13 birds were taken at low altitudes between 100 and 400 meters, and only one specimen came from 700 m. (Seboruco, November 20), whereas the breeding grounds PLATE 12



(Left) Male one singing on his look-out in avocado tree. Photograph by K. Koch. (Right) Second growth BETWEEN TERRITORIES ONE AND TWO. NEST-BUILDING MATERIAL WAS COLLECTED HERE. PHOTOGRAPH BY F. SCHAEFER.

Тне Аик, Vol. 70

in the Cordillera de la Costa range up to 1,800 m. (Colonia Tovar). Therefore, it might be assumed that *Tersina viridis* is a "hygrophil" species spending the dryer and cooler part of the year in the more humid parts of the country at rather low elevations.

Also, it seems most likely that the migration route of at least the tersina population of the Parque Nacional is in a north-south direction. It is interesting to note that in the Parque Nacional the population of *Tersina viridis* is almost entirely restricted to the south side of the Cordillera. On the northern slopes no tersina was observed below 800 meters. This fact is the more curious as the northern slopes are, especially during the dry season, much more humid than the southern ones and, at least from our human point of view, might therefore be considered as adequate wintering quarters. This, however, is apparently not the case.

Habitat.—Originally, *Tersina viridis* was undoubtedly a tropical bird. Compared with most of the other passerine species of the Parque Nacional, it has an unusually wide altitudinal distribution, ranging from the southern foothills of the Cordillera up to the building of the Estación Biológica itself (1,090 m.).

Tersina is not found in the widely distributed secondary savannas which cover the lower slopes towards the great alluvial plains of Lake Valencia. It is strictly a woodland species. The lower limit of its range is in the deciduous forests characterized by dense evergreen underbrush and widely scattered, often thorny, trees (*Hura crepitans*) the majority of which shed their leaves during the dry season.

At about 800 meters these deciduous seasonal forests merge insensibly into the semi-evergreen forests where only one-third of the trees shed their leaves during the dry season. The part-evergreen forest is characterized by an overwhelming growth of creepers and lianas, which cover nearly all the tree-tops in unbelievably thick masses. Here, between 800 and 900 meters, we found the optimum habitat for *Tersina viridis* in the Parque Nacional.

At approximately 900 meters, the part-evergreen forest merges with the evergreen montane cloud forest of the subtropical belt. Here, close to the watershed, the Estación Biológica lies at 1,090 meters above sea level. The half-ruined building lies in the middle of an ecological island of secondary growth, partly introduced and twenty years old. A high percentage of the bird population of this semixerophytic ecological island consists of aggressive invaders from the lower tropical belt. Only about half of the species belong to the subtropical cloud forest biocoenosis (rich in species but poor in numbers of individuals). This also explains why *Tersina viridis* has developed a rather large, isolated breeding community in and around the Rancho Grande building where human interference has changed the natural habitat.

Possibly all newly formed ecological niches are first settled by younger birds which, through population pressure, are driven out of their home areas. Because of competition from old birds of both sexes, these younger birds are often forced to content themselves with inferior biotopes. Once settled, however, they soon develop a strong homing faculty. Therefore, Tersina viridis is rather evenly distributed along the road wherever adequate breeding conditions are found. The ecological extremes of open savanna and heavily wooded, humid gorges are always strictly avoided. After the road reaches the humid subtropical cloud forest, Tersina viridis is absent, except around a few human settlements and, of course, the ecological island of Rancho Here, however, it has found exceptionally favorable Grande itself. breeding conditions and is even more abundant than in the semievergreen forest. Tersina favors a broken landscape with not too dense secondary woods and many clearings. It is a bird of the high tree-tops and even while foraging seldom descends to the middle or lower strata.

Contact with human beings appears to cause a decrease in the distance at which tersinas will flush. This depends on the experiences of individual birds during their life-time and might be considered a biological pre-adaptation for following human civilization.

The wide range of ecological tolerance of tersina seems also to be a matter of individual variation and is obviously not based on micropopulations which differ genetically in having narrow, but different, ranges of tolerance.

The surprisingly large number of breeding pairs (six) around Rancho Grande cannot be a measure for judging population conditions in other parts, where there is not such an abundance of excellent nesting sites, and where more natural enemies probably occur.

General Habits.—With the exception of the times of nest-building and the feeding of the young, their daily cycle of activity and rest is rather uniform. About half of the day (six hours more or less), they are inactive; another 3 to 4 hours are devoted to their social activities, and about two hours are spent in foraging.

The tersinas are rather late risers; they never appear before sunrise, long after the general chorus of thrushes, vireos, trogons, etc., has begun. From about 6 to 11 a. m. they stay in their territories, rarely foraging but alternately being (according to their semi-social way of life) very active or sitting quietly on their favorite vantage points, sometimes without moving. This is true of both sexes. From 11 a. m. to 3:30 p. m. they are usually absent from their territories. During this time most of the Rancho Grande birds fly down into the part-evergreen forests for foraging and resting in the course of midday hours. From 3:30 or 4 p.m. on, they are again present on their territories; the rest of the day is spent in the same way as the forenoon "activity" hours. At about 6 p. m. all birds (with the exception of breeding females) fly out of their territories to their roosting places, often far away. All the Rancho Grande birds roost in lower regions. I often observed the birds flying in a straight, almost horizontal line for 300 to 500 meters out over the deep erosion valley. Then, from above the semi-evergreen forest, they dropped vertically and vanished.

I have learned nothing about the actual roosting habits, but I am quite sure that during the breeding season the birds do not congregate in the night. In the mornings, the arriving birds are often very wet and sit for a long time preening and drying their feathers.

There were considerable differences in the sleep-wakefulness cycle during the different conditions of their residence at Rancho Grande. Shortly after their arrival in February and March their day was about one to one and one-half hours shorter than in April and May, when the breeding season was in full swing. Later, in June and July, after the main breeding season, the birds arrived much later in the mornings and again left earlier in the afternoons.

Approximate average times of arrival in and departure from territories:

	March	A pril	May	June	July
Arrival in territory	6:30 a.m.	5:45 a.m.	5:45 a.m.	7 a.m.	8 a.m.
Departure from territory	5:30 p.m.	6:20 p.m.	6:20 p.m.	5:30 p.m.	4:15 p.m.

It seems that the sleep-wakefulness and the daily activity cycles of *Tersina viridis* have no direct correlation with the absolute number of daylight hours.

Inherent as well as environmental factors are probably involved in the control of the cycles. In April, the inherent physiological factors seem to predominate, as this is the time of greatest sexual activity. The longer daytime activity is thus fomented. In May, both inherent and environmental factors control the necessity of caring for the young and promote the longer daily activity. In June and July, after the main breeding activities have ceased, the birds take no advantage of the longer daylight hours. In these months of excessive rains and storms, the delaying environmental factors are dominant. Also, with the onset of the rainy season (low temperatures, high humidity, minimum of sunshine hours with a corresponding maximum of fog), the tendency to omit the morning activity hours and to show social activity only in the early afternoon (3 to 4 p. m.) becomes stronger, especially after stormy nights.

There is always, independent of sex and age, a great conformity of action under such extreme circumstances. But under normal conditions the males are markedly more active than the females; and the latter arrive on the territories five to fifteen minutes later in the mornings.

Though bright daylight is essential for the full display of the optical signal code of the tersinas, they are not fond of excessive sunshine. The birds are very sensitive to changes of light intensity. At about 11 a.m., when the sun is nearing the zenith, the time of "social activity" is over and the bright, iridescent colors are not "needed" any more; the tersinas then leave their vantage points and dive into the shade.

During foggy hours their senses are noticeably dulled. Then they often go astray and invariably fly only short distances.

Protective Color, Enemies, etc.—Though the green females have an ideal camouflage, the males are very conspicuous in their native surroundings; it seems that protective coloration has only very slight significance in the preservation of the species. With the exception of several snakes and possibly large land crabs, which may prey on eggs and nestlings in natural nesting holes, and rats (Rattus norvegicus) in the building of Rancho Grande, the tersinas seem to have very few potential enemies. Small weasels are absent, small marsupials (Marmosa demararae) very scarce, and the great majority of the smaller Venezuelan birds of prey not only avoid the dense woodland areas but also feed mostly on reptiles and insects, which are most plentiful in the dryer, cultivated parts. Accipiter erythronemius, Micrastur ruficollis (both rare birds of the lower forest strata), and Falco albigularis (a tropical species which regularly visits the ecological island of Rancho Grande) may prey on tersinas. The reactions of tersinas to mounted specimens of these birds of prey will be discussed later.

Flight.—Though generally a sedentary bird, tersina is an excellent flyer, often covering long distances above the highest tree-tops in a straight, scarcely undulating, line. The flight resembles that of the true finches, but it is lighter and the birds are more agile. In some phases it even recalls the agile movements of kingbirds (Tyrannidae). Usually the tersinas confine themselves to short flights from one scantily leaved tree-top to the next.

Being semi-social birds, they have a very distinctive code of intention movements which indicate the movements to follow and usually affect other individuals present. They are ever ready to escape. The females, which usually sit lower and remain more concealed, are as a rule more timid than the males.

Bathing and Drinking.—Before the beginning of the rainy season and during dry weather, the tersinas are fond of bathing in pools and small streams. The act is always accompanied by a complicated ceremony of bobbing, wing-flapping, and hopping from stone to stone.

From May on, they did not bathe any more, but I often saw them drinking out of puddles on the flat roof of the Rancho Grande building.

Feeding Habits.—It seems very likely that the half-year residence of tersina in the Parque Nacional is strongly influenced by the fact that both fruit and insects are more abundant during the beginning of the rainy season than in any other part of the year. Tersina is an omnivorous bird; fourteen stomachs which I examined contained both fruit and animal matter, but the percentage of each varied considerably with the seasons. During the dry season, fruit seems to be the dominant source of nourishment, while from the beginning of the rains when insects crop out by the millions, until the time of departure, animal matter plays a very considerable part in the diet.

Great variations, possibly due to weather conditions which regulate supply of insects, were observed. During bad weather, fruit again dominated in the daily diet, because tersinas are accustomed to catch their insects flycatcher-like, on the wing. This method of catching insects was confirmed by the stomach contents, which seldom disclosed caterpillars, larvae, pupae, or cocoons, but consisted mainly of flying insects like small Orthoptera, flying ants and termites, and chiefly Diptera. Beetles and other insects with strongly chitinized cuticulae were rarely found. The only exception was "soft" beetles of the family Elateridae.

During certain periods, the young are fed mainly on insects.

In May, I repeatedly observed females hunting insects in the underbrush. This is unusual, as tersinas most frequently forage high in trees.

The tersinas have a strong predilection for big, pulpy fruit; small berries are rarely taken. Seeds are discharged whole with the excrement. Cecropia fruit, which forms a favorite dish for at least 25 species of Thraupidae and Icteridae, are apparently not liked by the tersinas. Only on rare occasions have I observed "lazy" males taking cecropia fruit from nearby trees to feed their young.

The favorite fruits of tersinas, like *Beilschmiedea roehleina* and the avocado (*Persea americana*), belong to the family Lauraceae. My pet birds also prefer the avocado to any other fruit, and they dislike

Oct.] 1953] bananas. According to Pittier, the avocado contains 10 to 30 per cent fat, 3.6 to 16 per cent carbohydrates, and 1.3 to 7 per cent proteins. It is therefore one of the most nutritious fruits. Nevertheless, each of my tame birds eats daily about 20 to 25 grams of avocado, which corresponds to two-thirds of their body weight.

Wild tersinas also consume great quantities of food, and their throat-pouches often overflow. Unlike many other fruit-eating birds, such as cracids, trogons, toucans, cotingas, etc., tersinas seem never to swallow and to regurgitate the hard pits, but rather nibble off the fleshy pulp and then let the pit fall. In this way the tersinas assist in the dissemination of many trees.

Only rarely I saw tersinas foraging for fruit in the vicinity of the Rancho Grande building. Usually, even during the time of feeding of their young, they flew distances of 200 to 400 meters to collect the fruit of their favorite trees. While the females usually filled their throat-pouches at the distant fruit trees, the males sometimes followed another practice. They hopped side-ways close to the fruit, seized it with strong, wide-open bill, and by tossing the head back with an upward jerk, opened the mouth, froglike, before bringing the whole fruit—which was often bigger than their head—back into their territory. Then they often sat displaying fully their gorgeous plumage, bill wide open with the big fruit in it, the velvet-black mask showing in the most impressive way; sometimes they sang with a muted voice. I observed this performance enacted by three different adult males. It might well be a ceremonial act, with the aim of impressing the female.

I never saw a foraging tersina hanging head down, a common habit of the tanagers. The act of feeding is very peculiar, resembling that of a snake: the widely opened beak, with its sharp and pointed tomia and the enormous throat-sac, literally creeps over the big fruit, which is many times turned and twisted until the fleshy pulp is scraped off and busily gulped down. The instinct of "scraping" is very strongly developed. Pet birds are constantly using their wide-open bills for scraping whatever comes within their reach: clothes, buttons, human noses, ear lobes, etc. Large butterflies and moths are also swallowed by pet birds in a similar snake-like way. They use their hooked bills only for catching or gripping and then slowly gulp the insects down.

Voice and Song.—Most of the utterances of tersina are unmusical. The vocal repertoire centers about a monotonous, sharply pronounced chirping which, however, is very characteristic of the species and cannot be confused with the voices of tanagers or finches. Males are vocally more active than females. Most of the following vocal expressions, with specific biological significance, are common to both sexes: 1. Calling, ordinarily a single note *tsee*, usually uttered by a male sitting on a perch in his territory. During periods of activity, it is repeated with monotonous regularity; it may also be given before the nest when the female is brooding. The corresponding note of the female is much weaker. While this call is being given, the bird sits erect and motionless except for the bill which is opened halfway and then quickly shut.

2. Caressing, se-se-se-su quickly repeated, probably uttered only by male before and during copulation.

3. Warning and "flight-escape," one syllable *tse*, sharply pronounced by both sexes before flying away, also uttered by pets when an object falls suddenly.

4. Defense, very sharp *tse-it tsu-it*, uttered by both sexes when an intruder enters the territory.

5. Fighting, three to six syllables, a rather long, nasal tsee wee it.

6. Nestlings, whispering we-we-we, from second and third day after hatching.

Only the males sing. While singing, they always sit still; no nuptial display flights were observed. Ordinary advertising song, a metallic clinking twitter of four to seven syllables *tsee-wi-tit-tit-tit*, is heard only on the territory. It is softest during nest construction, when stalks are often held in the beak; strongest on favorite singing perches (tree tops, telephone wires, roofs, pinnacles).

The song plays only a small part in the social life of tersinas. It seems to have slight attractive influence on females and almost no warning effect on other males.

Singing begins after pair formation and "engagement"; the urge to sing is strongest during time of nest-building: at that time it also occurs during the midday hours, even when it is foggy. It is given less often after copulation and during the periods of egg-laying and incubation. Otherwise, it is heard on clear mornings and evenings (activity hours) during the breeding season, with the exception of the time when males are feeding the young. No song is heard when the temperature falls below 15° C. After the young leave the nest, there is a second singing period which dies away after a lapse of one or two weeks unless a second nesting is attempted. Great variation in the songs of individual males was observed.

I have not as yet heard the young males sing in the wild before their departure. However, the first clumsy twitter was given by a captive male at the age of 36 days (June 3, 1952) and full juvenile song between the ages of 60 and 70 days. Astonishingly, this juvenile song, though only uttered in a soft voice, not only consists of at least 15 to 20 syllables but has a very variable succession of different sounds forming a real melody, faintly resembling the song of the European Siskin (*Carduelis spinus*). A similar, very rich, but very loud musical song of at least twenty syllables was repeatedly heard on June 8, 1952. It was uttered by an unmated male, one year old, sitting on top of a *Gyranthera caribensis*, 40 meters high. These observations indicate that young males have far more complex songs than the adults, the songs of which seem to be simplified in favor of special movement reactions, which will be described later.

CLIMATOLOGICAL DATA DURING THE 1952 BREEDING SEASON IN THE ECOLOGICAL ISLAND OF RANCHO GRANDE Month Temperature Rainfall in Insolation Breeding

Month	Temperature in degrees C.		Rainfall in millimeters	Insolation, total hours	Breeding activity
	High	Low			
February	27.5	13.5			arrival
March	26.5	14.5	18.0	194.5	engagement and pair formation
April	26.5	15.0	157.7	105.5	nest building and incubation
May	26.2	15.5	149.7	152.0	nestling time
June	25.7	15.0	254.0	110.0	under normal conditions, end of
July	24.5	15.0	340.2	102.0	breeding

Arrival and Pair Formation.—Comparative observations in 1950, 1951, and 1952 have proved that the entire breeding cycle of Tersina viridis in the Parque Nacional de Rancho Grande depends on the local weather conditions. While the years 1950 and 1951 had rather indistinct seasons, 1952 was, according to the information I received from Dr. Goldbrunner of the Meteorological Service of the Venezuelan Air Forces in Maracay, the only really "normal" year of the three. So, 1952 had a very pronounced dry season which lasted until March and was then followed by an extremely wet, rainy period.

General breeding records concerning the entire avifauna in the Parque Nacional give conclusive evidence that in 1952 the breeding ℓ season not only was much more uniform but also began and ended three to four weeks earlier than in the two preceding years. This also applies to *Tersina viridis*.

It was certainly because of the very dry weather in February, 1952, that the tersinas arrived at 500 meters as early as February 14. This was about 12 days earlier than in the two former years. Furthermore, the extremely dry conditions at Rancho Grande (1,000 m.) in Feb-





Adult males in curtsy positions while fighting. Photographs by K. Koch.

ruary, 1952, were certainly responsible for the short interval of only three days (twelve in 1950 and eight in 1951) between the arrival at 500 meters on February 14 and the first record in Rancho Grande on February 17.

Between February 14 and March 31 the dry weather with very little fog continued. During this time of pair formation, territory establishment, and "engagement," no differences in these activities between the populations at 500 and 1,000 meters were observed.

Though there was a slight predominance of male birds during the first days, females and first-year birds arrived at almost the same time. The time of arrival of the entire Rancho Grande population (6 definite pairs) extended over 10 to 15 days.

Pair number 1, consisting of obviously "old" birds, arrived on February 14 already "engaged." Male one immediately took possession of and defended an avocado tree in front of the building, which in the two preceding years had been the center of the territory of an adult pair.

Though it was rather difficult to distinguish individual birds during the first days of almost continuous commotion before the establishment of territories, I had the impression that at least half of the Rancho Grande population arrived already paired. For the first two weeks, the birds stayed only for about one hour in the forenoon and as long in the afternoon. If the weather was foggy, no birds were seen. All birds came and went together; sometimes as many as eight birds, half males and half females, formed little flocks.

During early March, the birds became more sedentary and the formation of definite pairs took place; new pairs formed and segregated themselves from the group. As the males did not sing at this initial stage, the females seemed to be mainly attracted by the sight of the striking colors of the adult male birds. From the beginning, the latter had a strong predilection for fixed lookout branches in the tops of the trees, where they exhibited themselves.

When a young and an old male were sitting on neighboring trees, the newcomers of both sexes were invariably attracted by the old male. Young males were often completely ignored. Experiments with mounted birds have clearly shown that a quietly sitting bird provides nearly as strong a stimulus as a moving one. Certainly the optical characteristics are most important as recognition marks of the sex partner as well as of competitors of the same sex.

In the process of pair formation, the female plays the dominant part. The following observation on February 20 is typical: an adult male and a young male (2 years old) sit quietly close together on a high pinnacle of the Rancho Grande building; a female arrives and alights 1.5 meters

Auk Vol. 70

away. Immediately she begins curtsying (a very complicated movement reaction which will be described later), takes a blade of grass in her beak, and approaches the older male with bobbing movements. While the young male remains passive, the old one first draws back, then also begins curtsying until the female, followed by the gallant, flies to the flat roof immediately below. Now the female takes up some small particles, possibly pebbles. The old male approaches her from behind and, trembling with excitement, feeds her in a symbolized action but without uttering a sound; during this ceremony the female stoops a little, spreads the tail, and lets her wings hang down as if before copulation. From now on, the male does not allow "his" female out of sight, follows her from stone to stone, from branch to branch, rarely sits farther away than one meter, and while sitting on tree tops always occupies the higher position, showing his silky brilliance and the black mask in the most impressive way. Often both partners sit close together for half an hour calling to each other at intervals of 4 to 6 seconds.

In the course of this phase, there existed only one movement reaction, in which the female promptly followed the male. This was a formalized act of "pebble-flicking" on the ground, the actual meaning of which was not clear to me. It was always initiated by tripping steps of the male while he pressed his plumage tightly to the body, stretched his neck, and let his head appear extremely flat.

The partners of an established pair always remain in very close contact, although the actual sex functions are still dormant. Knowing each other well, they seldom associate with other tersinas. The specific menacing position with which they formed their first ceremonial contact ceases completely. Several times I had the opportunity to observe that an already "engaged" male sat near, but completely indifferent to another pair.

After pair formation, the birds become much calmer. Very seldom one observes that several birds of different sexes are following each other, which was a daily occurrence at the time of arrival. Also, demonstrations of "tenderness" exchanged between the partners of one pair seem to be much rarer now.

Territory.—Another great change takes place while definite territories are being selected. This is a relatively slow, cumulative process, which sometimes occurs with pair formation but as a rule follows it. It takes definite shape only shortly before nest-building begins. In 1952 there was no definite sign of territorial boundaries until March 17. Several things may be responsible for the relatively late selection and establishment of territory. Among them are the semi-gregarious habits and the fact that the breeding and living biotope and the food biotope are very different and lie far apart. Also, the advertising song plays no essential part in the breeding habits.

The quantity, selection, and the relative dimensions of the territories are largely correlated with the density of population. General topography, human interference, and the structure of vegetation which have produced the almost universal edge effect are primarily responsible for the formation of 80 to 90 per cent of the breeding territories of the entire population of *Tersina viridis* in the Parque Nacional. They are concentrated along the road. I estimated the number of territories on a stretch of 10 kilometers at about 50. Under normal conditions we might expect a territory every 200 meters. Only where bridges are concentrated do we find more.

The average extension of the territories along the road is about 50 by 100 meters. Many of these territories are isolated and do not border on others. In and around Rancho Grande, however, we find a mosaic of territories with only small intervals between because of of the location of favorable nesting sites. Here, six territories were concentrated on a stretch of only 300 meters which means that the Rancho Grande population is four times denser than that along the road. Accordingly, the territories at Rancho Grande were very much smaller, the maximum being about 40 by 60 meters and the minimum about 15 by 30 meters. Along the road as well as around Rancho Grande, we were able to show that population pressure is so strong that if the exit of one nesting pair frees a territory it is immediately filled by a new pair.

Undoubtedly the main activity in founding a territory lies with the male bird, who is also its sole defender. The basic requirements seem to be good visibility, the proximity of at least one suitable nesting site, and one or more vantage points. Favorite vantage points are treetops with horizontal, sparsely leaved branches, telephone wires, roofs of building, etc., from which the territory can be watched and defended.

The main functions of the territory seem to be: first, to guarantee a certain isolation and equal distribution in a given breeding area; second, to advertise a nesting site; and third, to protect the nesting site.

All territories have two centers towards which all social activities, including defense, are concentrated. The first is the main vantage point of the male, who also "represents" the territory. This is not necessarily situated in the geographical center of the territory, but is determined primarily by visibility. The second center is around the nest itself. SCHAEFER, Life History of the Swallow-Tanager

Auk Vol. 70

Boundaries are sharply drawn only on the borders of small territories. When breeding activities are at their peak during the time of building and copulation, the borders are best kept. Later on, a certain negligence is observed.

The territories of old males nearly always occupy the "best" places of a given breeding area. The younger males, whose sexual activity begins later, have to content themselves with the rest; but as the younger males are always on the defensive, their faithfulness and homing faculty are greater.

In general, no other tersinas are tolerated in an occupied territory, but there are many exceptions which will be discussed later. In the



Territories of Tersinas at Rancho Grande in 1952.

Rancho Grande colony, a well balanced hierarchy existed. The dominant bird always was the old male of territory one, who seemed to be well known to all other males. Though not "agressive," male one seemed to be more "self-assured" than all the other males, and his presence was always respected. He was the "owner" of the first and largest territory (see figure 1); he was also the first to arrive (February 17) already paired, and the last to leave (July 12) together with his



MALE TWO ATTACKING MOUNTED MALE. PHOTOGRAPHS BY E. SCHAEFER.

female who was dominant over all the other females and probably the oldest. Their late departure was due to the fact that they were not able to raise any young in spite of three attempts. From his avocado tree male one dominated the whole Rancho Grande breeding colony. He had another vantage point in common with male two (of territory II) on the border of their territories.

The territory of pair two was the smallest of all; it was squeezed in between territories I and III. Male two shared the vantage point on the cecropia with male one but preferred his own on the roof of the building. Details will be given later.

Territory III of male three was on the edge of the uninhabited part of the building. Male three had his vantage point on a grapefruit tree. He had a tendency to enlarge his territory in the direction of the avocado tree of male one, who usually scared him away by his presence alone.

The first territory (IV-A) of male four was in a rather unfavorable position in the back of the inhabited part of the building. A small *Casuarina* tree served as vantage point for this young, very timid, probably two-year-old male. After the first young of pair four had flown, the territory (now IV-B) was shifted to the front of the building, where a new nest was built in a wall along the road. Here the telephone wire and a huge *Gyranthera* tree, 40 meters high, were selected as new vantage points by male four.

The territory of male five was small. It centered around a huge Gyranthera tree and a bridge. When the young of pair five were big and the boundaries of territory V no longer sharply watched by male five (an adult bird), male four enlarged his second territory (IV-B) in the direction of territory V without being molested by male five. Males four and five used the same tree as a vantage point.

The territory of male six (found last) was on the edge of second growth and virgin wood along the "water trail" east of the building. A large, isolated tree left from the virgin forest served as look-out, but two successively built nests were actually about 30 meters and 40 meters, respectively, inside the virgin forest, close to the man-cut embankment of the water-trail.

Co-inhabitants of Territories.—Many other species were found within the territories of the tersinas, but with the exception of actual competitors for nesting-holes, they were in no way molested by the tersinas. In fact, the latter never actively associated with other birds. On the other hand, their very favorably situated vantage trees also drew many other species of birds. Besides many purely accidental meetings I observed a kind of rank order.

Auk Vol. 70

The most prominent vantage point was the avocado tree in territory I, standing by itself and offering ideal resting or hunting conditions for flycatchers. It had a horizontal twig in its top, which not only was the favorite spot of tersina male one, but also attracted quite a number of other birds. On this very twig and in the space of a few centimeters I observed 21 other species during the breeding season (March to July) of tersina pair number one.

There were only a few birds which did not respect the tersina male when he was perched on "his" twig. These birds, which were definitely dominant over *Tersina viridis*, were a pair of *Tyrannus melancholicus* (banded), not breeding; a pair of *Thraupis episcopus*, breeding; and a pair of *Tachyphonus rufus*, breeding. It is interesting to note that all these birds are invaders from the tropical belt. If one of these birds appeared, tersina male one hopped quickly to another twig near by. There was never any fight nor defense observed for this much coveted twig. If tersina male one was not present, female one sometimes sat on the twig.

Tersina viridis shows altogether a very conciliatory attitude toward other species in and outside the territorial boundaries. Competitive fights for favorable nesting sites were observed against the swallow, Pygochelidon cyanoleuca, about 35 to 40 pairs of which breed in the building of Rancho Grande, and on one occasion against Philydor rufus. The latter fight took place on May 25, 1950. It clearly showed that a male tersina does not attack a territorial intruder, but very resolutely defends the nest with the young just as colonial breeders do. It must be mentioned that *Philydor rufus* generally digs its own nesting burrows in the virgin wood and that it therefore seldom competes with Tersina viridis. In the above mentioned instance, a Philydor rufus tried with great persistence to enter the nesting hole of a pair of tersinas with three young, 6 to 8 days old. During the first stage of the struggle, while the female tersina was on the nest and continued to feed her young, the fight was conducted by the male, obviously an old and experienced bird. His feathers ruffled, bill half open, he stood in a defensive position about 50 centimeters from the entrance hole of his nest, while the philydor was on the watch one meter in front of him, in smooth-feathered position. As soon as the philydor made a thrust forward to enter the nesting hole, he was seized by the male tersina with beak and claws and both birds rolled to the ground. where they soon separated and took up their former positions. This was repeated three times during twenty minutes. Then the philydor flew away.

The "Curtsy Reaction."-When dealing with or fighting against other birds, the tersinas never showed a fundamentally different bearing from other passerine birds. However, their own social code consists of a series of unique and rather eccentric movements and positions which completely dominate the social behavior in both sexes. I have called this innate, stereotyped, and rather complex signal code the "curtsy reaction."

Though this curtsy reaction seems to have a multitude of different meanings, which we will analyze later, it seems that in all cases the bird "enjoys" it. Undoubtedly it is correlated with sex functions and is intensified with age. Basically it may be interpreted as "play," in the strictest sense of the word, a self regulating reaction completely forming its own object. In principle it reminded me of the social dances of some Rallidae like *Porphyrula martinica*, or the vocal mass tumults of some Cracidae like *Ortalis ruficauda*. It may therefore also be classified as a surplus or extravagant reaction common among tropical birds and mammals.

The curtsy reaction involves more than one individual and is released either by sight or movement if two or more adult birds are together. It follows the avalanche principle, oftentimes "infecting" a whole group to participate in an orgiastic mass ecstasy of stereotyped movements. It has a blind reflex character without restraint or interruption and is often continued long after the original stimulus has passed.

In its most common form, the curtsy reaction begins with a pose of "boasting." The two or more partners or opponents face each other. All feathers are tightly appressed, the flat head is lifted, the wing tips hang down, the wings and tail sometimes tremble. Then a very characteristic and sprightly bobbing movement begins. From a distance it looks as though the birds are in mechanical contact with each other. The low bow of one bird almost exactly corresponds to the greatest erectness of the other.

During the first phase, the bow, wings and tail hang down, legs are bent, and the head is the lowest part of the deeply bent body. This movement is comparatively slow.

The second phase consists of a sudden upward jerk of the entire body which is then kept in a very stiff, almost vertical position. The head, now the highest part, is thrust backward, the beak directed upward. Though the bill may be half-open, I never heard a sound uttered during the whole procedure.

This mutual up-and-down movement may be repeated 20, 50, and up to 300 times, depending on the stimulus and the accumulated excitement. It is sometimes accompanied by bouncing hops through the horizontal branches of cecropia trees, the birds gamboling, chasing,

Oct.] 1953] and fencing with each other. During this rapid give and take, it is also a common practice to attempt to perch higher than the others' heads in order to gain advantage; but generally the birds do not strike against each other's bodies.

The whole curtsy reaction seems to be superimposed on a great many social and emotional actions. I was unable to differentiate the various components of this dominant reaction. We will therefore limit ourselves to enumerating only the most important stimuli which in the course of the entire breeding season automatically release the curtsy reaction.

During the initial phase of pair formation, when the birds do not yet "know" each other, both sex partners often curtsy in an almost hostile attitude. The curtsy is a display which is used under a variety of situations, such as "impressing each other," courting, display, challenge, and defense. After the partners are once accustomed to each other's presence, the action ceases completely.

The arrival of one or more strange males in a territory releases the action almost automatically. After the "owner" of the territory has chased the intruder in circles around and out of his territory, he immediately ceases curtsying and returns to his vantage point. Also, the sudden appearance of a known bird frees the curtsy reaction, which stops as soon as the unexpected visitor is recognized.

Among neighboring males, territorial defense curtsying is often observed, especially during the daily activity hours. This is particularly true if territories are small and boundaries sharply drawn. The male in whose territory the curtsy duel is fought generally "wins."

Although most pairs of the Rancho Grande breeding community lived in harmony, the potential preparedness for defense curtsying among adult males was maintained until the end of the breeding season. It seems to be weakest during the time of incubation.

With the exception of the already described "first meetings" of still sexually inactive males and females, the curtsy reaction is generally only performed by birds of the same sex. Males will then only curtsy with, or against, other males. This unisexual relationship also inhibits the increase of the reaction when two males curtsy in the presence of females. The females curtsy much less. When present, they act as onlookers. Females have a tendency to trespass territorial boundaries, and as they are frequently followed by their males, they give direct cause to territorial defense curtsying.

The oldest and most quarrelsome female of the whole Rancho Grande breeding community (female one) was the only one which often curtsied against other females. On March 25, when female two flew



(*Top*, *left*) Typical small nest with first egg, at low elevation (500 meters). (*Top*, *right*) Typical nest with full clutch. (*Bottom*) Young in nest two, 6 to 8 days old. Photographs by E. Schaefer.

close to the prospective nesting site of female one, the latter attacked female two, curtsying exactly like a male. Then she clawed female two and drove her away. On April 30, after the young had hatched, female one again "attacked" female two in the same manner. When female two did not respond, female one approached her neighbor to within 3 to 4 centimeters and curtsied about 150 times at this close distance before the completely inactive female two. In doing so, female one many times retched food out of her bulging throat sac and afterwards swallowed. it. On this occasion both females neglected their young for about two hours.

When old males are present, the young ones usually try to escape. Only in exceptional cases (to be described later) did I see young males engaged in territorial curtsy duels. Instead of participating in the curtsy activities of older males, they more frequently sang within the boundaries of their territories.

There is a possibility that in the evolution of the social life of tersinas, the curtsy reaction was substituted for the original song performance still maintained by young birds.

Very often the curtsy reaction culminates in a real mass ecstasy. We have mentioned before that neighboring birds know and, according to their rank order, also respect each other, at least under normal circumstances. As by nature tersinas are sociable, the territorial fights are rare after the rank order is once settled. The males, sometimes with their females, meet regularly during the activity hours. It was thus not uncommon to see several pairs peacefully sitting together in the same tree. This was mostly on the avocado in territory I, or the cecropia between territories I and II. Then, without any apparent reason, the whole group began curtsying in a frantic display. Sometimes, especially before nest-building time, but also even during incubation and feeding intervals, the females were infected to such an extent that they neglected their young for hours.

The young males of the Rancho Grande community generally did not participate in these mass curtsy dances. One exception, however, was noted on April 1, 1952, when nest-building began. That day, at 8 a.m., young male four and female four joined in an orgiastic mass dance conducted by twelve birds in the highest branches of a giant *Gyranthera caribensis* tree in front of the Rancho Grande building.

Mass curtsying often takes place in the early morning hours, after the males have arrived from their roosting places. Even when young were in the nest, adult males rather preferred their mass curtsy plays to feeding their young. Only when temperatures fell to 15° C., all curtsying activities stopped. This activity had a new climax in the beginning of June, after the broods were independent and many strangers arrived in the Rancho Grande community.

Mass Insect Catching.—Here we must also mention another activity of equally strong social character. Between the sixth and the fourteenth day after hatching, when insects were fed to the young, mass insect catching was almost completely substituted for the customary curtsy plays. The main difference seemed to be that the instinct for curtsy play was now overcome by the brood-rearing instinct. Independent of sex and age, all birds of the Rancho Grande community actually took part in these mass foragings, which seemed at the same time to be first indications of a gradual transition from breeding behavior to post-breeding flocking behavior.

Late every afternoon, the adult tersina population of Rancho Grande gathered in the tops of the casuarina trees belonging to territory III to catch insects for their young. There was a continuous coming and going between the nests and these trees. The strong social character of this action was accentuated by the fact that all birds remained in a flock even when moving to other tree tops. The main activity was always in one tree, often together with pairs of *Thraupis palmarum*, *Thraupis episcopus*, *Tangara heinei*, *Tyrannus melancholicus*, and *Myiozeletes similis*. Unlike the tersinas, the latter birds often changed trees. They were never molested by the tersinas, and *vice versa*.

This social insect-catching was done in the same manner as flycatchers do. The individual bird rose from 3 to 10 meters above the tree, often caught one, two, or three insects, and then went back to his starting point. The females were more agile and more dexterous. Usually they returned to their branches in beautiful glides, with tails spread fanlike. The old males were still partly governed by the curtsy instinct. This was obvious when an old male returned to a branch which had meanwhile been occupied by another old male. Still in flight, he began to curtsy (never observed on any other occasion), performing swinging, awkward-looking up and down movements before perching. Once he was perched, however, the curtsy movements were not continued.

Experiments with Mounted Birds.—With respect to sight recognition, fright and defense reaction, and individual behavior, many experiments with mounted birds were conducted.

For this purpose, mounted tersinas, males and females, a male of *Chlorophanes spiza* (a bird which to the human eye resembles the male tersina in the wild), a bat falcon (*Falco albigularis*), two small hawks (*Accipiter erythronemius* and *Micrastur ruficollis*), and two owls (*Bubo virginianus* and *Ciccaba virgata*) were fastened to long poles so that

they could be easily shifted from one place to another. The results follow.

The mounted tersinas were specifically recognized at a distance of at least 150 meters. They were treated by the live birds exactly as if they also were alive. The mounted males were more quickly recognized than the mounted females.

As could be expected, a confusion with *Chlorophanes spiza* never took place. Also no attention was paid to the mounted *Chlorophanes* when it was put close to the nesting holes. It was "nonexistent" to the tersinas.

The owls were neither feared nor attacked. There was a certain uneasiness shown (especially by timid pair three and young male four) but feeding activity was not interrupted, even when the mounted owls were exhibited three or four meters away from the nest entrances. This apparent ignoring of the owls may be explained by the fact that tersinas are strictly diurnal birds, going to roost by early twilight, and most owls of the Rancho Grande region feed almost exclusively on insects and land-crabs.

The sight of the hawks excited the tersinas to such an extent that they interrupted the feeding of their young if the hawks were put close to their nests. But actual fear was not demonstrated. Both hawks are quite rare birds and are seldom seen in high trees.

The only bird of prey specifically recognized and *really feared* was the bat falcon. When the mounted falcon was exhibited, no tersina dared to come close and none entered its nest.' If the falcon and an owl were exhibited together and the falcon then taken away, the tersinas immediately began feeding again. The bat falcon is (with the exception of the true eagles and the rare North American *Falco peregrinus*) the only "noble" predator of the Parque Nacional which hunts above and in the tree tops and has a predilection for small birds.

Reactions to mounted tersinas were in no way uniform. Male one, the leading male of the whole breeding community, did not attack the mounted male. After he became accustomed to the latter, he treated it in just as "friendly" a manner as he treated the males when they came as visitors into his territory. Several times he tried to induce the mounted bird to join in the curtsy play. Female one, however, was very aggressive; she attacked the mounted female many times, but paid no attention to the mounted male. The most interesting experiment with pair one was as follows: two mounted birds were fastened two meters away from the nesting hole; female one was on her nest and male one on his perch on the avocado tree. Male one immediately approached to 20 centimeters from the mounted male and began curtsying. This attracted male and female two and male and female three. All of them alighted close to the curtsying male one. Then female one came out of her nest and all three males began a frantic curtsy dance on the ground. The mounted male which had orginally stimulated the action was not given any more heed. Only female one did not join the orgiastic dance but with long bouncing hops, attacked the two living females and the mounted one with the obvious aim of driving them away from her nesting site.

Pair two, whose territory was squeezed in between territory I and territory III, was undoubtedly the most aggressive and therefore also rendered excellent results in these experiments. On May 7, at 11 a.m., the mounted birds were fastened to two poles five meters long. They were put three meters apart, to right and left of the nesting hole of pair two. Male one and male two alighted on the wall above nest two and began curtsying to each other in the usual "friendly" manner. Male one then flew away showing no further interest. Shortly afterwards, male two and female two alighted about one meter from the mounted male. Male two immediately began to curtsy before the mounted male but paid no attention to the mounted female. The latter was then slowly brought to a distance of only five centimeters from curtsying male two, yet male two showed no reaction. The mounted female was then put back in its original place. As soon as the mounted female "passed" the nesting hole, female two attacked the mounted female and curtsied about fifty times before it. Then female two calmed down and sat for about 20 minutes at a distance of 50 centimeters from the mounted female. After this, female two flew away and fed her young. Meanwhile male two had entered into the second phase of his attack. In full fighting rage he hovered around the head of the mounted male and tried to alight on its back. During the third phase, which lasted 47 minutes, male two threw himself on the mounted male, sat on its back or head, wildly picking at its eyes, head, and neck and trying to strangle it. While frantically beating his wings, he also regurgitated a pulp of insects and swallowed plucked feathers of the mounted bird. This he repeated about 10 to 12 times, and the mounted male was slowly torn to pieces. Next, the pole with both the mounted male and the vigorously fighting male two sitting on top of it, was carried to the nest hole and the mounted bird slowly pushed into it. As male two seemed to be only interested in fighting his "opponent," which had already lost a wing, not the slightest change in behavior was noticed. Female two made no attempt to defend the nest against the "foreign male." She sat passively on one of the iron girders and observed the fight. The mounted female was then put close to the nest. Immediately female two attacked "her" furiously. She also alighted on top of the mounted female and tried to strangle it. After this, both mounted birds with both live birds still sitting on top of them were carried in the direction of territory III. As soon as the inner border was passed, they flew back into their own territory, catching insects on the way, and the female started feeding her young again. Then the mounted birds were stationed on the border. About 15 minutes later, male three arrived and without passing the border instantly began curtsying before the mounted male. Male two and female two saw it and immediately renewed their attacks from their side. It is a very instructive sight to see both males fighting the same male "intruder" from their own ground and territories. Female two of course only fought the mounted female. Then, male two and female two again pitched onto the mounted birds and male three soon withdrew to the center of his territory.

Similar experiments were repeated on different days. The results were the same. Though the mounted birds soon looked very shabby and had to be stitched together, the tersinas always attacked them as though they were live birds.

Both male three and female three were very timid. While female three showed only fear and never attacked, even if the mounted female was put close to her nest, male three fought in a rather irresolute way and often merely watched attentively. Only if the mounted male was put in "his" grapefruit tree, the look-out center of his territory, he attacked courageously, sitting on the mounted bird in the same way as male two. On May 8, male three even tore a wing off the mounted male, swallowed feathers, and immediately after his "victory" fed insects to his female, who sat beside him on a grapefruit tree.

Male four and female four reacted very similarly. They were even more timid than pair three and often completely indifferent to the mounted birds. When the mounted male was put in the casuarina tree of male four, the latter continued feeding his young. Only once he tried to curtsy in a very awkward way before the mounted male. Evidently the instinct for territorial defense is little developed in younger birds.

Selection of Nesting Site.—Though I had the strong impression that old females like female one sometimes actively search for old nesting sites of the year before, there is no doubt that the primary selection is done by the male. This "searching" begins at least 8 to 12 days before the actual nest is built. In 1950, the searching time was April 1 to 10; in 1951, April 8 to 15; in 1952, March 23 to 31. No difference in time was observed between the population at Rancho Grande (1,000 meters) and that of the deciduous forest at 500 meters. This may be due to the fact that the main climatic changes which bring about the end of the dry and the beginning of the wet season affect both altitudinal belts, not only at practically the same time, but also in a very similar way.

Usually the male flies close to the prospective nesting site and the female follows him closely. During the entire breeding season, this is one of the few occasions when the female willingly follows the male. The female then sits quietly, sometimes calling at short intervals and watching attentively all movements of the male. The male is very active. Seemingly attracted by all dark objects, he hovers restlessly from one hole, burrow, or cavity to the next. Sometimes he also flies in spirals and circles in a kind of symbolic dance, which reminded me of a hummingbird flying from flower to flower. During the first days, there is no system in this hovering dance. The male seems only trying to awaken the interest of the female for a general place but not for a definite hole or burrow. The male often alights near the female and sings. During the next phase of "demonstration," the male takes up blades of grass or other light-colored material such as the inner bark of *Cecropia* or *Miconia* and sings a soft, muted song, holding the material in his bill. From this time on, the female becomes interested too. Often she follows the male and hovers in the same way he does. Then the male enters a hole with the material in his bill and after a few seconds looks out again, displaying fully his gorgeous plumage.

To the human eye, the effect of this peculiar signal is that of a "target": the center consists of the much distended velvet-black mask, surrounded by a turquoise ring, which with every turn and movement changes its vivid iridescent color from green to deep blue. The outer ring of the target is formed by the black of the entrance hole itself. Often I had the strong impression that the black-mask-signal not only released the "enter-the-black-hole" reaction, but also produced an association which led the female to search from now on for black holes herself.

The fact that young males lack the black mask has certainly selective importance in that it minimizes their chances for propagation. Through the "black-mask-effect," the male "invites" the female to search too, which she always does in a much more particular way than the male. As soon as she finds a nesting hole to her liking, she usually occupies it without further searching. Independently of the fact that the female may already have selected a nesting hole, the "searching" and "demonstration" instincts in the male continue in a rather undecided and playful way for many days, at least until the actual nest-building begins. There is, of course, considerable individual variation. One case was observed (pair two) in which the male and female first occupied different holes in close proximity until the time when actual nest-building began. Only then did the male change over to the hole of the female.

Conditions of Nesting Site.—Contrary to most statements, the tersinas of the Parque Nacional never selected holes in trees as breeding places. They invariably bred in cliffs, earth walls, road-cuts, or stone walls or under bridges. Of 28 nests observed during three years, I found only three constructed under completely natural conditions. Two of these were in cliffs and one in an earth wall caused by a landslide. Four more nests were in earth banks, five under bridges, and sixteen others in man-made perpendicular walls. The height from the ground seems to be of no importance; it varied between 1 and 3 meters. The nests constructed under natural conditions were found between 50 and 70 centimeters inside the tunnels; the majority of the other nests were found 1 to 2 meters deep, varying according to the depth of the hole. One nest was found only 5 centimeters from the entrance, the deepest was 2.3 meters from the entrance.

The natural nesting hole in the vertical earth wall beside a small stream was surrounded by about ten half-finished earth tunnels, which seemed to have been dug out by the tersinas themselves (see plate 16). In another case, the burrow was obviously constructed by *Philydor rufus*.

The diameters of the entrance holes of natural nests were between 6 and 10 centimeters; the entrances of the artificial holes showed much variation. Usually they were rectangular or square, and measured about 20 by 25 or 20 by 20 centimeters. With very few exceptions, the actual nests were built at the back of the holes or the straight burrows. The entrances of the nests were never camouflaged. In one case, an occupied nest of the tropical *Turdus leucomelas* was only 50 to 60 centimeters from the entrance to a tersina nest. The two species in no way disturbed each other.

Before the arrival of the tersinas in 1952, we constructed about 20 wooden nest-boxes and hung them close to the nesting sites of the previous year. Not one was used. The tersinas definitely preferred the deep holes in the stone walls.

Two out of three pairs which built second (or third) nests showed a tendency to choose more open, drier, sunnier nesting sites than those used for their first nests.

They moved from the shadier and damper back of the building to the sunnier front. This was apparently due to the very much heavier rainfall in June and July.

Nest-building.—Although in 1950 and 1951 no exact observations were made, it was impressive to see that after the very dry "dry season" of 1952, nest-building began rather "explosively" after the first rains. This applied not only to the entire tersina population of the Parque Nacional, regardless of biotopes and altitudes, but also to a great number of other species of passerine and non-passerine birds.

Of nine pairs of tersina whose nest-building activities were under observation, four began to build their nests on April 1 and 2: one and two days, respectively, after the first rains had fallen. Three of these nests were at about 500 meters and the rest between 900 and 1100 However, accurate nest-building observations were only meters. made with pairs one, two, and three at Rancho Grande. All three nests were situated in holes in the wall of the unfinished part of the building, and all three could be watched from one observation point, as the greatest distance between them was only 45 meters. The entrance of nest one could not be seen, as it was situated between two dark walls; the entrances of nests two and three, however, were plainly visible. There were iron girders before each nest, and these were favorite resting places on which the birds could be observed very closely. The progress of nest construction was observed with the help of flashlights.

Nest one was begun April 1 and finished on April 6 (six days); 81 construction trips of the female were observed. About 60 of these trips were concentrated in the first four days. During nest-building, the male sat singing or watching on the wall above the nest. Further activities of the male will be described later.

Nest two was begun on April 2 and finished on April 8 (seven days). Female two was a rather slow builder; only 54 construction trips were observed, about 30 of which were made in the first three days. Both male two and female two used to sit for hours on iron girders watching their nesting site during intervals between construction trips.

Nest three was begun on April 9 and finished on April 13 (five days); 62 construction trips of female three were observed, about two-thirds of them also concentrated in the first 3 days.

Though one sometimes gained the impression that the males also were taking an active part in nest construction, the main work was done by the females. The male's part was that of a stimulator or instigator rather than one of active cooperation. All the males' activities during nest-building seem playful compared with the

Тне Аик, Vol. 70



ONLY THE HOLE (Right)(Left) MALE TWO AND FEMALE TWO ON IRON GIRDERS BEFORE THEIR NESTING HOLE (BETWEEN CROSS AND ARROW). MARKED WITH AN ARROW WAS OCCUPIED IN 1953 WHEN THE PICTURE WAS TAKEN. PHOTOGRAPHS BY E. SCHAEFER. FIFTEEN NATURAL NESTING HOLES OF TERSINA IN A STRONGLY WEATHERED GRANITE BANK ALONG ROAD.

PLATE 16

strongly directed activities of the females. The females were also more secretive and cautious during nest-building, whereas the males were tame and even heedless. In spite of the fact that the "searching" instincts of the males had not yet completely died away, the females played the leading rôles.

The average nest-building day passed as follows: 6 to 6:30 a.m., first the male, then the female, arrive in territory. They sit close to nesting site; at short intervals, the male sings or both call to each other. After half an hour or a little longer, the female flies away to collect nesting material. The male follows.

Material is collected in the immediate neighborhood of the nesting site (within 10 to 60 meters), mostly in second-growth behind the Rancho Grande building, but sometimes also in empty rooms. No great stress is laid on the selection of any special material.

On April 2, a voluminous, ball-shaped nest of *Pachyramphus rufus* of the year before was looted and systematically taken to pieces between 7 and 9 a.m. The following birds, which were all simultaneously constructing their nests, took part: *Tersina viridis*, female one, male one, and female two; *Pachyramphus rufus*, female; and *Myiarchus tuberculifer*, sex undetermined.

After each 5 to 10 minutes, the female generally returns, closely followed by her mate. She usually carries a thick bundle of loose, dry material and, often without alighting, flies directly and very rapidly into the nesting hole where she remains from 2 to 3 minutes.

The male generally carries "blind" material. Very often this consists of green blades of grass, flowers, umbels, little sticks, etc., all material which is not, or only very rarely, used for construction. The male then either sits before the entrance to the nest and sings with his "show" material in his beak, or enters the nest and comes out again still carrying the material. Seldom does he leave it inside the hole. Often he lets it fall. Sometimes he carries it to another hole and leaves it there. All this is done without system. The female leaves the nest like a flash, always using the same route, and the male immediately follows her, often still carrying "his" material in his beak. In nearly all construction trips to and from the nest, the male is the faithful and ever playful companion of the industrious female. Though the male does not share the "work," he nevertheless is always active. Often, when the female rests between construction trips, the male flies back and forth to the nest carrying blind material or singing. All this activity may lead to the false conclusion that the male is even busier in construction work than the female.

The nest-building activity usually continues until 9:30 or 10 a.m. Then both birds leave the territory (male following the female) for foraging. Half an hour later construction work is resumed and continued till noon or, during the first days, even up to 2 p.m. Construction activity during the afternoon, 3 to 5 p.m., was only observed on the first, second, and third days. At most, 3 or 4 trips were made during these two hours.

In the course of the last two days of construction, quantities of fine black palm fibers are carried in. At this time, the female remains in the nest for 3 to 5 minutes; the weaving and cushioning with the fine inner lining apparently takes more time than the rough construction of the base.

Until the whole nest is finished, the male still brings blind material, particularly of light color.

Generally the tersinas accustom themselves quickly to the presence of humans in the neighborhood of their nests. When illuminated with flash lights in their nests, they usually make no attempt to escape, but remain completely still. Only one of the "natural" nests (5) was deserted after inspection, probably because some loose earth had fallen on it and partly covered the burrow.

Exceptional Observations during Nest-building Time.—April 1, 1952: 9 a. m., male one passes real construction material (inner bark) to female one on iron girder. Female one enters with material and obviously uses it for construction. Construction activity is continued in spite of heavy fog.

April 2: 7:29 a.m., male two enters nesting hole first, female two follows one minute later, both carry material. 7:33 a.m., both come out *without* material. Then male two catches insects and feeds them to female two.

April 3: 10:22 a.m., first female two, then male two, both with material, enter their hole. They remain inside six minutes, and I hear loud twittering several times. No other such observation was made.

April 4: 8 a.m., an unknown female arrives. Immediately pair one and pair two interrupt their construction activity and, curtsying, drive the strange female away. 9:23 a.m., male two "demonstrates," with black-mask-effect, in one of the neighboring holes. Female two leaves her construction material and "blindly" follows the male. 10 a.m., male two seems to carry material only if female two sees it. He still has the custom of "hovering" and "demonstrating" before other holes. 5:58 p.m., male one still demonstrates at this unusual hour; female one is absent.

April 6: 8:20 a.m., after finishing her own nest, female one "visits" the nesting hole of female two. While female one enters, female two waits quietly outside showing no excitement whatever. After female
one comes out again, female two curtsies four or five times and drives female one back to her own territory.

Consistency of Nests.-The nests of tersinas are loosely constructed, rather shallow cups with irregular, not circular, bases. They are always sufficiently cohesive to be removed from the holes in their original form. They are composed of two layers. The outer is roughly built and of light color. It reaches to the upper rim of the nest, where it is 3 to 4 times thicker than in the center of the nest. This layer consists of vines, creepers, moss, and especially the inner bark and the cambium of various light-wooded trees. The finely interlaced inner layer is a rather compact fabric of tiny palm fibers, which resemble roots. Though the material used in the outer layer is subject to great variation according to altitude, climate, biotope, etc., that used in the inner layer always appears to be the same.

Old nests do not, as a rule, serve as bases for new ones. Only one exception was found at the lower limit of distribution (500 meters) where favorable nesting sites were rare.

The nests show marked differences in shape, size, and weight, apparently an adaptation to differences in the altitudinal levels (500 to 1,000 meters), with their different climates. This is clearly shown in the following table:

WEIGHTS (IN GRAMS) AND MEASUREMENTS (IN MILLIMETERS) OF TERSINA NESTS BUILT IN APRIL, 1952, AT DIFFERENT ALTITUDES AND UNDER DIFFERENT CLIMATIC CONDITIONS

500 melers, aeciauous joresi										
Average yearly	temperature $\pm 24^{\circ}$	Average yearly rainfall \pm 1,000 mm.								
$W eight^1$	Circumference	Diameter	Height (rim)	Depth of cup						
5.0	28	12	2.5	2.0						
5.5	29	10	3.5	2.0						
6.7	31	10	4.0	2.5						
11.0	35	10	4.5	3.0						
	1,000 meters, Rancho Grande									
Average yearly temperature $\pm 18^{\circ}$ C. Average yearly rainfall $\pm 1,800$ mm.										
Weight	Circumference	Diameter	Height (rim)	Depth of cup						
8	39	13	5	3.0						
13	45	14	5	3.0						

500 meters deciduous forest

37 ¹ All weights are taken of the dry material.

38

26

14.6

The following table gives us weights (in grams) and measurements (in millimeters) of first, second, and, in one case (pair one), third nests of the same breeding pairs at Rancho Grande in different months and under different climatic conditions.

13

12

5

6

3.6

4.0

SCHAEFER. Life History of the Smallow-Tanager

er, Life	e History of the Swe	Auk Vol. 70	
e	Pair two	Pair four	Pair five

	Pair one		Pair two		Pair four		Pair five		
	A pril nest	May nest	June nest	A pril nest	June nest	A pril nest	June nest	A pril nest	June nest
Weight	8	22	25	13	22	26	40	14.6	34.5
Circumference	39	41	45	45	54	38	55	37	41
Diameter	13	14	14	14	16	13	18	12	14
Height	5	5	7	5	6	5	7	6	7
Depth of cup	3	3	3	3	3	3.5	4	4	3

At low elevations (between 500 and 600 meters), the nests of tersinas and their cushioning are much more uniform than the nests of Rancho The rim is always intricately interwoven with the outer Grande. laver. This consists of pieces of bark and macerated wood of dead dicotyledonous trees (15 to 20 cm. long and 2 cm. broad); strongly macerated wood of monocotyledonous trees (12 to 18 cm. long and 2 cm. broad); strips of macerated palm wood (10 cm. long and 1 cm. broad); grass stalks, grass blades (Panicum maximum), wool of silk-cotton tree (Ceiba pentandra); much-twisted tendrils of Cucurbitaceae (20 to 30 cm. long), sometimes also skins of ameiva lizards and feathers of doves (Leptotila verreauxi). All nests at low elevations are transparent in the center. In the nests at Rancho Grande (1,000 meters), there is much greater variation in size, shape, and choice of materials. The base is extraordinarily heavy, and not only is three to four times thicker than those of nests at lower altitudes. but often has no definite shape and structure. No nests here are transparent in the center. The construction is untidy with a great assortment of material, such as liverworts (Hepaticae, Jungermanniales), lichens, many mosses, whole wisps of dried Panicum maximum, clusters of Panicum roots with stalks (25 cm. long, 3 to 4 gms. in weight), xylem and macerated leaves of dicotyledonous trees, twigs of Casuarina (nest four completely built of this material), chicken feathers, and feathers of swallows (Pygochelidon cyanoleuca). The outer layer is always thicker than the inner layer. In two cases the inner layer of black palm fibers was almost entirely lacking. The second nest of pair four consisted only of very dirty creepers, tendrils (30 cm. long) of Vitaceae, with a little moss as the inner lining.

In summary, the nests at lower elevations and those made during the drier months are lighter, smaller, and much less massive than those at higher elevations and those made during the wetter months. This is undoubtedly a direct adaptation to climatic differences.

Mating.—With the exception of pair three, where a copulation was observed on the fifth day of nest-building, mating generally begins only after the nests are completed. According to my observations, the mating period lasts about 4 to 6 days. During this time both males and females are extremely shy. Though the nests are rarely visited,

the males sing more than during nest-building time. Males and females are nearly always seen together. No mass curtsy dances were observed. Both partners seem to be more closely attached to each other than during any other time of the breeding season. The males always follow the females. Frequently the birds were seen in their territories even between 1 and 3 p.m.

Copulation was observed only inside the territories, mostly on vantage points, as in tree tops, the flat roof, and iron girders. The usual time for copulation is between 7 and 11 a.m.; only one copulation was observed between 4 and 5 p.m.

The act is often inaugurated by ceremonial play on a flat surface, either on the ground or on a roof. With drooping wings, the male hops toward the female either from behind or from the side; then he opens his bill widely as if yawning and regurgitates fruit or insect pulp. The black mask is ruffled. Then, wings still drooping and tail tilted, he trips closer and feeds the female from behind over her back. While receiving the food, the female bends her head back and sits completely still. Then she gives the food back to the male. This latter act is often more conspicuous than the reception of the food; one sometimes has the impression that the female is actually feeding the male. Copulation either takes place immediately after the feeding ceremony, or the female flies a short distance with slowly flapping wings, male following in the same butterfly-like manner, uttering thin twittering notes.

During copulation, the female crouches down, flapping her wings; the male, also flapping his wings, covers her for 2 to 3 seconds. Trilling mouse-like notes are uttered. Most copulations are single acts, although in one case, I observed it repeated four times. After copulation both birds often sit close together for 15 minutes to half an hour. In one exceptional instance (pair one), the male flew into the nest and was immediately followed by the female. Both birds stayed inside for six minutes.

Egg-laying.—The span of time between the conclusion of the construction of the nest and the laying of the first egg varied with the different pairs from four to seven days. The daily examination of nests was accomplished with the help of hooked wires, with which the nests could be cautiously lifted in the rear to permit inspection.

During egg-laying, the behavior of the birds changed again. The males, with the exception of male three, became quite indifferent to the females, and mass curtsy plays were common during the activity hours.

With male one, the nest-searching instinct cropped out again for one or two days. Again he hovered from one dark hole to the next, often sitting in front of one peering about, as though waiting for his (or another) female to be attracted. He also showed the mask effect and "demonstrated" with a blade of grass in his beak, sang a soft, muted song, and tried to copulate again, which the female did not permit. At this time, female one showed no interest in her male. After the laying of the first egg, male one sat on guard on an iron girder while his female was in the nest.

The females were usually seen alone during egg-laying time. They spent large parts of the forenoon sitting quietly near their nests. They lost their suspiciousness and could be approached very closely.

Several times in the afternoon hours, I observed males and females together on the flat roof of the Rancho Grande building. The females were then busily picking small particles from the cement walls. Male and female three were often seen together on their grapefruit tree during activity hours. All males and all females still roosted outside of their territories.

With the exception of female one (who laid two eggs in the first, three in the second, and only one in the third clutch), all females laid three eggs (14 records of different nests). The eggs are porcelain-white in color. The shells are very thin; seen against the light, the yolk is visible, giving a suffusion of light orange in the center of the fresh egg. The variation in shape and measurement of the eggs is considerable. One egg from 500 meters measured 21×14 mm. and weighed 1.75 gm. Four from Rancho Grande measured 22×16.5 , 23×15 , 20×15 , and 20×14.5 mm. The last two were in the same clutch. The first two weighed 2.7 and 2.9 gm., respectively.

The great majority, if not all, eggs are laid between 7 and 9 a.m. For the purpose, the female remains in the nest for about one to one and one half hours. However before laying her first egg, female three entered the nest at 6:10 in the afternoon and stayed in the nest until 9:40 the following morning. The span of time between the laying of the different eggs varies individually. Females one and two laid theirs on consecutive days, with 23 to 26 hours between eggs. The obviously younger females three and four laid their eggs every second day.

Incubation.—The eggs were incubated between 80 and 92 per cent of the entire time, a very high percentage. The period of incubation varies between 13 and 17 days; the average seems to be 15 days. In most cases, incubation begins after the laying of the first egg. From this time on, the females remain overnight in their nests and only the males leave the territories. The only exception observed was female three, who spent the night outside the nest after the third egg was laid. From the first to the fourth day, the females leave the nest four to six times a day. From the fifth to the thirteenth day, the females sit nearly all day, leaving the nest only for two intervals of varying length. And from the fourteenth to the sixteenth day, the females leave their nests three to five times a day.

All females sit especially close during foggy hours, although they sometimes leave their nests during even torrential rains. Coming back after the rain they are always dry, indicating that they had been foraging in another, lower, region, as cloudbursts are often quite local.

There is great individual variation in the length of the periods spent by each female outside her nest. During the main incubation period (fifth day to thirteenth day), the female is generally off the nest for two short periods each day: a longer one in the forenoon and a shorter one in the afternoon, both usually during the common activity hours. These are also the only times when the incubating females meet with their males. Then they use a very peculiar greeting ceremony, lifting their wings and stretching their legs. Apart from feeding, the females use this time mainly for preening.

Female one had a tendency to leave her nest for 20 to 40 minutes between noon and 1 p.m., with high outside temperatures of 19° to 24° C. in April. Otherwise the periods of neglect were correlated with the activity hours between 7 and 9 a.m. and 3:30 and 5:30 p.m. Female one left her nest for 15 to 50 minutes at a time. She kept the same rhythm in June, on her third clutch, when the rains were very heavy. However, when outside temperatures dropped to 15° C., especially during times of heavy rainfall, she left her nest usually between 10 and 11 a.m. and 2 and 3 p.m. During "cold" nights she also slept in her nest with her head under her wing. This was never observed with any other female.

Female two sat very closely and left her nest only for very short intervals, usually between 7:30 and 8 a.m. and between 3:15 and 5:30 p.m. The periods of neglect varied from 20 to 40 minutes in the forenoon, and from 10 to 35 minutes in the afternoon. Only on the seventh day of incubation, a very sunny day, did female two leave her nest between 2 and 3:10 p.m.

Female three spent more time off her nest than the other two females. Though she was very suspicious in the neighborhood of her nest, during the entire incubation period she regularly remained away from her nest for 60 to 90 minutes between 7 and 9 a.m. and again between 3 and 5:30 p.m.

In contrast to all other pairs, female three and male three kept intimate companionship during the period of incubation, the male often feeding his female with insects on "their" grapefruit tree. During incubation, all females were shy and secretive. They approached and left the nest rapidly. However, they never appeared to be disturbed when examined on their nests with flashlights.

While incubating, they always assumed an extraordinary flat posture, sometimes with the body feathers ruffled and often hanging over the rim of the nest. During the day, they sometimes sat sideways, but during the night the heads were nearly always directed toward the entrance hole.

The males never enter the nests during the period of incubation, and no vocal communications between males and incubating females were observed. The general characteristic in male behavior during incubation is estrangement from the females and nests. Most males behave like "bachelors." They sing and call little. During activity hours they occasionally curtsy to each other, but their instinct for territorial defense is weak. They seldom attack mounted birds and often sit quietly together with strangers. When they meet their females, they recognize them at once but do not employ the greeting ceremony as females do. Usually, they sit together with their females in complete indifference. Then the females, after preening, fly back to their nests; the males do not follow.

For days in succession, the males is not seen in the neighborhood of their nests, and they spend only the activity hours in their territories. On foggy mornings, they arrive as late as 8 a.m.

Individual variation with the males are also considerable. Male one used to meet his female quite regularly; male two was the most "unfaithful" of them all, often being absent even during the activity hours; and male three, as was said before, remained most closely attached to his female. Another characteristic of the males during incubation seemed to be the change from a diet of fruit to one consisting mainly of insects. Flycatcher-like insect catching was often observed, but only male three fed his female regularly with insects. With males one and two, the estrangement ceased on the third or second day before the young were hatched. Then they again approached their nests, watching in a rather shy way before the entrance.

Care of Nestlings.—The percentage of young which hatched, in the nests that I had under close observation and which were not disturbed by humans, was nearly 100. I never found an unfertilized egg. With the exception of pair one, whose first two nests were raided by rats (the third brood of this pair died of starvation), and the second nest of pair four, which was disturbed by humans, no losses of eggs or young were observed.

The nestling period lasts 24 days.





(Top) Young, 12 days old. (Bottom) Young, 16 days old. Photographs by E. Schaefer.

Though the average outside temperatures at 500 meters were at least 6 to 8° C. higher than those of Rancho Grande at 1,000 meters, no difference in speed of the development of young was observed. In respect to relative growth and to the period of time spent in the nest, there was an astonishing conformity of dates. The only noticeable difference observed was that the young of the "lower belt" left their actual nests one or two days earlier, awaiting feedings halfway between the nests and entrance holes. But this was probably due to the fact that the lower "tropical" nests, as we have already stated, were much smaller and weaker than the "subtropical" ones.

No details of the actual hatching process were observed. The young usually hatch on two or three consecutive days. This was proved directly by numerous daily examinations and indirectly by the fact that three eggs of nest 4/2, after 10 to 12 days of incubation, contained embryos in very different stages of development (3 mm., 10 mm., and 15 mm. in length).

I never found an empty shell. As the males do not enter the nests during the time of hatching, they were presumably removed by the females. Whether they were swallowed or carried out, I do not know.

Some of the most striking changes in physical growth throughout the nestling period may be seen in the following table.

The most conspicuous characteristics of the newly hatched young are their enormous heads, their very thin necks, and their tiny bodies. The protuberant nostrils and the traces of the egg tooth are visible during the first days. At a distance, the juveniles seem completely naked, as the sparse natal down on the head and back is of the same yellowish-pink color as the rest of the body, giving the skin a peculiar light golden hue. The flat heads look rather deformed because of the greatly extended bills, with their conspicuous white corners, contrasting with the big protruding eyes.

Instinctive light reactions of young tersinas from shortly after hatching till the third or fourth day are the more interesting as the eyes are tightly closed up to the seventh or eighth day after hatching. During the first two days, the young respond spontaneously with nondirected vertical stretching of the neck and simultaneous bill-opening, when stimulated by the beam of a flashlight. These experiments were often repeated after watching in complete silence before the nest tunnel. On the second day, this reaction was much less pronounced. It disappeared on the third or fourth day.

The first very weak, chiming cries were heard on the second day, becoming stronger from day to day thereafter. From the fifteenth

Tail	naked	·	I	1	spiky sheath 1 mm.	sheaths 5 mm.	sheath 15 mm. plumage 1 mm.
Chest and belly	naked	l	ļ	I	pattern of tracts visible	side-quills 2 mm. bright yellow	center still naked
Back	naked	1	I	pattern of tracts visible	tracts of upper legs visible	sheaths 1 mm.	plumage 1 to 1.5 mm.
Average primary	naked	1	ų	first gray points visible below epidermis	elevated gray rem- iges in sheath 0.5 mm.	still in the sheath 10 mm.	sheath 18 mm. plumage begins to escape 2 mm.
Pigment of skin	pink	1	l	ł	orange	I	I
Natal down	sparse yellow down	on head and back	1	1	I	I	only little left on head and back
Head	pink	still pink	ł	I	1	I	gray quills emerge
Bill	light pink, inside orange	corners to eye 1 cm. white	I	I	lead color	corners 0.7 mm. white	ł
Eyes	closed, pink	closed, gray	closed, 7 mm. in diameter	snall slit	bigger slit	in acti- vity, open	in calm, still closed
Color of legs	pink	I	ł	, 	flesh	1	I
Age in days	1	3	S	Ч	6	11	13

440

SCHAEFER, Life History of the Swallow-Tanager

Auk Vol. 70

Tail	total 17 mm. plumage 3 mm.	total 21 mm. plumage 9 mm.	plumage 12 mm.	plumage 13 mm.	plumage 15 mm.	plumage 17 mm.
Chest and belly	plumage escapes 2 mm., yellow	plumage 8 mm.	plumage 10 mm.	all yellowish green		I
Back	plumage 4 mm.	all green plumage 8 mm.	all green	I	I	ł
Average primary	plumage 10 mm.	plumage 15 mm.	plumage 23 mm.	plumage 31 mm.	plumage 34 mm.	plumage 38 mm., but sheath still 15 mm.
Pigment of skin	Ι	light gray	I	Ι	I	I
Natal down	I	ł	1	I	natal down disappear- ing	ł
Head	quills dark lead	da 2	I		feathers emerge green	white ring around eye visible
Bill	corners still 0.5 mm. white	I	still very soft	I	l	corners still 0.2 mm. white
Eyes	open	I	1	I	l	ł
Color of legs	dark lead color	1	Į.	Ι	Ι	I
Age in days	15	17	19	21	23	24

Auk Vol. 70

day on, they can be heard at a distance of 30 to 40 meters from the nest. Under natural conditions, these chirping notes were uttered only when the adults were near, or entered the nesting holes, and while the young were being fed. The chorus of united voices continued for one or two minutes after the adults had entered the nest. Even when the adults were away for intervals between feedings, no sounds were uttered by the young. When touched or taken out for inspection, the young were always silent.

From the third day on, they usually responded to sounds (chucking of tongue) with the same still undirected vertical neck stretching and gaping described above. The only differences were that they chimed continuously with united voices, flapped the tiny stumps of their wings, and described circles by moving their heads and necks vigorously.

From the sixth day on, the stretching and gaping were definitely directed toward the light (tunnel entrance). The reaction was easily released by sounds, but not by touching the nest. Under the latter circumstance, the young pressed themselves flat into the nest cavity, showing the first indications of fear.

From the seventh or eighth day on, the young usually faced the entrance, their heads resting on the rim of the nest. Then the white corners of the bills and the pinkish throats were clearly visible. Only while defecating and at night did the young face in the opposite direction.

From the eighth (in one case seventh) day on, the females did not brood at night. This was also the time when the first eye-slits were visible. The aquisition of vision is a slow process (see pp. 440-441). Between the tenth and twelfth days, the eyes were completely open during activity (as when the young were hungry or being fed) but were still closed at times of rest.

Thereafter, many experiments were conducted with pieces of cardboard of different shapes, paper images of adult birds, and mounted tersinas and other birds, including birds of prey. The results showed that the juveniles were not able to recognize their own species or the birds of prey, they did not respond to motionless objects, and they stretched and gaped spontaneously in response to moving objects of any sort with simultaneous changes of light intensity.

From the tenth day on, the young began to clean and scratch themselves.

From the fourteenth day on, they had a tendency to leave the nest during the day to meet the feeding parents halfway between the nest and the tunnel entrance. During the night, they gathered again in the nest, and during cool nights (outside temperature: 15° C.), they even slept with their heads under their wings. They became very alert, and even shy, and invariably shrank back or dodged when they were inspected.

From the fifteenth day on, the young sometimes, but rarely, answered their parents when they approached the nests with food.

They were most shy before fledging. The last traces of natal down on the heads are lost, in some individuals, only after leaving the nest. The head and tail feathers are fully developed only after the young have started to fly (30th to 35th day). Then also the last traces of the white corners of the bill are lost.

The juvenal plumage, which shows much yellow in the underparts, is gradually lost by very slow, incomplete molt which begins within a month after leaving the nest.

On the sixteenth day, the first silky, glossy green feathers and the gray throat feathers are first seen. With the nineteenth day, the white ring around the eye begins to disappear. After 120 days, the young males look very much like adult females. After 140 days, primaries and secondaries are also changed, and in young males, the first iridescent blue feathers show on the back, tail, and breast. After 200 days, some iridescent blue feathers show over the whole body, but the general color is still green.

Weight of Juveniles.—As only three nests could be gradually drawn closer to the entrance with the help of wires and as there was danger that the adult birds might leave their broods, the following weight measurements are very incomplete and do not include the whole length of the nestling period.

With nest two, the weighing began on the fifth day after hatching, while the only young of nest 1/1 and nest 1/3 could only be weighed between the tenth and seventeenth, and the eighth and twelfth days, respectively. (See graph.) For weighing, the young were removed with their nest (or later simply taken out of the holes) and individually weighed on a balance and otherwise examined. This daily process lasted only 5 to 10 minutes for each nest.

Nest three, which was favorably situated for close visual inspection, was left completely untouched as a control until the twenty-third day, when the juveniles were banded. On the morning of the twentyfourth day, as was expected, they flew out. The general rhythm of growth and development of the juveniles of nest three was the same as that of the young of nest two.

Four rather distinct periods of growth could be distinguished. During the initial period, lasting from the first to the fifth day of post-natal

Oct.]

Auk

development, only visual observations could be made. Noticeable development did not begin before the second day. But the relative growth seemed very rapid. The great difference in size of the young of one brood just after the hatching of the last young, became less noticeable from day to day. Nevertheless, there was a decided difference in weight between the smallest and the largest until at the thirteenth or fourteenth day, when a strongly-marked period of



AGE IN DAYS

Weights of juvenile Tersinas. Solid lines, young of nest two; broken lines, young of nests 1/1 (upper) and 1/3 (lower).

fluctuation began. During the first five days, the single young of nest 1/1 appeared to be about three times larger than the young of nests two and three; later it grew more rapidly, and during the time it was weighed daily, it proved to be much heavier than the heaviest juvenile of nest two.

During the second period, from the fifth till the thirteenth day, the development was relatively uniform and rapid, but the increase in weight varied individually and according to the storage of food in the esophagus.

The third period, one of rapid feather sprouting, lasted from the fourteenth to the eighteenth day, was one of less increase in weight, and was marked by great fluctuations.

During the fourth period, the eighteenth to the twenty-fourth day, only very slight further increase of weight was observed; in two young, even a slight decrease was observed shortly before leaving the nest. *Brooding.*—After hatching, brooding and feeding activities are completely interwoven at least until the eighth day. During the first three or four days, the females invariably remain a long time in the nests, after returning from their food-collecting trips. They seem to feed only a part of the food contained in their throat-pouches at a time. They can be observed brooding for hours with throat-pouches still full of food. Though I have no conclusive evidence (as the females hesitate to feed in the beam of a flashlight), it is probable that they feed several times before leaving the nest again with empty pouches. There is, of course, the possibility that the brooding females regurgitate the food stored in their throat-sacs, to swallow it, or parts of it, themselves.

The juveniles themselves store so much food in their esophagi that till the 10th to the 13th day, they look enormously inflated, bulging out to one side of the throat. This strange faculty also seems responsible for oscillations in weight of between one and four grams. After the fourteenth day, I observed no further evidence of food storage in the young during the day. This may be due to the more rapid metabolic rate during the time of maximum feather growth. From this time on, the juveniles seem to be hungrier than before. On the tenth day, I obtained the first evidence that the young of nest three attempted to feed themselves or at least tried to swallow cherry-sized fruits brought in by the male.

The storage of food by adults as well as by juveniles is certainly an adaptive measure against the torrential tropical rains, which often prevent for hours the collection of food for the young.

The females brood more closely during the great rains. This indicates that the brooding rhythm after hatching is mainly controlled by outside temperatures, which fall from 2° to 3° C. during cloudbursts.

On the morning of May 6, when the outside temperature dropped from 18° to 15° C., none of the females left their nests before 8 a.m. On the other hand, with fine weather and high temperatures, I often saw the heads of the juveniles protruding beside the brooding females. Depending strongly on weather conditions, the number of hours of brooding can be extremely irregular on two successive days. However, there is no doubt that they decrease gradually up to the eighth day. On the first day, the female broods nearly continuously with only two or three intervals of 5 to 40 minutes in the morning and early afternoon.

Following is a summary of the length of time spent by females in brooding: first day, \pm 22 hours; second and third days, 16 to 20 hours; fourth and fifth days, 15 to 18 hours; sixth and seventh days, 14 to 17 hours; eighth and ninth days, no more brooding.

Oct. 1953] SCHAEFER, Life History of the Swallow-Tanager

Though the juveniles are still nearly naked, the change from brooding by day and night to leaving the juveniles over night without cover is very abrupt. It generally takes place on the eighth day.

Feeding of the Young.—The main task of feeding the young falls to the female. As the feeding activities differed in many respects at the various nests, details are given below. The numbers shown should be considered as approximate, as these observations were made by four different observers.

Pair one, nest one (May): only one young, which was killed by a rat on the seventeenth day after hatching. Though the male entered once on the fifth day, when the female was brooding, it fed the young only from the thirteenth day on. Approximate number of feeding trips: first to twelfth day, 97; thirteenth to seventeenth day, 94 (12 of which were by the male).

Pair one, nest three (July): only one young, which died of starvation on the twelfth day. Approximate number of feeding trips: first to twelfth day, 28 (only one feeding by male when female was inside nesting hole).

Pair two: three young, fed by the female only, during the first eight days. Approximate number of feeding trips: first to twelfth day, 229 (35 by the male); thirteenth to twenty-fourth day, 463 (150 by males 2 and 2a).

Pair three: three young. The male started feeding them on the third day. Approximate number of feeding trips: first to twelfth day, 220 (100 by the male); thirteenth to twenty-fourth day, 527 (220 by the male).

Pair four: three young. The male started feeding them on the thirteenth day. Approximate number of feeding trips: first to twelfth day, 200 (all by the female); thirteenth to twenty-fourth day, 511 (215 by the male).

NUMBER OF FEEDING TRIPS FROM HATCHING TO FLEDGING

		Number of		Number of	
Pair Number	Number of young	Trips by male(s)	Male started feeding Young	Trips by Female	Total Trips
2	3	185	Ninth Day	507	692
3	3	320	Third Day	427	747
4	3	215	Thirteenth Day	496	711

The rhythmic increase and the variations in the number of feeding trips can be best seen in the graph, in which the numbers are only approximate.

It may be added that during the first days, the intervals between feedings often amounted to many hours; this was true also during the last two to three days before leaving the nest. The long intervals in

THE AUK, VOL. 70



(*Left*) Young after fledging, 24 days old. (*Right, top*) Young captive males, 45 days old. (*Right, bottom*) Young captive male performing greeting ceremony. Photographs by E. Schaefer.

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the first days may be explained by the smallness of the young and their ability to store food. The intervals of the last days, however, may be interpreted as an attempt to "compel" the young to fly.

Besides the relationship between relative age (or growth) of the young and the number of feeding trips, there are also correlations with weather. With fine weather, feeding begins at 6 a.m. and ends at 6 p.m., with approximately the same number of feeding trips in the



Daily rate of feeding of young tersinas. The Roman numerals refer to the nests.

morning and afternoon. As the mornings are usually clear and sunny, there is generally less variation in feeding activity before noon than in the afternoon, when rains and cloudbursts are heaviest and most abundant. The maximum feeding activity was observed one or two hours *before* cloudbursts (eight or nine times per hour); the minimum, during continuous rains (three or four times per hour). Exceptions were observed on fine sunny afternoons when activities were even greater than in the preceding forenoons. This was probably due to the high outside temperatures with simultaneous abundance of flying insects.

With the exception of flying insects, which are usually caught inside the territories and which are immediately fed to the young, the food for the young is nearly always brought from far away. On several occasions, I observed females covering distances of 300 to 400 meters to collect fruit.

Oct.]

Auk Vol. 70

The males as a rule did not participate in these long collecting trips. They stuck more or less to their territories. The adult birds always used the same routes in approaching and leaving their nests. These flightways never led over open ground. The birds always took advantage of the smallest cover, such as bushes, trees, and walls. Before entering their burrows, they often alighted near by, waited for some minutes (if feeling insecure, they even waited with bulging throat-sacs for 15 to 20 minutes) and then rapidly flew into the holes to feed their young.

Judging from the relative volume of their throat-pouches, the females invariably brought a much larger quantity of food than the males. The females also played the leading rôle. Only very exceptionally did the males make independent feeding trips. In the great majority of cases, both partners arrived together, the males always following the females. Then the male invariably waited outside until the female had finished feeding the young and had left. The male stayed inside only half as long as the female. I often had the impression that the male only acts as a follower or companion of his female.

With the exception of male three, the males joined the feeding activity when the young had grown to such an extent that the females alone could not supply the demand for food. So it could easily be predicted that male one, which had only one young to care for, would begin his feeding activity much later than males two and three, each of which had three young.

Also there was a great deal of individual variation among the different males in the degree of attachment to their females. Male three, which was most closely "united" to his female, was also the earliest to share in the feeding activity. Since male three fed his female much more frequently than the other males and often entered his nesting hole when his female was inside, it is very probable that he also fed his female when she was brooding. With males one and two, the feeding activity was inaugurated by first feeding their respective females with insects. This was done in a rather "shy" way, two or three days before the males fed their young for the first time.

The males still engaged in their curtsy play during activity hours, even when food demand was at its maximum and feeding trips had reached their greatest frequency.

They always preferred to bring insects, which they could catch on the wing. If males brought fruit at all, they tended to collect the easiest obtainable, Cecropia seeds or whole lauraceous fruit, with which they first played, as described earlier. In one instance, male one brought one of these fruits and after 20 minutes of playing with it on one of the iron girders, he cut it into small bits and fed it all to his female, who had just arrived with food in her own throat-pouch. She then entered the nesting hole to feed the single young, while her mate flew away.

Before beginning their own share in feeding, the males were very timid. Often it seemed that they wanted to follow their females into the nests, but that they somehow were stopped from doing so by an unknown psychological factor. At this time I also saw the males' throat-pouches filled with large insects. They hovered undecidedly for three to five minutes in front of the entrance holes of their nests before they finally dared (or dared not) to enter.

On the fifth day after the eggs hatched, male one (nest one) sang with insects in his bill before clinging to the nest entrance. Then female one came out of the nest, where she was brooding the young, and her male tried to copulate.

The act of feeding the young could be observed only in nest four, which was situated only five centimeters inside the wall of the building. After the nest entrance had been enlarged with a chisel, I was able to see with strong field glasses directly into the nest from the opposite slope, a distance of 15 meters.

At nest four, the female invariably came first. Generally she alighted on the rim of the nest for one or two minutes. She gave equal shares to all three young. A few seconds after she had left, male four arrived and invariably fed only one young; accordingly he stayed a much shorter time in the nest before following the female.

Defecation.—After feeding the young, the adult birds leave the nests extremely rapidly and the surroundings were difficult to survey, so little definite knowledge was gathered on the question of whether and for how long the adult birds swallowed the droppings of their young. My observations on this were again made at nest four.

During the first six days, it seems that the females, who nearly exclusively feed during this time, swallow all or nearly all droppings. From then on, the feces, which are enveloped in a gelatinous cover, are carried away by the female after each feeding and less frequently by the male. After leaving the nests with the excrement in their bills, the adult birds first invariably drop down, fly very low, and after about 10 to 20 meters, let the droppings fall.

The parent birds never wait for the defecation of their young. In the early morning hours, one usually finds a row of droppings lined up on the front rim of the nests. These droppings are carried away, one after each feeding. The individual young appear to def-

Oct.] 1953] ecate every one to two hours during the day. Before doing so, they turn the anus toward the light, make a bow so the anus points out straight into the air, and deposit the dropping on the rim of the nest. Defecation stops at 9 to 10 p.m.

The individual droppings are large, and they vary considerably in size, weight, and color. If the predominant food consists of insects, the droppings are dark gray, bluish, or purple, with a big white rim of albumen; they measure 20 to 30 mm. long and 3 to 5 mm. thick, and they weigh 0.3 to 0.7 gm. When the diet is mainly fruit, the droppings are dark green or yellowish, with only very little white. They are 35 to 40 mm. long, 0.3 to 0.5 mm. thick, and weigh 0.4 to 0.8 gm.

The continuous analysis of fresh droppings during the daily cycle as well as during the entire nestling period, has shown interesting irregularities: in the morning and early afternoon, the food is predominantly (80 to 100 per cent) fruit; in late afternoon, the food consists chiefly of soft, flying insects, especially Diptera and Hymenotera (75 to 100 per cent). This relationship depends largely on daily weather conditions and the habit of the tersinas of catching insects in the late afternoons, if the weather is fine. After excessive rain, the evening food consists mainly of fruit, sometimes even entirely of Cecropia, which under normal conditions is fed only by the "lazier" males.

During the first six days, insect food predominates, while between the seventh and fourteenth days at least 40 per cent fruit is fed. From the fifteenth to the twentieth day, the main period of feather sprouting, a change from fruit to insect food was noticeable, while during the last days before fledging, the food consisted chiefly of fruit.

Second and Third Nestings.—Only one second brood was observed under completely natural conditions, though the males were still in breeding inclination and faithfully stuck to their territories after the young had fledged. If the first nest, with eggs or juveniles, was destroyed, the birds began to build a second nest, usually in the same territory. Sometimes the territory was enlarged in the direction of the least biological resistance.

The second nest of pair four, a very large, untidy structure, was built in only four days. But as a rule, the instinctive actions involved in second and third nestings are slower and less pronounced than those of the main breeding period. Also, the curtsy activities of the males gradually diminish.

Leaving of the Nest.—While in 1950 and 1951 the majority of juveniles fledged between June 15 and 25, in 1952 almost all left during the last week of May. The young of all nests under observation in 1952 left the nest between 6:45 and 9 a.m. They never returned to their nests. Though they were able to fly for 40 or 50 yards, they were easily recognized by their flat, scantily feathered heads and short tails.

During the first day, they usually sat quietly on branches of middlesized trees 50 to 100 yards from their nests. They were generally fed by the females, while the males alternately protected them actively against birds of the same or other species and flew back to their territories.

By the second or third day, they leave the territories, accompanied by their mothers, for lower regions. Only one case was recorded in which a banded juvenile, which fledged on June 3, returned on June 18 with three unbanded juveniles (not hatched at Rancho Grande) and an adult female.

After leaving the young by themselves 8 to 10 days after fledging, the females return to their territories to join their males. The males do not follow their females and young but remain in their territories. As soon as their females return, they try to induce them by "searching" demonstrations to start a second brood, but they are seldom successful.

Then, during June, the breeding and territorial instincts of the males slowly die away, and they all join the juveniles in flocking. These changes, doubtless under hormonal control, seem to be mainly regulated by temperature: a comparatively short spell of bad weather with heavy rains and low temperatures actually extinguishes the breeding disposition even in the old males. Tropical birds are as a rule much more sensitive to small temperature variations than are birds of temperate zones.

Flocking.—Single acts of aggression or defense against other species of passerine birds are now very common. They are soon coordinated with a completely different behavior which quickly culminates in a very strong species consciousness. The tersinas congregate in companies of 10 to 30 individuals, with strong social ties, which were absent during the breeding season. Thenceforth they are never seen in company with other passerine species (unlike Furnariidae and tanagers, which after the breeding season form mixed flocks of up to 25 species). Even stronger and bigger birds, such as *Thraupis* espiscopus, *Thraupis palmarum*, and *Tyrannus melancholicus*, are then often vigorously fought off and sometimes followed with open bills and hissing noises.

All tersinas now adopt a very pronounced "follow-me" reaction which regulates the movements of the flocks. These flocks move from one high tree top to the next in a loose order, often covering great dis-

Oct.] 1953] tances. Often they follow insect swarms. Even the old males act just like ordinary members of the flocks without assuming a leading position. There is little individual freedom in these tersina flocks.

Between June 2 and July 6, one large flock visited the high (50 m.) tops of *Gyranthera caribensis* trees in front of the Rancho Grande building every afternoon.

The last single tersina in Rancho Grande, a female, was seen on July 17, 1952. At 500 meters the last bird was observed July 20.

Individual Characteristics and Exceptional Behavior of Different Pairs.—Pair one: May 13, noon, the only young of this pair is found dead in entrance to nesting hole. The juvenile had left the nest on May 10, when it was fourteen days old. The dead young is half eaten by a *Rattus norvegicus*, which probably killed it. During the afternoon female one lost her instinctive feeding shyness; she sat passively on iron girders in front of the nest entrance. Male one also changes his behavior after a few hours. He is always present, does not leave his territory during the whole afternoon, and often sits beside the "mourning" female and sings for hours without interruption.

Between 4 and 6 (activity hours), both birds are extremely restless and often trespass into other territories. It seems that territorial boundaries have no significance to the pair. The female leads, always followed by the courting and singing male. Through this behavior, the whole breeding community falls into disorder. Males two and three leave the feeding activities of their own young entirely to their females, who do not join in the general excitement. A one-hour, very hostile curtsy duel between males one and two and male three takes place on the uppermost roof of the building, and no territorial boundaries are observed by any of the males. The site of the duels is determined by mourning female one, who is continuously followed by all three males. Also young male four timidly tries to participate, begins to curtsy, but is immediately driven away by the three old males. During most of the time, female one sits quietly preening, often surrounded by the three duelling males. At 6:12 p.m., female one and all three males fly down to spend the night outside the Rancho Grande island.

May 14. Female one arrives at 6:05 a.m. and flies, followed by male one, to the old nesting site, where she sits passively while the male sings two yards away. Males two and three are again feeding their own young and the "old order" is restored. No further territorial invasion by female one takes place. Actions of female one determine the behavior of the males. At 7:40, male one stops singing and very actively begins searching for a new nesting site about 4 to 6 meters from the old nest. Female one remains passive. At 10 a.m., both birds vanish and do not return until 3:30 p.m. From 4 to 5:30 p.m., male one searches and demonstrates with stalks in his bill, but the female still is completely indifferent.

May 15. At 7:05 a.m., male one demonstrates and carries little stalks close to his female, who still shows no reaction and at 7:14 flies off, immediately followed by male one. At 7:16 a.m., female one again arrives, followed by the two-year-old light gray bachelor male (number 2a). This male immediately begins searching and hovering between all the holes which surround the still sitting female one. Male one returns at 7:21 a.m. and throws himself at once on male 2a, drives him out of the territory, and alights several centimeters from female one. Then they both fly to the avocado tree where they quietly sit for an hour close together: a new "engagement" seems to be accomplished.

During afternoon activity hours, male one demonstrates again and female one responds to the black mask effect. New nesting site is selected. May 16, building of second nest begins; May 22, nest completed; May 23, copulation observed; May 26, first egg; May 27, second egg; May 28, third egg; May 29, 6:00 p.m., rat is surprised eating all three eggs; rat charges and bites observer's finger.

May 30. 6:20 a.m., pair one arrives and without paying further attention to old nesting site, immediately chooses new one on lighter, more open, and less damp southeastern front of building, only 15 meters from the avocado tree. The female leads; at 7 a.m., after hovering, she enters a 2.5-meter hole in wall, which contains a swallow nest (Pygochelidon cyanoleuca) with three nestlings which are nearly ready to fledge. Female one remains 17 minutes in the swallow nest while male one sits on wire one meter from hole. Both adult swallows are circling around, timidly shrieking but not attacking. 9 a.m., one adult swallow enters the hole to feed her young. Female one follows the swallow, drives her out and chases her in three large circles around the territory and then away. Then female one alights on the avocado tree, where male one has been sitting quietly for a long time. The fight between the attacking female one and the two adult swallows continues all day long. Male two does not participate in this final fight for the nesting site but has a very vigorous curtsy duel with four unknown adult males, which come up at 4:30 p.m. and are all beaten off and out of his territory. In the evening the swallows still occupy their nest. Both adult swallows are, as usual, brooding their young over night.

May 31. Fight against swallows continues all day. Now male one also joins in, enters the nest hole at 7 a.m., and soon afterwards demonstrates with stalk in bill. Again the adult swallows circle for hours around the nesting hole, probably to induce the young, which have already left the nest, to fly out. The fight ceases at 4 p.m., when male one and his female both join in curtsy duel with strangers. Then, usual pebble-flicking on the roof follows. At night the swallow family is still on the nest. June 1 and 2, fighting continues in the same way, outcome still undecided; it seems as though the tersinas will wait until the young swallows have flown out.

June 3. Immediately after the young swallows have flown out, between 6:30 and 7 a.m., female one begins building nest. The material is brought from the same place, behind the building where material for the first two nests was collected. Nestbuilding activity ceases at 9 a.m. (wind, rain, drop of temperature to 16° C.). At 5 p.m. when the young swallows fly to their old nest again, they are immediately attacked vigorously by male one, who follows into the hole. After 3 or 4 minutes, male one drags out a young, already half-dead swallow, holding it by the throat. He throws the young swallow to the ground, follows, and strangles it on flat ground. During this last phase of the "murder," female one has approached to within 20 centimeters of the scene and watches it. The adult swallows again circle around without actively defending their young. After the "murder," male one sits on the avocado tree during heavy rain and sings several times. But again both adult swallows and the two remaining young enter the hole and spend the night inside.

June 4. Swallows fly out at 6:15 a.m., before the tersinas arrive. Both tersinas are now very tame, as place in front of nesting hole was much used during last days as a parking space. Flushing distance has now diminished to about 3 or 4 meters. Nest building by female one continues, but is much slower than it was with first and second nests. Between 8 and 10 a.m., only four construction trips are observed. Nest three is constructed on back wall of the hole, 0.3 centimeter behind swallow nest. During the building activity of female one, male one sits inactive on wire before nesting hole. No singing. No construction in the afternoon. After tersinas have left at 6:05 p.m., the swallow family again enters hole and sleeps in nest.

Oct. 1953] June 5. Nest-building activity still slower than on preceding day: only from 8 to 9 a.m. After interruption for my own breakfast, second young swallow is found dead on ground in front of nesting hole (same place where first young swallow was killed by male one). The three remaining swallows (two adults and one young) do not sleep in nest again.

June 6. Rain, storm, 15° C.: no nest-building activity; male one arrives alone at 9 a.m. and demonstrates with stalk in beak.

June 7. Fine sunny day, 24° C., great building activity: 8 to 10 construction trips between 8 a.m. and noon. Male one joins in and follows female on each trip behind the building (50 to 70 meters distance) but carries only one third as much as female. Female often brings thick bundles of grass and inner bark of Cecropia and Miconia. These bundles are often larger than her body and hang 20 to 25 centimeters behind like little streamers. Before flying into the hole, both birds always alight on the avocado tree, then on wire in front of nest. Male always enters 3 to 4 minutes after female, often reappears with material, plays undecidedly, demonstrates, etc. Yet male one actually seems to take part in construction work. This is proved by inspection with a flashlight after both birds have been in the nest ten minutes: while female sits on the rim of the new nest, the male makes weaving movements; he was not disturbed by the light. All of the material of the swallow nest is by now used by the tersinas to build their new nest. After two or three minutes, male one tries to escape, flies against my hand, then squeezes through my fingers, alights on the avocado tree, and immediately begins to sing. Female one, as usual, remains in the nest, leaves after seven more minutes. No nest building in the afternoon. During activity hours, 4 to 5 p.m., both fly to old nesting site, then indulge in pebble-flicking on the roof. 5:15 p.m., one whole hour before sunset, both fly "down."

June 8. Last observed building activity, only by female, 8 to 10 a.m. Male alternately sings on wire in front of nest and demonstrates with stalks in bill.

June 9 to 12. Both birds shy, copulation twice observed.

June 13. The only egg is laid, female on nest from 7 to 10:30 a.m., male not visible.

June 14. Female incubating 7 to 10 a.m., and from 4 p.m. to 7 a.m. of next day. Male not seen.

June 15 to 22. Incubation very lax compared with first brood. On June 18, female stays out of nest during heavy cloudburst, 2 to 2:50 p.m. Male one does not approach the nest; curtsy and defense reactions die down. Male is seen daily on his avocado tree for only a few minutes during activity hours.

June 22 and 23. Female incubating very closely, absent from nest only from 8:30 to 9 a.m., and from 4 to 4:43 p.m.

June 24. Female incubating very closely, male on wire in front of nest from 8:20 to 8:25 a.m., then disappears for whole day.

June 25 and 26. Female incubating tightly, male daily on his avocado tree for only 15 minutes to half an hour, inactive.

June 30. The young is hatched, male not visible.

July 1 and 2. Very few food trips of female, mostly brooding. Male one on the avocado tree only between 8 and 9 a.m. for very short intervals, inactive; otherwise absent from territory.

July 3. Male very shy, at 8:45 a.m. on wire in front of nest, throat-sac full of insects, hovers but does not enter.

July 4. Very few feeding trips by female. 11:25 a.m., male with full throat-sac perches on wire in front of nest, hovers about 20 times, then leaves again.

July 6 and 7. For the first time, young is not brooded over night though still very small and completely naked.

July 8 to 11. Female neglects young, makes very few, short feeding trips, brood rearing instinct dies away. Starvation of young is foreseen. Male seen in territory only for a few minutes during morning activity hours; twice he hovers with bulging food sac in front of nesting hole but does not enter.

July 12. Young dies of starvation. Stomach is empty, weight: 10.1 grams. Parents not seen again, have disappeared from Rancho Grande.

Pair two. May 2. For the first time, the juveniles are taken out of the nest, weighed, measured, etc. Immediately, female two arrives with bulging throat-sac. Male two follows without food, after one minute. Both alight 5 meters away on iron girders. While female is very excited, male begins to sing repeatedly. Ten minutes later the young are restored. In order to keep nest in level position, a small supporting stone is placed in front of it. Now, from 10:50 a.m. till nearly 1 p.m., female two makes 26 vain attempts to enter the nest, hovering before the hole and flying back to the girders. Also about 20 times she retches the food out of her throat-sac and "chews" it excitedly. Finally, at 12:42 she swallows the pulp and with empty throat leaves nesting site to collect new food. She is followed by male, who was singing the whole time. The supporting stone is removed. Female arrives with bulging throat-sac, hovers, and sees that obstacle has been removed, then clings to entrance hole in a vertical, woodpecker-like position. Then enters, feeds, looks out again, feeds, and flies away to collect new food.

May 12. Fifteenth day after hatching of first young: male feeds insects to female during "social" insect catching (evening activity hours).

May 15. Eighteenth day after hatching. To understand the incidents of this day, some of the preceding events must be taken into consideration: On April 24, a two-year-old (?), light gray, bachelor male (male 2a), very easily recognized by green feathers on left chest only, in a very peculiar pattern, arrived for the first time during morning activity hours at Rancho Grande. He was driven away by adult male two. On May 5, the same young male came again at 7:30 a.m. and sat for two minutes in territory of male four. Male four was present, but being a young male himself in similar juvenal plumage, neither curtised nor showed inclination to drive male 2a away. At 7:30 a.m., male 2a flew into territory of old male two, obviously only for the purpose of foraging, which none of the resident males ever did at that hour. Males one and two then appeared on the scene, vigorously curtsying and fencing with male 2a. Female one also appeared, with throat-sac bulging with food. Constantly curtsying and regurgitating her food, she attacked male 2a much more vigorously than male one and male two had and after a short struggle drove male 2a Meanwhile, males one and two were so much engaged in their curtsy cereaway. mony that they did not realize that the intruding originator of their own excitement had already left the scene. They went on curtsying at least a hundred times before following the intruder from tree to tree. Then with female one, they drove him out of the breeding community. During the whole struggle, which was directed solely against him, young male 2a did not curtsy once. He was not observed again until May 15.

On May 15, young male 2a had tried to win female one, but was driven away by returning male one. This happened at 7:16 a.m. The sex-consciousness of male 2a was obviously aroused by female one, whose cycle had been interrupted by the death of her young with the result that, to all males, she seemed to be "free." At 10 a.m., male 2a descends precipitately from roof onto male two. Both struggling males fall to ground, form a heap of feathers, and after five minutes, old male two is defin-

Oct.] 1953]

Auk Vol. 70

itely beaten by young male 2a. Male two flees low over ground out of the territory and *is not seen again*. After his victory, male 2a remains in territory II, approaches female two, and is accepted without ceremony. Female two immediately follows male 2a from one girder to another. Then at noon, also without any apparent ceremony, male 2a begins feeding the young in nest two.

May 18. Twenty-first day after hatching, the juveniles of nest two have left the nest and are nearly ready to fledge. Female two and "foster father" male 2a are very lazy in feeding. From 7 to 9 a.m. instead of feeding the young, male 2a, sings a great deal around the nesting site and demonstrates from the roof with stalk in At 10 a.m., male 2a feeds the young again, while female two sits passively bill. nearby. Then male 2a "searches," female two joins in, and both fly hovering from hole to hole, also doing same performance before their own nest, as though no young were inside. During this searching action, female enters territory I. Immediately male one charges her and drives her back into territory II. Oscillation between brood-rearing instinct and nest-building instinct, the latter prevalent, is now obvious in "newly married" female two. Same behavior continues for the rest of the day. At 5:40 p.m., male 2a enters territory of male three, obviously for the purpose of enlarging his own small "inherited" territory, and immediately meets male three. Male 2a is driven out of territory III, begins singing in front of the old nesting site, and feeds female two with insects.

May 19. Twenty-second day, 8:30 a.m.: male 2a again tries to enter territory III and is immediately attacked by male three. After a short period of curtsying, both males take to wing and try to soar over each other's head. In mid-air they seize each other and fall down like a feather ball into a mud hole. A deadly fight goes on Both birds are completely wet, seemingly unable to fly, but they for 4 to 5 minutes. are clasped so tightly together that it is hard to follow the details. Finally, male 2a succeeds in seizing male three by the throat, pressing him down into the water. When male three seems half dead, he frees himself with a jerk and without hesitation attacks anew, clawing male 2a and pounding his opponent's head with his beak. This decides the struggle. Male 2a flees, hopping back into his territory. With effort, he reaches an iron girder where he sits for an hour drying and preening his feathers. Male three does the same on his grapefruit tree. At 10 a.m., when both seem to have sufficiently recovered, the fight continues with the same violence. Again both birds fall to the ground and again they try to strangle each other. This time male three is the agressor. After the fight, male three flees and remains unseen during the rest of the day. Male 2a remains in the territory. During the fight, no female was present. In the afternoon hours, victorious male 2a sings but also continues feeding his "step-children." At 5 p.m., both female two and male 2a independently again begin searching for new nesting sites. The female does so in spite of having her throat-sac bulging with fruit pulp for the young. Male 2a (who has no black mask) demonstrates in entrance of different holes, with stalks in his bill, but female pays no attention at all. She continues her own independent searching and finally shows great interest in a hole in which swallows (Pygochelidon cyano*leuca*) are nesting, about three meters from her old nest. At 5:28 p.m., she enters the swallows' nesting hole for first time. Male 2a follows at 5:35, both come out at Nest is immediately examined and one young naked swallow (2.2 grams) is 5:39. found dead, still warm, with blood on his head and throat, half way between entrance and nest. As female two still has her mouth full of fruit pulp, the "murder" was probably done by male 2a. At 5:47 p.m., the swallows' nest is again visited by female two and male 2a; both sit in entrance hole. The adult swallows enter shortly afterwards and cover their remaining two young for the night.

May 20. Twenty-third day, a pair of thrushes (*Platycichla flavipes*) are beginning to build their nest in a recess in the wall, in territory II. They are neither attacked nor otherwise molested by the tersinas. With the exception of midday hours, searching goes on under the leadership of female two during the whole day. The young are rather neglected. Continuous demonstrations by male 2a are not watched by female, though they are visible to each other. Female two definitely decides on the occupied swallow nesting hole. During the afternoon, male 2a sings on the wall and iron girders near the nesting site, and he feeds female two with insects.

May 21. Twenty-fourth day, young fly out at 7:15 a.m. to the Casuarina tree. Female two feeds; male 2a defends them with curtsy movements (first time seen) against other males and other species of birds. Between 7:15 and 9 a.m., male 2a returns twice to old nesting site. At 10 a.m., he comes again with female two and a second female, which I had not seen before. While the male is again demonstrating in old nest hole, the two females curtsy energetically against each other. Meanwhile, male 2a enters again and brings out the whole old nest. With great difficulty, he flies with it in the air and after two or three meters drops it to the ground. He then descends on the fallen nest, tears some material from the inner layer and demonstrates it to his female two, who meanwhile has driven the strange female away. Instead of responding, female two enters the still-occupied swallow nest. At 10:45, both birds fly to the young in the Casuarina tree. During the rest of the day, male 2a comes six times, female only once into the territory.

May 22. Female two is not seen, the young have also disappeared from Rancho Grande, and male 2a is only seen between 8 and 9 a.m., still searching for new holes in territory II.

May 23. 8:25 a.m., male 2a again tears roots out of old nest (which was still lying on the ground), enters with them into the old nesting hole, and demonstrates in vain. Then he drops roots and flies into two other holes. Female also appears for a short time and sits passively on girders, then is not seen during the rest of the day.

May 25 and 26. Male 2a is still demonstrating during activity hours; female is absent.

May 27. 4:30 to 4:50 p.m., male 2a demonstrates, then carries long fibers of inner bark and grass into the old nesting hole and leaves them there in disorder. Later, he feeds female and sings. Female sits passively on girders.

May 28. Again no bird seen in the morning. Female two seems to have left her young. At 3 p.m., both arrive and female immediately occupies the swallow nesting hole and begins nest building (afternoon). After third construction trip with much material, she remains for 20 minutes in swallow hole. After anxious twittering, adult swallows feed their remaining two young while female two is still in the hole. A check with flashlight shows that female two had scrambled over the swallow nest. She sits close to back wall, where she has begun a new nest. She leaves at 4 p.m. Now male also enters the swallow hole. Both remain in territory till 5:35 p.m.

May 29. 8:45 to 10 a.m., female two makes two construction trips, while male 2a is demonstrating in occupied swallow nest hole, stimulating the female to build her own nest behind the swallow nest. No building activity in the afternoon. After darkness the nesting hole is checked and the two remaining young swallows are found dead between their nest and the hole entrance. Whether male 2a or female two had dragged them out of the nest and killed them cannot be ascertained. The new tersina nest is well under construction in the back of the hole. The swallow nest is now removed for better observation of the building progress on the tersina nest.

May 30. Male 2a and female two arrive at 7:05 a.m. Female observes the change and does not enter. The male, instead, enters freely and after continuous demonstra-

Oct. 1953] tion female also enters, but very reluctantly. Construction work, however, is not continued.

May 31. No construction work; instead both birds search again between 9 and 10 a.m. Neither is seen during the rest of the day.

June 1. Rain and storm: no birds seen in territory.

June 2. 6:25 a.m., both birds arrive, male feeds female. 8 to 9:30 a.m., searching activity, male 2a again concentrates on "his" old nesting hole and female seems to accept it as she enters three times.

June 3. 8 to 10 a.m., male 2a is demonstrating and female is building in old nesting hole.

June 4. 8:20 to 11 a.m., female building in her old nesting hole.

June 5. 8:15 to 10:20, birds very secretive and shy in their nest building, male 2a carrying only "show" material, singing in between trips. After nightfall, the nest, which seems nearly ready, is pulled closer for better observation.

June 6. No nest building, birds very secretive and shy, male tries to copulate.

June 7. 7:50 a.m., male 2a sings on girder in front of nest; female is squatting down inside entrance to hole. At 8:34, female leaves and immediately I see a white egg, which she laid on the bare stones, obviously not having dared to enter the nest I had moved from its original position on evening of June 5. Male enters at 8:36, takes egg in bill and tries to roll it further inside. The egg slips and male flies away; female follows. Immediate inspection shows that egg shell is cracked. Nevertheless, the egg is put into the nest. 5:20 p.m., both birds again back in territory, male sings and feeds female with insects.

June 8 to 12. During morning activity hours, male 2a still sings and searches. Female is sometimes present, but the nest is deserted and breeding "mood" of female is obviously exhausted.

June 13 to 16. Male 2a still holds territory during activity hours. No singing. Female not seen after June 12.

June 17. 7:40 a.m., male 2a seen in company of a *new*, very light green female easily recognized as not previously belonging to the Rancho Grande colony. Male searches and demonstrates, obviously tries to show "his" territory to the female, is very active, sings. But new female shows no interest and passes over into territory I. Male 2a follows and tries to feed her, whereupon female defends herself by curtsying. She apparently is not in breeding inclination.

June 18. 8:30 to 9 a.m., male 2a and new light green female again in territory, male searching, female always passive.

June 19. Rain and storm: no birds seen.

June 20. 9:15 a.m., male 2a alone, last time seen in territory.

Pair Number Three. (As mentioned before, this pair keeps closer together than any other and is more strictly limited to its territory.)

May 20. Eighteenth day after hatching of first young. Maximum feeding activity: 9 trips between 11 a.m. and 12 noon. (5 by female, 4 by male) followed by a three-hour cloudburst with no feeding trips.

May 26. All three young fly out, sit in Casuarina tree 40 meters from nesting site, but still in territory. Female three feeds, male actively defends the young. Fierce battle occurs in the air between male three and male one; the latter is driven away. Then male three attacks a *Thraupis episcopus*, chases this bird in three large circles around the territory and drives it away.

May 27. Female three and all three young have left Rancho Grande. 8 a.m., male three brings a cherry-sized fruit to his grapefruit tree and chews it for 15

minutes. Then, for first time, engages in curtsy duel with male one. At 8:45, he flies to old nesting site, alights, and sings.

May 28. Female still absent. Male three still defends his territory and every one or two hours alights for several minutes close to the old nesting hole and sings.

May 29. 4 to 5:30 p.m., both male three and his female in territory, quietly sitting side by side in their grapefruit tree.

May 30. 3 to 5:30 p.m., both male three and his female in territory; male searches with stalks in bill in grapefruit tree where female sits passively. Then, with show material flies to old nesting site, demonstrates in entrance to old nest hole, but elicits no response from female. Then male flies to neighboring hole occupied by a pair of swallows (*Pygochelidon cyanoleuca*) with three young, enters and demonstrates again while adult swallows shriek and circle around. Then three strange males arrive, and male three engages in a long curtsy battle, defending his territory.

June 1 to 10. Both birds usually absent during morning activity hours, but always present on fine afternoons from 4 to 5:30 p.m. Female three is already totally inactive, while male still searches and demonstrates without success. On rainy afternoons, only male is present, sometimes close to the old nesting hole.

June 12. Exceptionally fine sunny morning. 8 to 9 a.m., both male three and female three are in their grapefruit tree. Then male hangs head down on dead Mosonia tree, seizes a long piece of bark, lets himself fall, swings into air like a pendulum for one or two seconds and using own weight tears off a strip of bark 15 cm. long, flies with it to the old nesting hole and demonstrates first there and then in the entrance of occupied swallow nest. That evening I found one dead young swallow in hole, half way between nest and entrance.

June 12 to 18. While female remains inactive and at most appears only during sunny hours (activity hours), male three is still searching and demonstrating during fine weather. Territory is still occupied and weakly defended.

June 19. New awakening of propagation instincts, activated by arrival of new unknown pair (a young one-year-old male very active in curtsying, and a completely inactive gray-throated female). This new pair tries to install itself in territory III, on the outer sunny front of the building. The young new male is continuously searching and also singing. Male three, now very active again, attacks newcomer, drives it out of territory many times, and afterwards regularly searches, sings, and demonstrates before old nesting site. Even female three has become slightly active, and for the first time since the young have left the nest, she is seen again on girders, one meter from the entrance of the old nest.

June 20. Duelling between newcomer and male three, but with less vehemence. The newcomer yields and leaves Rancho Grande.

June 21 to July 9. Male three and female three visit their territory only every second or third day for a few minutes when weather is fine, during activity hours. No searching, no demonstrating.

July 10. Both male three and female three seen for the last time in territory. They are still "married."

Tersina viridis as Pets.—I have never had more enjoyable pets among passerine birds than my two tame male tersinas. Both were taken out of their nest shortly before fledging and soon became very tame.

Observations can be summarized as follows:

Oct.] 1953] 1. They do not recognize natural enemies (cats, birds of prey, etc.) but learn quickly to fear them.

2. They are instinctively afraid of rapidly falling objects.

3. They show no preference for certain colors if fruit, beads, berries, etc., of different colors are offered them for food or play.

4. They are extremely sociable between themselves, and they also actively seek the company of their masters. They follow us hopping or flying and alighting on our heads or shoulders, even when they are not hungry.

5. For passerines, they are very intelligent; they recognize their master and greet him by stretching their wings and legs. They always like to "play," parrot-like using their bills.

6. They have a preference for dark places outside their activity hours, which correspond to those in nature.

7. They fight each other with open bills, uttering nasal hissing noises and employing the same method against their master.

8. They go to sleep early and are very late risers, as in nature.

9. The first awkward curtsy movement was observed at the age of 230 days.

Summary

1. In Venezuela, tersinas are migratory, wintering in the humid lowlands and breeding in forested areas at elevations of from 500 to at least 1100 meters.

2. Fighting and a display, the "curtsy," are employed in territorial activities. Song appears to play but a small part in their social life. Away from the breeding territories, tersinas are gregarious. Their food consists of fruit and insects taken on the wing.

3. Nests are built in holes in building, bridges, etc.; or the birds may excavate holes in vertical banks. Three eggs constitute the usual clutch. The incubation period varies from 13 to 17 days (mean, 15 days) and begins with the laying of the first egg.

4. The nestling period lasts for 24 days. The young are fed fruit and insects by both parents, but only the female incubates the eggs and broods the young.

Instituto Botánico, Ministerio de Agricultura y Cría, Dirección Foréstal, Caracas, Venezuela, February 11, 1953.