

THE BREEDING ECOLOGY OF THE PAINTED REDSTART

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The Painted Redstart (*Setophaga picta*) is a conspicuous bird of those southwestern riparian habitats with dense overstories, thick undergrowth, and permanent or semi-permanent water. Although the bird is easily observed because of its persistent calling, singing, and acrobatic tactics, its general behavior and breeding biology are not well known.

Bent (1953) gives a brief account of the life history of this species, and Brandt (1951) and Marshall (1957) discuss the peculiar tail-fanning behavior that these birds so frequently exhibit. Verner and Willson (1969), in their extensive review of reproductive patterns of North American passerines, indicate no references for the Painted Redstart. The purpose of this study is to provide information on the behavior, breeding habits, and life history of this species at the northern edge of its breeding range. Further, the taxonomic status of the Painted Redstart has not been totally resolved (Parkes 1961; Phillips et al. 1964), and field studies may supply valuable information to help resolve this problem. The American Redstart (*Setophaga ruticilla*) is much better known than the Painted Redstart because of the studies by Hickey (1940) on territoriality, those of Baker (1944) and Sturm (1945) on nesting activities, and the varied works by Ficken (1961, 1962, 1963, 1965) and Ficken and Ficken (1965, 1967).

STUDY AREA AND METHODS

This study was done in Oak Creek Canyon, Coconino County, Arizona, from April through September 1969 and 1970. Although the study area was approximately 5.5 miles long (elevation 4970–5700 ft), our efforts, in 1970, were concentrated along 1.5 miles of permanent, riparian stream bottom (fig. 1). The area lies along the canyon floor (400–800 ft in width), and is bordered on the east and west by steep walls that rise approximately 2000 ft. Except for areas altered by human habitation, the vegetation is very dense and diverse (fig. 2). Arizona alder (*Alnus oblongifolia*), Arizona sycamore (*Platanus wrightii*), and Fremont cottonwood (*Populus fremontii*) are dominant along the creek. From

mid-April to mid-May a noticeable increase in canopy cover occurs as the leaves appear on these deciduous trees. Ponderosa pine (*Pinus ponderosa*), Douglas fir (*Pseudotsuga menziesii*), and several species of live and deciduous oaks (*Quercus arizonica*, *Q. turbinella*, *Q. gambelii*, *Q. emoryi*) are abundant in all areas except those directly bordering the creek. The presence of 63 species of shrubs and herbaceous plants on the study area indicate the high plant-species diversity of the understory. Ground cover is dense due to the heavy growths of canyon grape (*Vitis arizonica*), Virginia creeper (*Parthenocissus inserta*), wild rose (*Rosa arizonica*), wild blackberry (*Crataegus erythropoda*), and other plants. Near dwellings, ivy (*Hedera helix*) and myrtle (*Vinca major*) cover steep banks near the creek and most rock walls. Several resorts, public campgrounds, and private homes are located within the study area.

Highest temperatures recorded on the study area occur in June, July, and August while night-time low temperatures often reach freezing during March and April. The precipitation is seasonal. Rain and some snow fall during March, followed by a dryer period. The summer rainy season usually begins in mid-July and continues into September.

Territorial boundaries were determined by observing individual birds during the reproductive period. Territories were mapped with a compass and steel tape, scaled to map size, and areas were determined by using a polar planimeter.

For identification, individual eggs were numbered and the nestlings' toes were marked with ink. Eggs were measured with a vernier caliper, and eggs, nestlings, and nests were weighed on a triple beam balance. For determining nestling growth, the right hallux, the tenth primary, and the outside tail feather of each young were measured daily. Measurements were made at precisely the same time each day to assure a 24-hr span between measurements. To our knowledge, these intrusions did not cause desertions by the adults nor lead to excessive predation.

Some adults and young were marked with color bands. The young were banded before they left the nests and the adults were banded after capture with mist nets. No adult that was captured deserted a nest.

Data on nest attentiveness during incubation and feeding rates of the nestlings were obtained by observation at nest-sites for 8 consecutive hours per nesting phase. No blind was used. Data on nest attentiveness and feeding rates were recorded at four and seven nests, respectively. Nest material of seven nests were analyzed by separating the nest materials into categories, and the contents of each were counted and weighed.

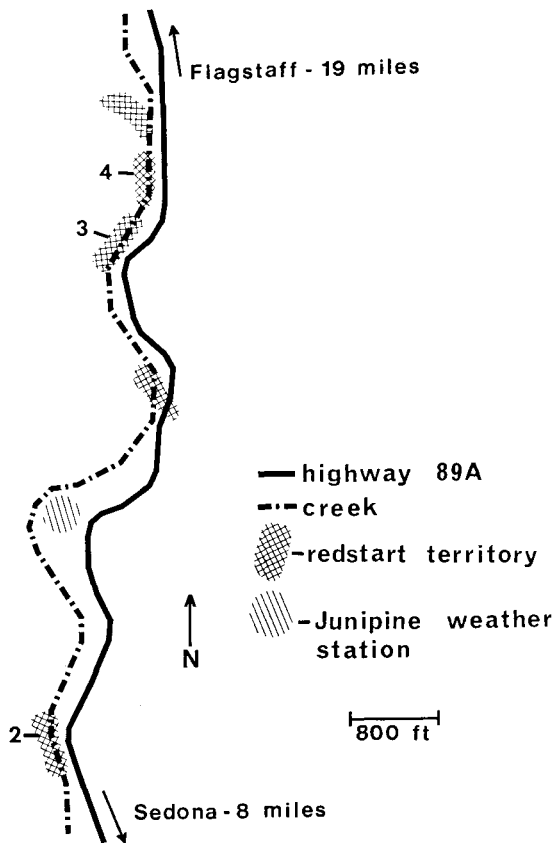


FIGURE 1. Map of a portion of the study area. Numbered territories are from 1969, unnumbered ones from 1970. Note distance between active territories in each year.

RESULTS

FEEDING BEHAVIOR

We found that the diet of the Painted Redstart consisted primarily of small to medium-sized insects obtained in a feeding range that extended vertically from ground level to the tips of the highest trees, and to every type of foliage available.

Both male and female redstarts characteristically fed in three ways: (1) individuals gleaned insects from leaves, needles, and surfaces of trunks, branches, and twigs, frequently moving parallel to branches and larger twigs, and examining the surfaces in a deliberate manner. They often hung upside down while gleaning insects from tree trunks, and moved either up or down the trunk. (2) Individuals commonly hovered in place, picking insects from tree foliage, trunks and branches, and from spider webs. (3) Individuals were observed hawking insects over open water or, at dusk in spring, at lights near dwellings. This strategy was like that of flycatchers.



FIGURE 2. Photograph of a portion of a Painted Redstart territory showing stream and adjacent dense and diverse vegetation.

Members of a foraging pair kept in contact by calling, singing, and posturing. The latter consisted of abruptly turning from side to side, exposing flashes of red, black, and white. These rapid 180° turns were performed during short, quick hops. A slight fanning of the tail may occur during these movements. These patterns are similar to the pirouette movements of the American Redstart (Ficken 1962). During the period of nestling and fledgling care, adults also performed rapid tail-fanning, independent of the pirouette movement.

VOCALIZATION

The songs and calls of the Painted Redstart are classified as follows:

Primary song. Both the males and females sing a song composed of seven syllables. Peterson (1961) appropriately described this as *weeta, weeta, weeta, wee*. Males sing this song throughout the spring and summer, whereas females sing it while dueting with or answering the males during courtship and egg-laying. While the females are building nests, the males may sing near them but the females make no response. While the females incubate, males continue to sing throughout their territories, but rarely approach the nest sites. After the young hatch, the males curtail their singing and it is heard only between trips to feed the young. The females also sing low, quiet versions of the primary song when they are away from the nests.

Location call. This is best described as *cheree*. It apparently is a signal between parents and young and between adults before and after pair formation. Unmated males

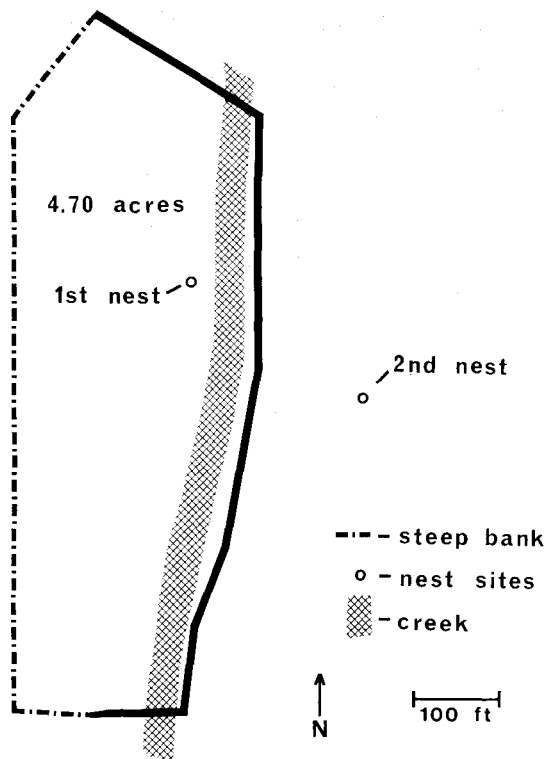


FIGURE 3. Territory of a male Painted Redstart showing the locations of the female's first and second nest.

typically give this call while foraging. The *ee* is a slightly higher note than the *cher* and, when the two are combined, the vocalization sounds much like a question. Both adults give this call while foraging. It may signal the location of the partner in an often dark or shady habitat. More often, however, it is directly associated with the nest and if heard repeatedly, it is a good indication that a nest is close by. Adults give *cheree* calls near the nests before and after feeding the young. Occasionally, the males approach the nests in complete silence. Unduly excited adults emit *cherees* in rapid succession. A 7-day-old young was heard emitting a *cheree* as loud as those of adults.

Warning call. A *zeeettt* is uttered commonly when a hawk, crow, or Steller's Jay (*Cyanocitta stelleri*) flies overhead, causing both adult birds to hide immediately until the danger passes. When adults arrive near the nest and give their *cheree* call, the young sit up, stretch their necks, and look about. If the warning call is then given, the young immediately duck down, lying flat and still in the bottom of the nest until a *cheree* is given by one of the adults.

Courtship sound. This sharp, high-pitched

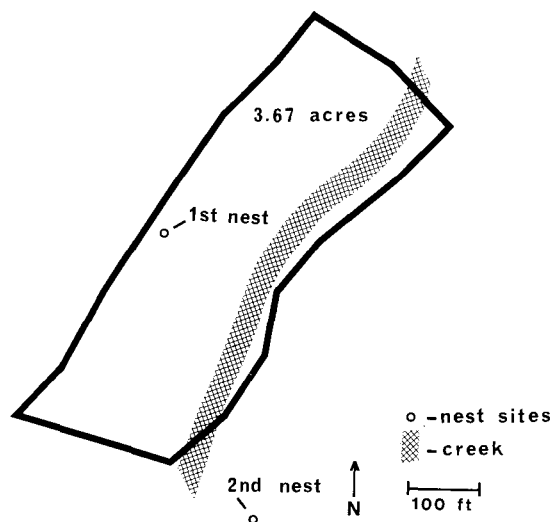


FIGURE 4. Territory of a male Painted Redstart showing the locations of the female's first and second nest.

dee-dee-dee, made during courtship flights, lasts but a few seconds. We seldom heard this sound, and could not determine which courting bird gave it.

Nestling responses. These are the first audible sounds given by the young. At 4 days of age they are soft *peeps*; they soon develop into louder *squeaks* given in response to the presence of a parent, even while the young are handled.

Begging sounds. These sounds are very squeaky and can be described as *chee-chee*. They are emitted by fledglings when the adults approach with food and are given continuously until the young are fed.

ARRIVAL IN SPRING AND ESTABLISHMENT OF TERRITORIES

Males arrived in the area from 2 to 10 days prior to the females, with the first sighting in 1969 on 5 April and in 1970 on 27 March. At this time temperatures were often below freezing at night and ample moisture in the form of rain or light snow occurred. Upon arrival, males usually gave only *cheree* calls while foraging. Within 2-5 days thereafter, we heard occasional songs which increased daily in volume and number.

The males began establishing territories 2-5 days after arrival, signified by singing all morning and into early afternoon. During this period, the males perched in trees at the boundaries of their territories and sang loudly for 15-30 min, often with only 5-sec intervals between songs. At territorial boundaries, certain song posts were used consistently

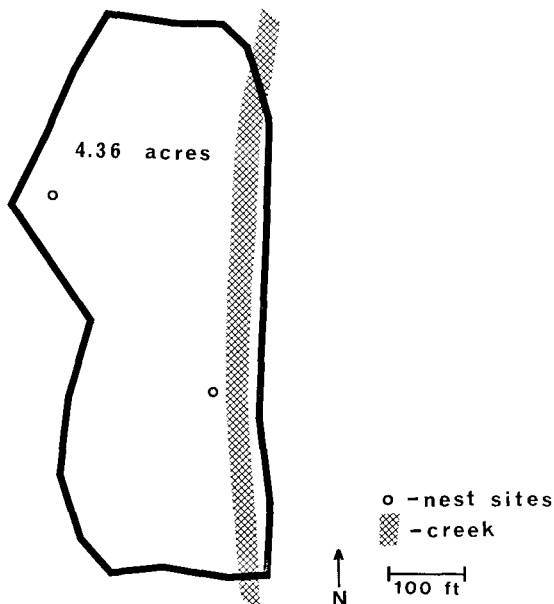


FIGURE 5. Territory of a polygynous Painted Redstart showing the location of the two nests.

throughout the spring and summer. On five occasions small birds (e.g., chickadees or nuthatches) in nearby brush caused the males to cease singing and to begin giving *cheree* calls. When no response was given by the small bird, males resumed singing.

Once, while a male was performing his territorial singing, another redstart, presumably an unpaired male, entered the same tree. Both birds sang alternate, loud songs as they flitted about in the tree, never getting closer than 1 ft from each other. This behavior continued for about 15 min, until the original male flew to the other end of his territory and the intruder flew off.

At the time the early arriving males were establishing and maintaining territories, several migrating redstarts were observed in these territories. Most resident males attracted mates quickly; within 4 days most territories contained a male and at least one female. Later in the season we discovered males with more than one female. Painted Redstarts were tolerant of other species of birds in their territories, but aggression was common when other birds approached a nest. When a House Wren (*Troglodytes aedon*) landed approximately 5 ft from a nest, the female ceased incubating and pursued the wren for about 100 yards.

Redstart territories were used for courting, nesting, and feeding, type A of Nice (1941). All territories we observed were along the stream (fig. 1), and the four that were plotted

were approximately 4 acres in size ($\bar{x} = 4.15$; range, 3.9–4.7) (figs. 3, 4, 5).

Both sexes recognized territorial boundaries and restricted their daily movements to the territory. In double-brooded pairs, the females left the territories (or perhaps extended them) to build their second nests about 4 or 5 days after the first broods left the nests. The new nests were placed from 100 to 300 ft beyond the original territorial boundaries (figs. 3, 4). The first broods left the territories about 28 days after they fledged. It is not known if they were actively driven out or simply departed.

After the first broods left the territories and the second broods hatched, the males shifted their territorial boundaries to include the extended areas chosen by the females. The fledged second broods formed small family groups. These groups stayed within the territories for several weeks. Vocal advertisement of the territories by the males, however, continued throughout the season.

PAIR FORMATION AND COURTSHIP

Female redstarts appeared to be attracted initially to territories by singing males. After approaching the males, an antiphonal duet began which lasted throughout the morning and into early afternoon, with 1–3 sec intervals between the male's and female's songs. Female song is unusual in parulids and may be a vehicle for keeping males and females in contact on large territories. The birds remained closely associated, flying together and foraging in the same or nearby trees. On occasion, a male dove at a perched female which then flew up to avoid contact. The male pursued the female through the trees as the female turned and swerved to evade him. During these short, fast, erratic courtship flights, the *dee-dee-dee* sounds were heard. After about one day, a pair bond was formed. During the following days, the male and female stayed within 150 ft of each other while foraging. The *cheree* call was frequently given by both birds during this time.

NEST SITE SELECTION AND NEST CONSTRUCTION

The male and female appeared to select nest sites together. They hovered around possible nest sites and darted in and out of depressions and sheltered areas. Upon entering such sites, both birds pivoted around and examined them closely. Often when females entered a depression or went behind overhanging vegetation, the males joined them. The pair

TABLE 1. Composition of Painted Redstart nests.

Nest no.	Hair lining ^a		Fine grass		Coarse grass ^b		Pine needles		Leaves		Other ^c wt	Nest location
	no.	wt ^d	no.	wt	no.	wt	no.	wt	no.	wt		
6	980	0.3	1082	7.2	69	3.9	9	1.0	29	0.6	1.5	rock wall
7	1420	0.7	1182	6.1	241	4.9	1	0.1	48	1.9	0.1	grass clump
8	1235	0.3	1047	6.0	112	2.6	2	0.1	49	1.2	5.4	grass clump
9	2816	2.3	1648	5.4	16	2.4	4	1.0	22	1.0	1.9	pine needles
11	1454	0.7	663	4.0	102	6.0	3	0.2	7	0.4	5.1	dirt bank
14	571	0.5	624	4.2	225	6.2	67	3.0	12	0.6	1.1	grass clump
15	509	0.9	896	2.9	67	1.3	21	1.0	95	3.1	0.3	grass clump

^a Includes deer hair, horse hair, fish line, and an occasional feather.

^b Includes bark and rootlets in addition to coarse grass.

^c Includes fecal wastes, feather shafts, dirt, and pebbles.

^d Weights given in grams.

spent up to a week searching for a nest site, with the female signaling the final decision by bringing in nest material.

Nests were located on the ground, on steep banks, or in rock walls. Generally, protective overhangs sheltered the nests. If built in a wall, the overhead shelter was a rock; if at the base of a tree, the trunk afforded the shelter; if in a bank laden with pine needles, the pine needles generally covered the nest; and if at the base of a grass clump, roots and dead grass formed the shelter. One nest had no natural overhead shelter. Here, the female constructed the back and sides of the nest much higher than usual and then formed a roof out over the bowl. All nests were shaded from direct sunlight early in the season and remained dry during summer rains. The entrance direction varied and followed no pattern. From our general impressions, there seemed to be many suitable nest sites in each territory.

Females built the entire nests. During the first few days of construction, males accompanied females to the nest sites and sang loudly from nearby perches. Near the end of nest construction, males sang in other parts of the territories, seldom visited the nest sites, and were possibly attempting to attract a second mate.

Most nest construction was accomplished in the early morning, but sometimes females worked all day. Construction time of the nests varied from 4 days to 2 weeks. No reason was discovered for this wide variation.

When beginning the nests, females first put down a base of dead, dry leaves, then formed the general shape of the nests, using coarse grass and pine needles with smaller leaves sometimes entwined with these materials. Fine grass and hairs were used for the linings. Often leaves and coarse grass were gathered very close to the nests, whereas

lining materials were gathered within the territories but from more remote areas.

Coarse and fine grass made up the majority of the nest material in all nests analyzed (table 1). The total numbers of nest materials given in table 1 do not represent the total trips to the nest, for often the females brought in more than one piece of material per trip. Nests 6 through 11 were first nests of the season, whereas nests 14 and 15 were second nests of double-brooded females. We found no statistically significant differences in the composition of nest material of the early and late nests. Later nests did show a mean increase in coarse grass, pine needles, and leaves and a mean decrease in hair lining and fine grass. There were no significant correlations between size of nest and clutch size (table 2).

EGGS AND INCUBATION

The eggs generally were laid early in the morning at one-day intervals. They were white to cream-colored with brown speckles heavily concentrated at the larger ends. Average dimensions of 32 eggs were 13.1×17.1 mm, with extremes 14.2×17.6 mm (high width), 12.3×15.7 mm (low width and length), and 13.7×18.8 mm (high length). The average clutch size for nine nests was 3.7 eggs.

Incubation generally began on the day when the last egg was laid, but it sometimes began on the day before or after the last egg was laid. Only the females incubated and possessed brood patches. Overall, females incubated 75% of the observation time (table 3). During the earlier stages of incubation, females apparently left the nest more often but for a shorter time than during the later stages. As incubation proceeded, females took fewer feeding trips but each trip was of longer duration. Females usually took slightly

TABLE 2. Dimensions of Painted Redstart nests and clutch size.

Nest no.	Diameter (cm)	Height (cm)	Cup diam. (cm)	Cup depth (cm)	Total weight (g)	No. of eggs
6	9.5	5.5	5.5	3.0	14.5	3
7	12.0	7.0	5.5	4.0	13.8	4
8	11.5	7.5	5.0	3.5	15.6	0
9	11.0	8.0	5.5	3.0	14.0	4
11	9.0	6.0	4.5	3.0	16.4	3
14	10.0	6.5	5.0	3.5	15.6	4
15	8.0	6.0	5.0	3.5	9.5	4

longer feeding trips in the afternoon than in the morning (table 3), possibly due to the warmer afternoon temperatures. Occasionally, males came to the nests during incubation and called softly; females then left with them on feeding trips. The females always returned alone.

The incubation period (Nice 1954) was found to be 13 days at five nests and 14 days at one nest. The eggs usually hatched early in the morning, but at one nest two eggs hatched in the morning and two hatched in the afternoon. Only at one nest did the eggs hatch over a 2-day period.

CARE AND FEEDING OF NESTLINGS

After the young hatched, the females either ate the egg shells or carried them away. The males came to the nests on the day of hatching and both males and females called continuously as they flitted about the nest sites.

At early nests the females brooded the young for 2 days, departing only to feed. At later nests, the females left for several hours when the young were only one day old. By this time, air temperatures had increased markedly, averaging 17°C in 1969 and 1970.

Occasionally, males brought food to the young while the females were brooding. In response, females either left the nests while the males fed the young or stood up, took food from the males, and fed it to the young.

The females brooded the nestlings at night. We observed one female brooding 6-day-old

TABLE 4. Rates of feeding nestling Painted Redstarts.

Nest no.	No. of young	Age of young (days)	No. of trips/8 hr	Trips/hour	Trips/young
13 ^a	4	2	22	2.75	5.5
6 ^b	3	4	21	2.63	7.0
13	4	4	31	3.88	7.8
9 ^b	4	4	28	3.50	7.0
13	4	7	45	5.63	11.3
9	4	7	40	5.00	10.0

^a Second nest of year for female.

^b First nest of year for female.

young during the middle of the day. At this nest we had removed the overhanging vegetation to facilitate observations. The female probably was shading her young from the direct sunlight.

Both adults removed fecal sacs. For the first 4 days, the females ate the fecal sacs and after that time, carried them off. Males often carried fecal sacs to tree branches where they were deposited. After each feeding trip, the adults wiped their bills on tree branches.

Observation revealed that the food brought to the nestlings consisted exclusively of adult and larval stages of insects. Insect larvae and transparent insects' wings could be seen protruding from the birds' bills.

Feeding of the young was generally divided evenly between the males and females. The number of feeding trips made by the adults was directly related to the number and age of the young, and the time of nesting (table 4). Nestlings 7 days old were fed more than twice as frequently as those 2 days of age (nest 13, table 4).

GROWTH AND DEVELOPMENT OF NESTLINGS

Descriptions of the nestlings at various ages follow.

0 days old. The young were feeble and helpless. Their only response appeared to be opening their mouths, the insides of which were a deep tangerine-orange color. Their legs hung limp. They were pink-skinned,

TABLE 3. Incubation and foraging times of female Painted Redstarts.

Nest no.	Day of incubation	No. of morning trips	Time off nest (min)	No. of afternoon trips	Time off nest (min)	\bar{x} time off nest/trip	
						AM	PM
13	3	5	44 (18) ^a	4	55 (22) ^b	8.8	13.8
14	6	2	44 (18)	2	50 (21)	22.0	25.0
14	11	2	70 (29)	2	75 (31)	35.0	37.5
15	12	2	76 (32)	2	80 (33)	38.0	40.0

^a Per cent of morning female was off nest.

^b Per cent of afternoon female was off nest.

TABLE 5. Average growth measurements of Painted Redstart nestlings.

Age (days)	No. of birds measured	Weight (g)	Hallux length (mm)	Outer primary length (mm)	Tail feather length (mm)
0	10	1.36	3.0		
1	10	1.9	3.3		
2	14	3.1	4.2	1.1	
3	13	4.3	5.5	3.5	
4	13	5.9	6.1	6.2	0.2
5	13	6.5	6.5	9.5	2.4
6	13	7.9	7.1	12.9	4.4
7	13	8.6	7.2	15.8	6.8
8	12	8.8	7.3	19.2	9.3
Adult average	5	9.7	7.5	52.5	56.5

¹ Numbers in parentheses are % of adult average.

with a small amount of black down on the dorsal portion of their heads and backs.

1 day old. The young lifted their heads in response to a noise or when the nest was touched. Their mouths were opened wide and held gaping upward. Feather tracts were visible as darker areas below the pink skin. Leg movements were not coordinated.

2 days old. Feather shafts of the alar tracts were emerging through the skin. When the young were handled, they moved their wings and legs slightly in attempts to balance.

3 days old. The feather shafts were emerging from all feather tracts and down was still present. The eyes were beginning to appear as small slits. Grasping was attempted when the chicks were handled.

4 days old. The eyeslits were very evident. While weighing and handling the chicks, they were heard to *peep* softly. When removed from the nests, the young grasped firmly onto the nest lining, often pulling it out with them.

5 days old. The eyes were completely open. The wings were often flapped as the young were handled. The bills and claws were darkening. The nestlings sat up and balanced themselves.

6 days old. The young were able to stand on their feet for short periods. The skin on the legs was turning darker brown and the feathers were opening from the sheaths.

7 days old. The young sat up, looked about, and appeared to be very alert. They *squeaked* loudly when answering their parents' *cherees*.

8 days old. The completely feathered young stood and balanced themselves well and called as loudly as the parents. By using their wings for balance, they could walk short distances.

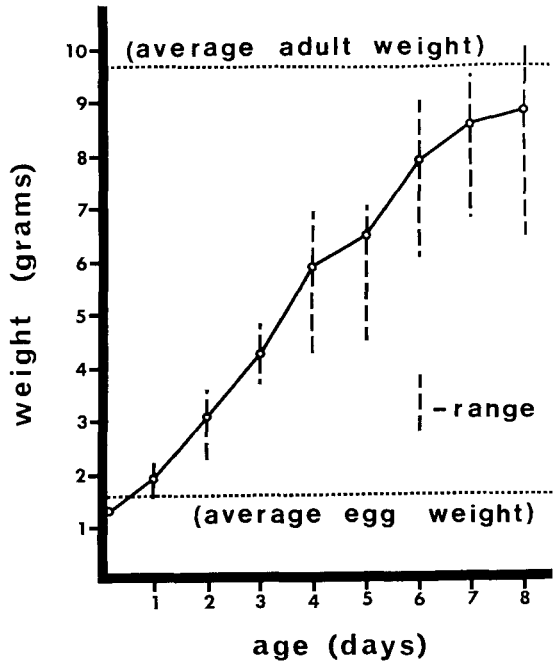


FIGURE 6. The average weight gain for nestling Painted Redstarts.

As we handled the young, they attempted to escape.

9 days old. At this age, most young left the nests. Although they flapped their wings they could not fly, and fell downward. By hopping from branch to branch, they stationed themselves off the ground in shrubs or thick vegetation. They were well concealed, especially in the shadows.

Skutch (1954) found that handling the young of the Slate-throated Redstart (*Myioborus miniatus*) caused premature departure from the nest. We believe the 9-day nestling period we observed reflected our handling of the young. At one nest, the nestlings were not disturbed after day 8, and did not leave the nest until day 13.

Table 5 shows the averages of all the growth measurements taken and the average measurements of the same parameters for adults. Since the young could not fly when they fledged prematurely, they depended greatly on their feet for locomotion and support. The most noticeable change in the young after premature fledging was the rapid increase in the length of the wing and tail feathers. Four to five days after leaving the nests, or when they would normally fledge, the young began making short flights.

Figure 6 shows the average growth curve for Painted Redstart young. Obtaining 90% of the average adult weight in 8 days meant

TABLE 6. Nesting success of the Painted Redstart.

Status	No. of nests with eggs	Eggs laid	Eggs hatched	Young fledged
First broods	9	32(3.6) ^a	29(91) ^b	22(76) ^b
Second broods	3	12(4.0) ^a	4(33) ^b	4(33) ^b
Total	12	44	33	26
Overall success (%)			75	59

^a Average clutch size.^b Per cent success.

an increase of approximately 10% of the average adult weight per day. As the young increased in age, the range of weight increased for individuals of the same age. This increase was most noticeable below the mean and is probably a result of the slower weight gain by individuals in larger broods. Figure 7 shows average growth curves for young from three early nests. Nest 4 contained two young; nest 6, three young; and nest 9, four young. When the growth curves for nestlings from nests 4 and 6 are compared, they show a fairly similar and uniform increase with age. This indicates that adequate food was available and was brought to all nestlings. Although the growth curve for nestlings from nest 9 shows an initial uniform increase, at the age of 5 days, the growth rate begins to slow down and becomes somewhat erratic. When the young departed from this nest, they were lighter than young from smaller broods. This may indicate that adequate food was not brought to these nestlings to allow for their optimum growth.

The growth rate, calculated as suggested by Banks (1959), decreased as the nestlings aged. The index of this growth rate was 0.23. The growth rate, calculated as suggested by Ricklefs (1967), was found to be 0.140 per day, with the total growth rate being 0.560. This is well within the range of growth rates for six species of parulids presented by Ricklefs (1968).

DEPARTURE FROM THE NESTS

Fledglings flapped their wings as they jumped from the nests, and they often tumbled down the banks. If we were near a nest when the young fledged, both adults came within a foot of us and feigned injured wings until the young were hidden and quiet.

The young remained hidden in areas surrounding the nest sites for 3–5 days while the adults brought them food. The adults

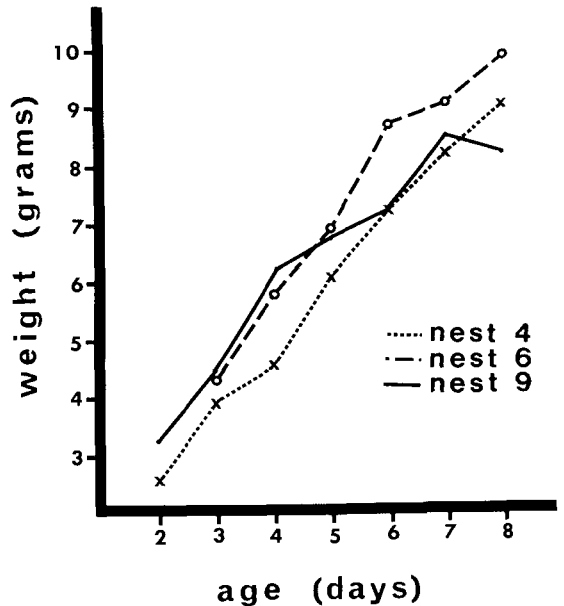


FIGURE 7. The average growth of young of three different nests. Nest 4 had two young, nest 6 had three young, and nest 9 had four young.

alternated between young, feeding one young up to three times, then feeding another. When the young began making short flights they and the adults formed family groups and traveled about within the territory. The young began feeding independently and usually left the territory when 27–30 days old.

NESTING SUCCESS

Nesting success of the Painted Redstart was high (table 6), in spite of our many visits to some nests. Overall, 75% of the eggs hatched and 59% of the eggs resulted in fledglings. Seventy-eight per cent of the young that hatched also fledged. Nesting success was notably greater from the first nests of the year.

Production was similar for both clutch sizes for early nests: nests with three-egg clutches ($n=4$) produced 2.5 young per nest and early nests with four eggs ($n=5$) produced 2.4 young per nest. Double-brooded females ($n=3$) all produced four eggs in their second clutch but only 1.3 young per nest survived.

POLYGYNOUS BEHAVIOR AND DOUBLE-BROODED PAIRS

On several occasions before nesting began, three adult redstarts were observed traveling and feeding together. None showed any aggressiveness toward any of the others. Since Painted Redstarts are not sexually dimorphic, the sexes could not be determined at this time. However, in 1970, one polygynous male (banded) was observed and, in 1969, another

(unbanded) male was suspected of polygynous behavior. The territory and location of both nests of the 1970 male are shown in figure 5. At one nest (number 6), containing three eggs, incubation began on 11 May. At a second nest, containing three eggs, incubation began about 16 May (± 2 days). The earlier clutch hatched on 24 May and both adults cared for the young for the next 7 days. When the young were 4 days old, the male and female fed them 12 and 10 times, respectively, in 480 min. Three days later, however, the male ceased caring for these young and was not seen again at the nest. The female fed the three young until they fledged at 9 days of age. Although figure 7 shows a slight decrease in rate of weight gain for the young on day 7, all were at least 1 g heavier than the average on the day they left the nest. After deserting the earlier nest, the polygynous male fed young at the later nest. It is not known if the male also contributed food during the first 2 days of nestling life, but we suspect he did as most females spent considerable time brooding at this stage.

Later, banded young from both nests were observed in a single group within the territory. The banded male was seen feeding banded young from both nests and showed no preference for young from either nest. The females also fed the young for about 7 days before leaving the group with the male. We strongly suspect one of these females built a second nest but we could not locate it as she spent most of her time off the original territory. Three other females began to build a second nest after leaving their young in the care of their mates.

Sixteen days after four young left nest 10, the banded female from that nest was found incubating a clutch of four eggs (nest 14) located about 200 ft south of the original territorial boundary. The male of this pair had sole responsibility for the first brood at this time. The eggs of the second brood were destroyed before they hatched.

Twenty-five days after four young left nest 9, their banded female parent was found incubating a clutch of four eggs in nest 15, about 200 ft west of the original territorial boundary.

Nest 13 was situated about 150 ft west of an unmapped territory where four young fledglings had earlier been observed. It contained four eggs, all of which hatched, and the young fledged.

There appeared to be two definite peaks in initiation of nesting in 1970. Incubation

began about the second week of May and again in the third week of June. From our data we project that at least 25% of the females are double-brooded. Polygyny was not as common but is probably a normal event, at least for a segment of the population.

TAIL-FANNING

The peculiar tail-fanning behavior of the Painted Redstart (cf. Brandt 1951; Marshall 1957) was performed by both males and females. It consisted of a rapid partial spreading and closing of the rectrices while the bird foraged and displayed. The tail was often, but not always, fanned in unison with wing-spreading.

Tail-fanning was not seen during territorial establishment or courtship. At this time, the deciduous canopy along the creek bed was very open and the ground brightly lit. Tail-fanning behavior was first performed during the latter stages of incubation, and when feeding of the nestlings began. By this time, the overstory canopy was complete and the forest floor only dimly lit. When young birds began foraging for themselves, they also began fanning their tails. The fledglings' dark, comparatively drab plumage provided them with excellent camouflage as they foraged in the shadows.

The tail-fanning display, however, made the birds very conspicuous. This display by the young possibly allowed other individuals to be located with ease. It may also have helped the adults to locate the young when bringing them food. The adults continued to feed the young for at least 10 days after the young began to forage. Males fanned more frequently around nest sites than did females. Both males and females continued this display until the young were independent.

Adults of double-brooded pairs continued tail-fanning while raising both broods but pairs that failed in their second attempt ceased tail-fanning after the young from the first nest left the territory.

We believe that tail-fanning by young and adults aids the birds in locating one another in the relatively dark and thickly foliated habitat typical of the riparian communities used for nesting. Dickey and van Rossem (1938) came to a similar conclusion with reference to the closely related Fan-tailed Warbler (*Euthlypis lachrymosa*).

DISCUSSION

The nesting habitat of the Painted Redstart contains a high diversity of plant species,

topographic relief, substrate type, and climatic conditions. Although Marshall (1957) described the Painted Redstart as the most characteristic bird of pine-oak woodland in his extensive study of southern Arizona and adjacent México, he noted the species' habit of foraging in "shady places," "canyon bottoms," and "wooded north slopes." Balda (1967) found a breeding density of 22 pairs per 100 acres of dense riparian habitat and only six pairs per 100 acres in pine-oak-juniper woodland in the Chiricahua Mountains of southeastern Arizona.

The dense canopy and poorly illuminated floor of the riparian woodland, during a major portion of the breeding season, may be very important in determining the type and constancy of the communication system used by this bird. The bright colors, high activity, and vociferousness of the Painted Redstart allow it to attract a mate easily and remain in constant contact with the mate and young on large territories (see below) in this dense habitat. The apparent plasticity of foraging techniques and overt methods of communication leads us to conclude that this warbler is highly specialized morphologically and behaviorally for foraging and communicating in this habitat. This habitat association may, in part, account for its somewhat spotty distribution in the Southwest.

One must, however, be cautious in describing the vocal behavior of the Painted Redstart as solely adapted to fit the habitat. The breeding strategy and success of the redstart may also be in part determined by its ability to advertise, attract, and retain a mate(s). Verner and Willson (1966, 1969) state that polygyny may possibly be identified by observations that show that males play little role in nest construction but continue to advertise for additional mates after the initial mating. The male redstarts continued to sing and did not help in construction of the nests; this agrees with the reasoning of Verner and Willson.

TERRITORY SIZE

The territory size of the Painted Redstart in northern Arizona was surprisingly large when compared to that of other warblers. Hickey (1940) and Sturm (1945) found that territories of the American Redstart are about 1 acre or less. Ficken and Ficken (1967) found that American Redstart territories range in size between 0.75 and 1 acre. They noted that "many males were isolated or had only one neighboring male in an area of several

acres." This situation was also true in our study. Stenger and Falls (1959) found the average utilized territory of the Ovenbird (*Seiurus aurocapillus*) to be 2.3 acres, the largest, 4.3 acres. Both species are reported to be polygynous (after Verner and Willson 1969). Kendeigh (1947) found that the average territory size of nine species of warblers inhabiting a coniferous forest during a spruce bud-worm outbreak was much smaller than that of the Painted Redstart. Meanley (1969) reports an average territory size of 1.6 acres for the Swainson's Warbler (*Limnothlypis swainsonii*), including one isolated territory of 4.8 acres. Balda (1967) found that the average territory size for the Painted Redstart in a riparian habitat in southeastern Arizona was 1.51 acres ($n = 13$). Thus, redstart densities were higher and territories smaller in southeastern Arizona than at the northern edge of the species range.

There are at least two possible explanations for the large size of Painted Redstart territories in northern Arizona. First, males arrive in late March to early April. Phillips et al. (1964) state that this bird is "the first warbler to appear in the higher oak regions. . . ." Hubbard (pers. comm.) observed that Painted Redstarts arrived 2-3 weeks before other summer resident warblers in the Pinos Altos mountains of New Mexico. The mean arrival date for a 3-year period was 2 April. At this time nightly low temperatures are extreme enough to put a strain on the total energy budget of the bird, and the deciduous trees are bare. Consequently, foliage-inhabiting insects may be scarce. Large territory size may reflect the higher energy demands made on the birds in early spring, since males obtain their food from the territory. One could then argue that territories should shrink in size as productivity within the territory increases. This did not occur as males advertised for additional mates from the same song posts well into July. Second, the long, narrow territories containing well-spaced song posts bestow maximum exposure on the male as he continually advertises for more mates. The holding of these song posts is obviously economical if reproductive success is enhanced by polygyny. Our scant evidence leads us to believe this is so, as each polygynous male had two successful nests. Defense of these long, narrow territories had to occur only at the narrow north and south borders because all territories were situated along the stream (see fig. 1). Thus, lesser amounts of energy need be expended in this

situation than in one where neighboring territories are placed on all sides.

Females that initiated a second nest always moved to areas adjacent to the primary territory. We believe this was done to avoid the begging young from the first brood and possibly in response to the lower abundance of food on the original territory. This may be especially true if two breeding females are present, as they must forage for themselves, and foraging time may be at a premium. Only after the young from the first nest fledged did males increase their territory to encompass the second nest.

NESTING TIME

Males arrived on the study area and began advertising for mates 9 days earlier in 1970 than in 1969; however, the first eggs were laid 10 days later in 1970 than in 1969. April temperatures consistently averaged 3–5°C lower in 1970 than in 1969. Consequently, new foliage appeared later in 1970 than in 1969, and foliage-dependent insects probably appeared later in 1970. There was no difference in clutch size between the 2 years. Lack (1966) cites evidence that the time of egg-laying is dependent on the energy requirements of the female. Egg-laying occurs only after the female has obtained ample food to form eggs. Our data fit this hypothesis. Two peaks of nesting occurred. The first peak occurred about the time the foliage was leafing out (five nests in 1970) in early May. The second peak (three nests in 1970), formed primarily by females laying their second clutch, occurred during a warm, dry period when there was a noticeable increase in insects hatching and leaving the warm-water pools. The second brood was then raised during the July rainy season when insects were obviously abundant. Three double-brooded females laid four eggs in both early and late clutches. Nesting success was markedly different for these three females, however, as 100% of the young fledged from the early nests while only 33% fledged from the later nests.

REPRODUCTIVE STRATEGY

The fact that the Painted Redstart is both double-brooded and polygynous suggests that it is maximizing its reproductive potential. It is difficult to compare these features of its reproductive strategy to that of other warblers as many are so poorly known. Double-broods have been reported (Bent 1953) for the Palm Warbler (*Dendroica palmarum*),

Yellow-throat (*Geothlypis trichas*), Hooded Warbler (*Wilsonia citrina*), Lucy's Warbler (*Vermivora luciae*), and Yellow-rumped Warbler (*Dendroica coronata*). We believe double-broods are rather common in the Painted Redstart. This suggests that the riparian habitat provides ample food over a rather long period of time. The amount of food present on the territory can be critical because after one week postnestling, the male alone fed the young, while the female performed all nesting duties at the second nest. This is similar to the situation in the Painted Bunting (*Passerina ciris*) (Parmelee 1959). By the time the young redstarts left the second nest, the young from the first nest had left the territory and were not seen in the area. The male then fed the young from the second nest.

An additional means of maximizing reproduction is the polygynous behavior of males. On all 15 territories males continued to sing vigorously after mating, but we were able to identify only one positive case (banded adults) and one highly probable case (unbanded male) of polygyny: In one instance a polygynous male was mated to a (suspected) double-brooded female. This unusual circumstance was also reported by Parmelee (1959) for the Painted Bunting. Verner and Willson (1969), in their extensive review of mating systems in North American birds, list seven species of Parulidae in which polygyny is judged by them to be abnormal and one species (Prairie Warbler, *Dendroica discolor*) in which polygyny is normal. We do not consider polygyny to be abnormal in the Painted Redstart. Verner and Willson (1966) point out that polygynous mating systems are prevalent in two-dimensional habitats where production of food is limited to a narrow horizontal band of vegetation. This is not the case for the Painted Redstart as herb, shrub, and tree layers are dense and diverse. The above authors note that, in North America, the Winter Wren (*Troglodytes troglodytes*) is possibly the only polygynous passerine to nest in dense forest. The Painted Redstart can now be added to this list. Willson (1966) and Verner (1964) have actually correlated or suggested correlations of various parameters of male's territories with the number of mates acquired. The availability of nest sites did not play a major role in the redstart's breeding pattern, as Zimmerman (1966) suggests it does for the Dickcissel (*Spiza americana*). Rather, the Painted Redstart's ability to maintain successfully large, type A terri-

teries and to feed in all strata in a variety of ways is advantageous in providing adequate food to support this type of mating system.

The reasons for the (unusually ?) high reproductive rate of the Painted Redstart in north-central Arizona are varied and complex. Our study area was located at the northern edge of the species' known breeding range (Phillips et al. 1964). Densities were certainly lower (we estimate about 10 pairs per 100 acres of suitable habitat) here than in the Chiricahua Mountains of southern Arizona. There is less usable habitat available in northern Arizona and what is available is widely scattered. Mortality may be high during fall migration as the species passes through the very hot, dry environs to the south. Miller and Stebbins (1964) were impressed with the poor physical condition of warblers passing through the Mohave Desert during fall migration. The bright plumage and the overt foraging behavior of the Painted Redstart may make it extremely conspicuous to potential predators. Also, the bird arrives in north-central Arizona in early spring when climatic conditions can be harsh. Nesting densities are thus low, and territories can consequently be large without undue energy expended in their defense. In the very productive riparian habitat, the Painted Redstart, without the pressure of high population, marshals enough time and energy to be double-brooded and on occasion polygynous.

In the terminology of MacArthur and Wilson (1967) the Painted Redstart is probably r-selected at the northern edge of its range. Pianka (1970) discussed the various habitat and species correlates of both r- and K-strategists. Some of the factors that are highly correlated with r-selection (variable and unpredictable climate, catastrophic density-independent mortality, type III survivorship curve, constant recolonization of an area) also pertain to individuals of a species at the edge of its range. Thus, a stenotopic bird such as the Painted Redstart may be a K-strategist in the center of its breeding range and, relatively, an r-strategist at the edges of its range.

SUMMARY

The breeding biology of the Painted Redstart was investigated at the northern edge of its breeding range. Fifteen nests belonging to 10 females and 12 males were located and studied.

Males arrived on the breeding grounds in

a riparian canyon in late March and early April and immediately established territories. Territories were very large when compared to those of other warblers. Females arrived shortly after the males and pair bonds were established quickly.

Nest-building and incubation were carried out solely by the female. During this period the male did not feed the female but spent considerable time singing at the territorial boundaries.

Nesting success was quite high as 75% of the eggs hatched and 59% of the eggs resulted in fledglings. The average clutch size was 3.7 eggs and the incubation period was 13 days.

On territories with only one nest, care of the nestlings was evenly divided between both parents. The young left the nest between the ages of 9 and 13 days. Double-brooded females initiated their second nests from 5 to 7 days later. The male cared for the young until they left the territory at about 30 days of age. The male then helped feed the young of the second brood.

Two cases of polygyny were observed. In the best documented case the male helped feed the nestlings at both nests. The young from both nests formed a small flock and were fed by the three parent birds. High mortality between nesting seasons probably resulted in low densities at the northern edge of the species range. Individuals can thus occupy large territories in the productive breeding habitat and expend more energy for reproduction and less in intraspecific conflict.

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