NOTES AND COMMENT

OUTLINE FOR AN ECOLOGICAL LIFE HISTORY OF A BIRD, BASED UPON THE SONG TANAGER *RAMPHOCELUS PASSERINII COSTARICENSIS*

Introduction

Throughout the Caribbean lowlands of Central America, from western Panama into southern Mexico, one of the first birds to draw the attention of the traveller is a tanager of medium size, attired in velvety black plumage with an intensely scarlet rump. This is the male Scarlet-rumped Black Tanager. *Ramphocelus p. passerinii.* The female is a bird of very different appearance, clad in nondescript shades of brown, gray and yellowish-olive. This tanager is confined to clearings in regions where the natural vegetation is rain-forest; it often nests in dooryard shrubbery as well as in the tangled vegetation of neglected pastures and in abandoned fields once cultivated. In the Pacific lowlands of Central America typical rain-forest is the dominant vegetation only in southern Costa Rica and adjacent parts of the Republic of Panama. Here, separated by the high Cordillera from the Caribbean slope, occurs a very distinct race of the same species, *R. passerinii costaricensis.* The males, strangely enough, are not separable by appearance from those of the nominate race; but the females are distinguishable at a glance by their brighter plumage, with the chest and rump ochraceous or even orange, instead of pale yellowish as in the eastern form. In suitable habitats this western variety is no less common than its relative across the Cordillera; it is the most abundant of the birds which nest in my yard in the Térraba Valley of Costa Rica. Here it is resident throughout the year, and comes regularly to eat bananas at my feeding-shelf. The males have a pleasant although not brilliant song; in my experience they sing far more persistently than the birds of the nominate race. Indeed, they produce more music than any other passerine bird in the neighborhood, with the possible exception of Gray's Thrush, *Turdus grayi.* This is the more surprising when one recalls that the multitudinous species of tanagers in tropical America are more renowned for their amazingly varied plumage than for their musical ability, and that this is a non-territorial species. Hence I call it familiarly the "Song Tanager," although technically perhaps the designation of the western race should be "Pacific Scarlet-rumped Black Tanager."

The Pacific slope of southern Costa Rica is a region of heavy rainfall. From April or May until December showers, often torrential, fall almost every afternoon or evening. The single annual dry season is shorter and less pronounced than farther north, extending usually from early or mid-January to early or late March, and varying a good deal in length and severity from year to year. The Song Tanagers begin to nest with the return of the rains in March, starting early when these come early, late when the dry season is prolonged. Although with migratory birds in the North the males as a rule begin to sing before the females arrive and long before they start to nest, with the Song Tanagers males become songful at about the same time that females begin to build. The loose flocks, in which males outnumber females, persist throughout the nesting season; territories are not chosen and defended; fighting has never been observed. The birds are not colonial, however; nests are well scattered through suitable habitats; yet occasionally two or even three occupied nests will be found within a few yards; and once two active nests were separated by only four inches. The female builds without help, although often a male accompanies her and sings while she works.

The two eggs, pale blue blotched and spotted with black and shades of brown, are laid early on consecutive mornings; very rarely (in possibly one or two nests per hundred) there are true sets of three eggs; and with equal rarity two females lay in the same nest. The female alone incubates, hatching the eggs in 12 days and a few hours, rarely as long as 13 days. The male usually begins to help his mate feed the nestlings a few hours after they hatch, but is scarcely ever quite as assiduous in this occupation as the female. At some nests a male was never seen in attendance, a circumstance which suggests that polygamy sometimes occurs, as indeed is to be expected from the preponderance of females. The nestlings, unless frightened, remain in the nest between 12 and 13 days or sometimes longer, then depart spontaneously with no parental persuasion. Already well clothed with plumage, they go into hiding in low dense vegetation until their tails are grown and they fly well. They are fed for some weeks after leaving the nest, chiefly by their mother. Young males begin to acquire the brilliant adult dress soon after attaining full size, and when a few months old quite resemble the mature birds. Two broods may be reared in a season. By the end of June most birds have finished breeding for the year; but a few belated nests are found in August, exceptionally in September.

The following outline, although based upon the writer's experience with the Song Tanager,

has been extended so that it might serve as a guide for the study of other land birds, chiefly by the inclusion of sections on migration and territory, neither of which applies strictly to this species. Although it suggests observations more varied and more prolonged in years than most workers will be able to undertake, what one can accomplish with any species of bird varies enormously with its habits—whether it is shy or confiding, whether nests are easy or hard to discover and reach, whether it is readily trapped and banded—no less than with the time and energy of the investigator. Most of the questions here suggested were actually studied in detail for a single species by Mrs. Margaret M. Nice; the results are presented in her monumental "Studies in the Life history of the Song Sparrow."

Outline of Study

I. *Range and climatic requirements*
- A. General geographical distribution
  - 1. Physiographic barriers to dispersal
- B. Altitudinal limits
  - 1. Do these vary in different portions of the range, as between north and south?
- C. Migration
  - 1. Does the bird inhabit the same portions of its range at all seasons?
- D. Climate
  - 1. Mean annual temperature in the warmest part of the range and in the coldest
  - 2. Mean annual rainfall in the wettest part of the range and in the driest
  - 3. Annual march of temperature in a typical part of the range, or in the locality where the bird was most studied
  - 4. Annual march of rainfall and humidity as in (3)
  - 5. What climatic features appear to limit the bird's range in area and altitude? (If the species is migratory, breeding and wintering areas should be considered separately. See also VIII E 3.)
- E. Relation to cognate forms
  - 1. What relation does this bird's range bear to that of congeneric or conspecific forms that might compete with it?
  - 2. That might interbreed with it and cause it to lose distinctness?

II. *Habitat*
- A. Vegetational types which the bird frequents
  - 1. List the dominant species of plants
  - 2. Does the bird use different types of vegetation for feeding, for nesting, for roosting, for refuge?
  - 3. Is the bird restricted to particular levels within the vegetational association(s) it frequents?
  - 4. What causes the bird to avoid certain types or levels of vegetation within its range? (In tropical regions the restriction of birds to vegetational formations is often striking. A bird of the clearings may never be seen a hundred yards within the neighboring forest, and some of the forest-dwellers seem never to venture into the clearings. Very little is known of the physiology or psychology underlying this restriction. A study of microclimates might be illuminating.)
- B. Associated species of birds
  - 1. List the principal avian associates
  - 2. What are the bird's relations with the non-predatory species with which it normally associates?
  - 3. How does it react to a harmless strange bird, e.g. a straggler from a neighboring plant formation which it avoids?

III. *Food*
- A. Principal food plants and their seasons of bearing
- B. Principal insects and other animals eaten and their seasonal occurrence
- C. Special food requirements (if any) of the young
- D. Relation of the season of reproduction to the annual fluctuations in the kind and abundance of available food (see also VIII D 3)
- E. Methods of capturing or gathering animal and vegetable foods

IV. *Structure and plumage*
- A. Consider bill, feet and other structures in relation to the bird's food and manner of foraging
- B. Consider the length of the bird's wings in relation to its migratory or sedentary habit
- C. Other structural modifications of ecological significance
- D. Coloration
  - 1. Does the bird's plumage blend with the background?
  - 2. How is the diverse coloration of the sexes related to their participation in the activities of the nest?

V. *Social habits*
- A. During the non-breeding season
  - 1. Does the bird live solitary, in pairs or in flocks?
    - a. If in flocks, of what range in size?
    - b. Is there segregation of sexes and ages?
    - c. Is there a "leader"?
    - d. Do some members of the group "dominate" others?
  - 2. If the bird forages in mixed flocks, what are its associates and how do they interact?
  - 3. Does the bird roost alone or in company?
  - 4. What means does the bird employ to maintain contact with its mate or companions?
- B. During the nesting-season

1. Is the bird solitary or gregarious during the breeding-season?
2. If it claims a territory, what are its relations with its neighbors (see also IX A 2)?
3. If sexually immature grown birds, or mature but mateless birds, are present during the nesting-season, what are their relations with the breeding birds?

C. On migration
1. Does the bird migrate singly, in flocks of its own kind, or in mixed flocks?
2. Is there segregation of sexes or ages on migrations? Do males precede females? Do young precede old?

VI. *Enemies and hazards*
A. List the known avian, mammalian and other animal predators of the adults. If possible, indicate frequency of predation by each
B. The bird's reactions to the approach of potential enemies
1. Notes used to warn of approach of (a) aërial, (b) terrestrial enemies
2. Mode of taking refuge from (a) aërial, (b) terrestrial enemies
C. Effects of adverse weather—storms, hurricanes, protracted rains, drought, etc.
D. Effects of human activities—hunting and malicious persecution, agricultural operations, forest or brush fires, buildings, traffic, etc.
1. Are human activities on the whole beneficial or deleterious to the species?
E. Is the bird subject to diseases?
F. What external and internal parasites are known?
G. Predation on nests (see IX H I)

VII. *Diurnal rhythm*
A. Time of beginning day's activities
1. Relation of time of arising to light intensity
2. Variations with weather
3. Do males or females become active first?
B. Are special periods of the day devoted to foraging and resting? To singing? To nest-building?
C. Does the bird divide its day between various parts of its habitat in a more or less methodical fashion?
D. Manner of taking shelter from rain and storms. Does a light rain inhibit feeding? A torrential rain?
E. Time of retiring to roost, as related to light-intensity, weather and sex

VIII. *Annual cycle*
A. Plumage
1. How many molts are there in a year? At what seasons? Are they partial or complete?
2. Are there seasonal changes in coloration of males? Of females? Are these effected through molting, plumage-wear, or by other means?
3. How are the molts related to the annual march of temperature and rainfall?
4. If changes in coloration occur, how are they related to changes in the vegetation?
B. Weight (If birds are trapped and banded it will be well worth while to weight them.)
1. Are there daily rhythms in the weights of the birds? (It will be necessary to know this before fluctuations over longer periods can be studied.)
2. Are there annual fluctuations in the weights of adult males? Of adult females?
3. Can these fluctuations be correlated with:
a. Migratory or non-migratory habit?
b. With annual curve of temperature or precipitation?
c. With variations in available food?
d. With reproductive activities?
C. Song
1. Do both sexes sing?
2. Is singing seasonal or does it occur throughout the year?
3. What are the factors which influence the inception and decline of song, or its fluctuations in volume, if these occur?
D. Nesting
1. In what months does the bird nest? (When sufficient information is available, it should be presented in a graph or table, showing the distribution of nests by months. Each nest should be entered under the month when the eggs were laid, as observed or calculated from subsequent study.)
2. Can the nesting-season be correlated with the annual curve of temperature, of rainfall, or other meteorological conditions? How is it related to variations in the quantity or quality of available food?
3. How does the date of the inception of nesting (or of maximum nesting) vary from year to year with variations in weather, or in abundance of food?
E. Migration
1. Trace the chief migratory movements, with dates of arrival and departure at various points
2. Where possible, distinguish times of arrival of males and females, old and young
3. Attempt to correlate these movements with external conditions as in VIII D 2 and 3

IX. *Reproductive activities*
A. Territory (Does the bird select for purposes of nesting an area from which it attempts to exclude others of its kind?)
1. Character of the territory
a. Is the defended area merely a nest-site, or does it include sources of food?

b. What must the territory contain in the way of trees or other sites for singing and for nests? Of vegetation for refuge? Of sources of food? Of water?
c. Range in size of territories
2. Selection and defense of the territory
a. Is the territory chosen by the male or both sexes together?
b. How do the birds announce the possession of territory?
c. How do they react toward invaders of their own species? Is there any distinction in the treatment of male and female trespassers? Do the owners of both sexes defend the territory against invaders of both sexes?
d. How do the birds behave when birds of other species, or animals of other kinds, enter their territory?
3. Period of tenure
a. How long before the inception of nest-building is the territory claimed?
b. Is the defense of the territory relaxed after incubation has begun? After the young hatch? After they leave the nest?
B. Relations between the sexes
1. Is the bird monogamous, polygamous, or otherwise?
2. How long does the bond between mates endure?
C. Nest-site
1. Which sex selects the nest-site?
2. Character of the nest-site
a. Kinds of trees, bushes, etc., that may be chosen
b. Height above ground (Give extremes and average. Heights under one yard should be measured to the nearest inch; from one to two yards to the nearest half-foot; when above reach height may be estimated in feet.)
c. Concealment—is nest exposed or well hidden?
d. Protection. Are thorny trees favored? Is nest placed near a wasps' hive? Can other concealing or protective devices be detected?
3. Relation of nest-site to male's singing posts
D. Nest-building
1. Activities of the sexes during nest-construction
2. Kinds of materials selected
a. How are they gathered?
b. Are they brought from near or far?
3. Time of day when building is most active
a. Number of trips per hour during sample periods
4. Number of days required to complete nest
5. Structure of nest
a. Form (cup-like, oven-shaped, pensile, etc.)
b. Dimensions, internal and external (Measurements should refer to compact body of nest, not to loosely projesting ends of straws.)
c. Weight
d. Materials of foundation, walls, lining, etc.
e. Special features for concealing contents, sheltering them from rain, or the like, if they occur
E. The eggs
1. Time of laying
a. Interval between completion of nest and laying first egg
b. Hour of day when egg is deposited
c. Interval between eggs
2. Description of eggs
a. Shape, color and texture of shell (Describe common types and extreme variations.)
b. Is the color cryptic?
c. Size (Measurements may be made with calipers at nest, to nearest half-millimeter. In presenting data, state number of eggs measured, average to 0.1 mm., and dimensions of longest, shortest, widest and narrowest eggs. Fifty eggs of each species should be measured if possible.)
d. Weight of eggs in relation to weight of bird (Its fluctuation with differences in age or weight of the layer might be studied.)
3. Size of sets
a. General (Too often only averages are stated. It is important to know the actual number of sets of each size, e.g. 5 sets of 1, 90 sets of 2, 4 sets of 3, etc. This may be abbreviated $5 \times c/1$, $90 \times c/2$, $4 \times c/3$.)
b. Analysis (The size of sets may vary with the month of laying, peculiarities of weather, first or subsequent broods, young or old layers, etc. This information is of great ecological importance.)
c. Geographical variation (If nests were found in localities differing much in latitude, altitude, rainfall, etc., the data for each locality should be given separately.)
4. Replacement of lost nests
a. How soon after eggs or nestlings were lost does the female lay again?
b. How does the replacement set compare in size with the original set?
5. Number of broods (Distinguish between replacement nests and true second broods following fledging of earlier brood.)

a. Interval between departure of young from nest and laying of next set
b. Is the same nest used for more than one brood?
c. Relation of number of broods to seasonal variations in weather
d. Relation of number of broods to latitude, altitude and other regional variations

F. Incubation
1. Role of the sexes
2. When does incubation begin (with laying of first, second, last egg, etc.)?
3. Rhythm
a. Sessions on eggs (Give extremes and average in minutes, or frequency curve.)
b. Recesses (the same)
c. Per cent of day eggs are covered (May be calculated by the formula $T = \frac{s}{s+r} \times 100$, where T = per cent of time on eggs, s = average length of observed sessions, r = average length of observed recesses.)
4. Period of incubation (If eggs are marked in order of laying, the incubation period is the interval between the laying of the last egg and the hatching of this egg. Otherwise it is the interval between the laying of the last egg and the hatching of the last egg. The period may be stated in this form: 12 days 20 hours ± 10 hours. We need to know many more incubation periods in hours.)
5. How long will the bird continue to incubate eggs that fail to hatch?

G. The nestlings
1. Feeding
a. Which parent(s) feed(s)?
b. How soon after hatching does the mother begin to feed? The father?
c. Kinds of food and how obtained
d. Mode of delivery, whether brought in bill, throat or crop
e. Rate of food-bringing for nestlings of various ages, with various numbers in nest, with changes in weather, etc.
f. Do the parents receive assistance from other birds?
2. Brooding
a. Which parent(s) brood(s)?
b. Variation of amount with age of nestlings
c. Variation with weather
3. Sanitation of the nest
a. Are the empty shells swallowed or carried away by the parents?
b. Manner of disposal of droppings
c. Removal of ants, lice, or other insect pests
4. Development of young
a. Condition at birth as to covering of down, eyes open or closed, etc. Note color of interior and corners of mouth.
b. Trace the development of the nestlings' limbs, plumage, eyesight, etc.
c. Increase in weight, as determined by daily weighings
d. Development of reactions and activities: gaping, exercising, preening, fear reactions, etc.
e. Departure from nest, whether spontaneous or induced by parents. Time of day?
5. Nestling period (Care should be taken not to cause premature departure by handling or frightening the young. The nestling period may be stated in the same manner as the incubation period, e.g. 13 days 12 hours ± 14 hours.)
a. Variation of nestling period with number in nest
b. Variation of nestling period with weather or abundance of food
c. Regional variation
6. Regulation of brood-size
a. Is there any indication that the number of eggs in the set has been adjusted, through natural selection or otherwise, to the parent's ability to nourish the young?
b. How might the brood-size be affected by the hours of daylight available to the parents for hunting food?
c. What is the relation between brood-size and the average annual mortality of the species?
7. Defense of nest and young
a. Do the parents ever attack trespassers at the nest?
b. Have the parents a diversionary display to lure trespassers from the nest?
c. Does this behavior vary with the kind of trespasser or potential enemy?
d. Does it vary with the contents of the nest, whether eggs, newly hatched nestlings or older nestlings?
8. Care of young after leaving the nest
a. Do the fledglings go into hiding or follow their parents about?
b. How long do the parents continue to feed the young?
c. At what age do they become antagonistic to the young?

H. Reproductive success
1. Causes of loss of eggs and nestlings
a. Predators of specified or undetermined kinds
b. Adverse weather
c. Desertion of nests
d. Falling of nests
e. Miscellaneous

2. Causes of failure to hatch of eggs
   a. Infertile
   b. Death of embryo
3. Causes of death of nestlings which died in nest
   a. Competition with nest-mates
   b. Insufficient food
4. Calculation of reproductive success
   a. What per cent of the nests produced at least one fledgling?
   b. What per cent of the eggs hatched?
   c. What per cent of the nestlings which hatched were fledged?
   d. What per cent of the eggs produced young that survived up to the time of fledging?
   e. What per cent of the breeding females succeeded in rearing nestlings by dint of repeated trials?
   f. Average number of young fledged per breeding pair?

X. *Development and dispersal of juveniles*
A. Feeding
1. At what age do the young begin to find food for themselves?
2. At what age do they become self-supporting?
B. Voice
1. At what age do the juveniles begin to sing?
2. Follow the development of the song
C. Plumage
1. At what age does the post-juvenal molt begin?
2. At what age does the bird acquire adult plumage?
3. Describe the sequence of plumages
D. Dispersal
1. At what age do the young leave the parental territory?
2. How far do they go before settling down?
E. Survival
What per cent of the young are lost during the post-nestling stage?
F. Reproductive maturity
1. At what age do the young birds acquire nesting territories?
2. At what age do they pair?
3. At what age do they breed?

XI. *Population and vital statistics*
A. Density of the population
1. In the non-breeding season (Give method of taking census.)
2. During breeding-season, as determined by counts of nests or singing males, and making allowance for non-breeders
B. Longevity (This can be learned only by trapping and banding.)
1. How long may the bird live under the most favorable conditions?
2. What is the life-expectancy of full-grown young birds?
3. Are full-grown young birds more likely to meet accidents than older and more experienced individuals?
4. Determine the composition of the population by age-groups
5. What are the chief causes of mortality (see VI)?
C. Sex-ratio
1. Determine if possible the ratio of the sexes at fledging
2. Determine the sex-ratio of adults.

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