The Condor 96:1095–1099

NESTING ECOLOGY AND HELPING BEHAVIOR IN THE AZURE-RUMPED TANAGER IN MEXICO[1]

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Key words: Azure-rumped Tanager; nesting ecology; helping behavior; Mexico.

Tanagers are among the most conspicuous birds throughout the Neotropics. In spite of this, only a few of the 240 species of tanager have been studied. The nests of less than half of the 51 species of *Tangara* have been described, and published observations on breeding biology exist for only 10 (Isler and Isler 1987).

One of the poorly known species is the Azure-rumped Tanager *Tangara cabanisi,* which occupies a very small range in the Sierra Madre de Chiapas in Mexico and adjacent Guatemala. Distributional records consist of only five specimens from four localities and sight records from five additional areas (Heath and Long 1991). Its humid forest habitat is rapidly being destroyed, mainly for expansion of coffee plantations (Heath and Long 1991) and consequently it is listed as threatened (Collar et al. 1992).

The Azure-rumped Tanager is a social species, usually seen in flocks of six to eight individuals in the canopies of trees (Hilty and Simon 1977, Isler and Isler 1987, Heath and Long 1991). It does not usually join mixed-species bird parties. The sexes are alike, but subadult birds have a duller plumage (Isler and Isler 1987). Here, we present information on nest-site selection, duration of incubation and nesting periods, parental care, and helpers at the nest. These data augment the breeding data in Isler and Isler (1987), which were based on observations of one nest.

STUDY SITE AND METHODS

Our studies were carried out on the Pacific slope of the Sierra Madre de Chiapas at Cañada Honda (15°37'N, 92°48'W), within the El Triunfo Biosphere Reserve. Observations were made along 6 km of trail, ranging in elevation from 1,200 m to 1,500 m. Here the species inhabits humid evergreen broadleaf forest. Elsewhere we have described the physiognomy of the local plant communities and characteristics of the tanager's habitat (Long and Heath 1991, Heath and Long 1991).

The Azure-rumped Tanager has been regularly sighted at Cañada Honda since 1973 (Hilty and Simon 1977; G. Lasley, pers. comm.). Prior to our study, two nests were found: the first in April 1983 (Isler and Isler 1987; B. M. Whitney, pers. comm.), and the second in April 1987 (G. Lasley, pers. comm.; A. Huc, pers. comm.). We refer to these as nests A and B respectively.

During 1989 and 1990, we visited Cañada Honda in all months of the year except July, August and January. Throughout the year we found groups of Azure-rumped Tanagers in the same areas along the 6 km trail, suggesting that the species is territorial and does not undergo altitudinal migration. We estimated that there were five groups along the trail. Groups and pairs of tanagers were followed. Trees to which the tanagers regularly returned were watched carefully to locate nests. Tanagers were observed at nests during their breeding cycle and data collected on nest construction, incubation and parental care.

We collected the following data on the nest trees, including those of nests A and B: species, diameter at breast height (dbh), tree height, nest height, and the position of the nest in relation to the main trunk and to the edge of the tree. We compared nest trees with 148 other trees along the trail, which we sampled using the point-centered quarter method (Müller-Dombois and Ellenberg 1974).

RESULTS

We found evidence of breeding activity only in the early wet season, from mid-April through to mid-June (Table 1): the wet season lasts until September. We located six nests and observed two throughout the breeding cycle. Three of our nests and the two found prior to our study were located along a 200 m section of trail and may have involved the same social group of tanagers.

Nest-site characteristics. All nest trees were over 15 m tall, with a dbh of 0.43–5.35 m, and a wide canopy of spreading branches (Table 1). All nests were placed in the top half of the tree, some distance from the main trunk, approaching the end of a long horizontal branch, at a point where the branch forked. Tanagers nested in the taller trees of the forest (Fig. 1).

The trees selected by the tanager were of four species, with *Ficus cookii* selected for five of the eight nests. There are over 60 species of trees in the tanager's habitat at Cañada Honda, of which *Ficus cookii* is the dominant species (Heath and Long 1991).

Nest construction. Nests were cup-shaped, as with all *Tangara* species for which nests are known (Isler and Isler 1987). At three nests where construction was watched, both adults stripped lichen from nearby trees and flew with the material into the nest tree. They flew separately or together, often making their way to the nest in cautious stages. One nest was observed for 15

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[1] Received 22 March 1994. Accepted 27 May 1994.

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TABLE 1. Characteristics of *Tangara cabanisi* nesting trees, the position of the nests, and date of nesting.

Nest	Trees species	Dbh of tree (m)	Height of tree (m)	Height of nest (m)	Distance from edge of tree canopy (m)	Distance from trunk (m)	Dates of nesting
A	*Ficus cookii*	1.3	25.0	12.0	1.5	4.5	April 1983
B	*F. cookii*	1.6	25–30	20.0	—	8.0	April/May 1987*
1	*Rhamnus sharpii*	0.43	15.4	9.7	1.0	3.0	April 1989
2	Rubiaceae	0.8	22.6	15.0	1.5	9.0	May 1989
3	*Ulmus mexicana*	1.7	36.1	32.5	0.5	—	June 1989
4	*F. cookii*	5.35	30.0	22.0	1.0	—	May 1990
5	*F. cookii*	2.1	29.4	17.4	2.0	14.0	May 1990
6	*F. cookii*	1.25	30.0	26.5	1.0	>10.0	May 1990

* Two nests were built in this tree.

hr during two days of construction: the average visit was 32 ± SD 14.4 sec ($n = 54$).

Incubation. Incubation was monitored at nests 1 and 2. The percentages for daylight incubation (constancy), calculated by Skutch's (1954) method, were 73.9% for nest 1 and 81.7% for nest 2. The average length of an incubation session was 18.7 ± 6.8 min ($n = 34$) at nest 1 and 20.7 ± 10.2 min ($n = 26$) at nest 2. Recesses lasted 6.7 ± 3.4 min and 5.7 ± 3.2 min for nests 1 and 2 respectively.

During incubation the off-duty adult did not remain nearby. Instead, it returned about every 20 min, giving a rising inflected "*se-a-weet*" call in the general area and gradually approaching, but rarely entering the nest tree. The incubating bird normally gave a harsher and longer call (the "*chip chup weet*" described in Hilty and Simon [1977]) before leaving the nest to join its mate. The pair recessed and returned to the nest tree together. The off-duty bird occasionally fed the incubating bird, especially during heavy rainstorms.

Calculating the incubation period for the species is difficult, as the full cycle of nest building, copulation, incubation and nestlings was observed only at nest 1, and because the eggs and new-born nestlings could not be seen from our vantage position. At nest 1, a single copulation was seen on 27 April and incubation of the eggs was presumed to begin on 28 April when an adult was seen on the nest. The first indication of hatching was on 12 May, giving an incubation period of around 14 days. At nest 2 one of the pair was on the nest when discovered on 1 May and the first signs of hatching were on 13 May, making the incubation period at least 13 days.

Feeding the nestlings. Observations were made at nests 1 (59 hr) and 2 (24 hr). At both nests two nestlings were seen, and presumably the clutch size was two.

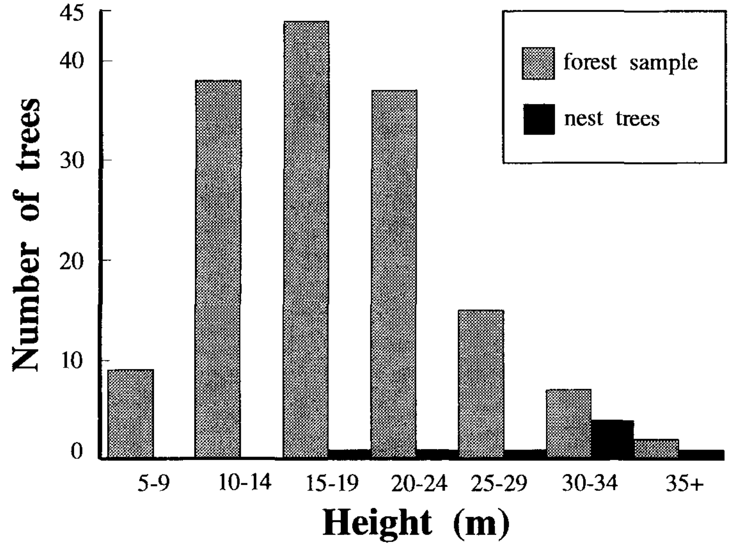

FIGURE 1. Frequency distribution of *Tangara cabanisi* nesting tree heights compared with a sample of 148 trees (>12 cm dbh) taken along the trail. The null hypothesis, that nest trees and a random sample of trees do not differ, is rejected ($t = 4.1$, $P < 0.001$).

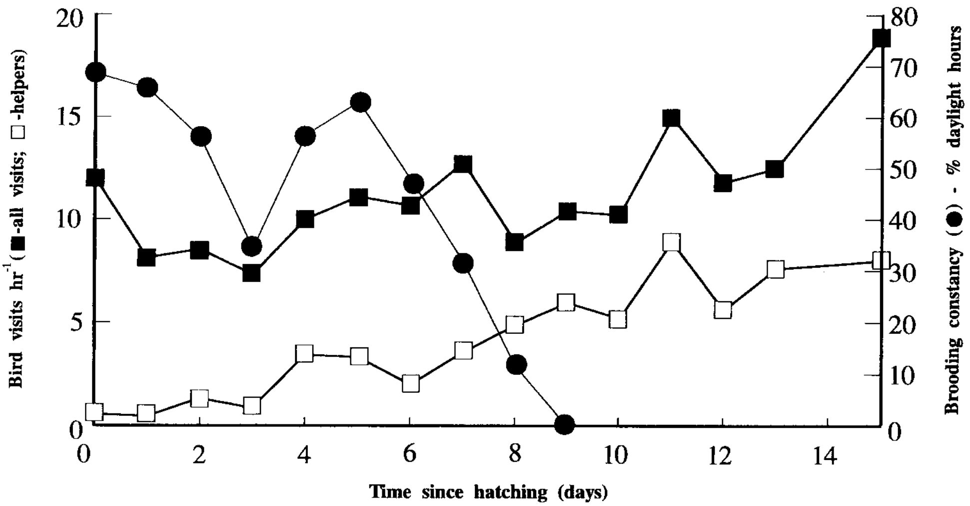

FIGURE 2. Brooding constancy (filled circles) and nest visits by adult birds at nest 1. A nest visit by an adult was defined as a visit to the nest rim and not to the general vicinity of the nest tree. The total number of nest visits by all adults (filled squares) and the minimum number of the total visits that were made by helpers (open squares) are shown. In nest visits in which more than two adults arrived together, the extras above two were counted as helpers. Nest visits consisting of one or two birds were marked simply as adults, but could have been helpers.

After hatching the brooding bird at nest 1 still spent a large proportion of daylight hours on the nest, but this decreased substantially after six days and stopped after nine days from hatching (Fig. 2).

Sometimes it was unclear whether the visiting adult actually fed the nestlings. However, if we assume that each nest visit did in fact equal a feed for the nestling then the average number of feeds per nestling at nest 1 from day 3 after hatching until the departure of the nestlings was 8/hr, and during the nestlings final five days in the nest each would have received more than 11 feeds per hour. At nest 2, from day 2 until day 6 after hatching, the average was 5.6 per hour for each nestling.

The food items brought to the nest consisted of both insects and fruit. Incidental feeding observations were of birds hunting insects in aerial sallies from tree-top positions or at fruiting trees, notably *Ficus cookii* Standley (Moraceae) and *Oreopanax sanderianus* Hemsley (Araliaceae). Visiting adults also collected fecal sacs which they swallowed whilst on the nest rim. For the last five days at nest 1 prior to fledging, each nestling on average produced a fecal sac every 15 min (173 fecal sacs in 21 hr 31 min of observations).

Helpers. A prominent feature at both nests was that the nestlings were fed by more than two birds. These helpers were indistinguishable from the breeding pair, all birds being in adult plumage. At both nests the adult group normally consisted of four or five individuals, although on one occasion at nest 1 six adults were seen together.

The first helpers were seen at both nests 1 and 2 at the end of the incubation period. At nest 2 this was the day before the eggs hatched, and ended with the incubating bird chasing off one of the two attending adults. However, by the end of the next day two tanagers came and fed the incubating bird.

The total number of nest visits by all adults and the minimum total of those that were made by helpers over the nesting period for nest 2 are shown in Figure 2. This demonstrates clearly that the contribution of helpers in terms of nest visits is substantial and increases steadily over the nesting period, rising from 4% of all visits at day 1 to a minimum of 38% the day before the young left the nest.

Fledglings. The young birds left nest 1 on 27 May, making the nestling period 15 days. Over the next two days they were sighted several times not more than 30 m from the nest tree, flying weakly between branches and trees. The group of adult tanagers continued making regular feeding trips to the two fledglings, and tended to stay for longer periods in their vicinity.

Reproductive success. From the limited data it seems probable that two or three of seven Azure-rumped Tanager nests (29–43%) fledged young. Nest 1 was the only successful nest in the first year, nest 2 being predated during nightfall of day 6 after the young hatched and nest 3 some time during incubation. In the second season one or two of the three nests reared young. This was nest 4 or 5, or both, it being impossible to tell which as two fledglings were seen moving between both nest trees. Nest 6 was depredated during incubation. Nest B was predated shortly after the young hatched (A. Huc, pers. comm.), and the fate of nest A is unknown. Renesting in the Azure-rumped Tanager, following the success or failure of a first nesting, was not seen during our study. However, in May 1987 a pair was observed beginning to build a nest in the same tree in which nest B had failed one month previously (A. Huc, pers. comm.).

DISCUSSION

Our results indicate that the preferred nest-sites of Azure-rumped Tanagers are in the largest trees in the forest with the majority of nests located in *Ficus cookii,* a canopy emergent and the dominant species in the study area. Nests were built where the foliage is at its densest, giving the nest maximum concealment.

Many of our results on the duration of the incubation and nesting periods are similar to the findings of previous studies on other tanager species. The clutch size of two is normal for non-cavity breeding birds at this latitude (Skutch 1954, 1984); most tanagers keep their eggs covered for 60–80% of daylight hours (Skutch 1989); the length of each incubation session is consistent with the usual 20–30 minutes session recorded for Central American tanagers (Skutch 1954), although Willis (1961) noted much longer sessions in the two species of ant-tanagers *Habia rubica* and *H. gutturalis* in Belize; and the 14 day incubation period is typical for tanagers (Isler and Isler 1987, Skutch 1989).

Similarly, the recorded nestling period of 15 days is about the same (within one day) as has been observed in eight of the ten other species of *Tangara* for which similar data exist (Isler and Isler 1987, Skutch 1989). According to Skutch (1989), 4–6 meals per hour is normal for tanager nestlings over two days old, but higher feeding rates have been observed in some species, such as the Scarlet-rumped Tanager *Ramphocelus passerinii,* with about 8 feeds per hour.

The Azure-rumped Tanager is highly social intraspecifically during the year but the breeding pairs we monitored constructed their nests alone. It was not possible to determine if both sexes had equal roles in nest construction, but the behavior of pairs at the nests observed suggests that one of the pair played a more active role than the other. Among other *Tangara* species the female nearly always plays a greater part in nest construction (Isler and Isler 1987, Wood et al. 1992), but commonly the male accompanies the female during nest building (Skutch 1989). Similarly, the female incubates the eggs in virtually all tanager species (Isler and Isler 1987, Skutch 1989), but often with the male attending her.

Our study showed that conspecific helpers contribute to the breeding activities of the Azure-rumped Tanager. Helping in other *Tangara* species has been recorded for Golden-masked *T. larvata,* Speckled *T. guttata,* Plain-colored *T. inornata,* Gilt-edged *T. cyanoventris* and Turquoise Tanagers *T. mexicana* (Skutch 1961, 1986; Isler and Isler 1987). The social breeding behavior of the last species, which Skutch (1989) found as complex as for any tanager studied, is very similar to the Azure-rumped Tanager but its breeding season is longer: February to October in Colombia, April to October in Trinidad (Isler and Isler 1987). Snow and Collins (1962) postulated that within a Turquoise Tanager social group pairs come into breeding condition at different times, thus ensuring ample food and protection for the young at all stages. However, this would not be possible within the short breeding season (as currently recorded) of the Azure-rumped Tanager.

It is possible that, for each social group of Azure-rumped Tanagers, more than one pair could be formed during the breeding season and that a group of tanagers could feed more than one brood at a time. Although we do not think this was the case for nests 1, 2, 3 or 6 it may have occurred at nests 4 and 5. These two nests were located less than 75 m apart and during the two seasons of fieldwork we saw only one group of tanagers in this area. Both these nests were found with eggs at the same time and thus their nestling stages would have overlapped; and later on, the five adults were attending two fledglings and using both of the nest trees as feeding posts.

This study indicates that the Azure-rumped Tanager has a cooperative breeding system as complex as for any tanager studied. We anticipate that social breeding will be found in other *Tangara* species that tend to occur in intraspecific groups.

We carried out this research whilst in receipt of scholarships from the Consejo Nacional de Ciencias y Tecnología (CONACYT), under the Anglo-Mexican Cultural Exchange Programme, and were based in the Instituto de Historia Natural (IHN), Tuxtla Gutiérrez, Chiapas. We thank Ramón Peréz Gil, former Assistant Director of IHN, the staff of the El Triunfo Project, the Natural Protected Areas and the Botany Departments of IHN. We are indebted to the wardens of the El Triunfo Biosphere Reserve, especially Ismael Gálvez and Rafael Solis for sharing with us their great knowledge of the area and for their help during the fieldwork. We thank Drs Nigel Collar, Martin Kelsey and Frank Lambert for their useful comments on earlier drafts. We also are indebted to two anonymous reviewers whose comments greatly helped us improve the manuscript.

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The Condor 96:1099–1103

REPRODUCTIVE ANATOMY OF THE CHAFFINCH IN RELATION TO SPERM COMPETITION[1]

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Key words: Sperm competition; Fringilla coelebs; *reproductive anatomy; sperm storage; testes.*

Competition among male birds to fertilize the eggs of females has the potential to infuence many areas of avian biology (Birkhead and Møller 1992a). This is particularly true of reproductive anatomy and physiology which provides a link between behavior (such as copulations) and parentage. The study of male reproductive parameters, such as testis size, the number of sperm stored and ejaculate volume, has revealed numerous adaptations to sperm competition at the anatomical level (e.g., Møller 1988, Møller 1991, Birkhead et al. 1993). For example, relative testes mass is generally greater in species in which females engage in extra-pair copulations (Møller 1991).

One important factor that determines which male fertilizes eggs is the mechanism of sperm precedence (the way in which order of mating affects the chances of fertilization). All experimental studies to date have revealed that when copulations are separated by at least 4 hr the sperm of the last male to mate have precedence. For example, last male precedence averages 80% in the Zebra Finch *Taeniopygia guttata* (Birkhead et al. 1988) and between 77% and 93% in chickens *Gallus* (Warren and Gish 1943, Compton et al. 1978). The aim of this paper is to describe the reproductive anatomy of both male and female Chaffinches *Fringilla coelebs,* and to interpret features of their anatomy with reference to sperm competition and sperm precedence mechanisms.

METHODS

A single pair of Chaffinches was collected (under license) close to their nest in the early morning of 13 May 1992, on day +3 of the female's laying cycle (where day 0 is the day the first egg is laid). In addition, we dissected a freshly dead male (killed by a weasel *Mustela nivalis* in mid April), and a female (road kill in mid June). Methods for dissection and measurement of sperm storage tubules (SSTs) in females and testes and number of sperm in sperm stores of males followed Briskie (1993) and Briskie and Birkhead (1993). SSTs containing sperm were photographed under Normarski illumination using a Leica Laborlux microscope. Although the sample size is small, it is reasonable to draw general conclusions from such a sample as Briskie and Montgomerie (1992, 1993) found that variation between species accounted for most (60.1% or more) of the total variance in sperm length, SST length and SST number in a sample of 20 North American passerine species. Values are given as means (±1 SD) unless otherwise stated.

RESULTS AND DISCUSSION

Male reproductive anatomy. Both males had enlarged testes and cloacal protuberances (CPs), indicating that they were reproductively active when collected (male 1: CP volume, following Briskie (1993), 308 mm^3; volume index following Birkhead et al. (1991), 20.3 mm^3g^{-1}; male 2: 322 mm^3 and 21.6 mm^3g^{-1} respectively). The right and left seminal glomera of male 1 weighed 0.0740 g and 0.0748 g respectively, a combined weight of 0.1488 g (0.73% of the male's body weight [20.25 g]) and contained an estimated total of 33.6×10^6 ($\pm 3.88 \times 10^6$ SE) sperm. The seminal glomera act as a store for matured sperm prior to ejaculation (Briskie 1993). The combined weight of the testes was 0.4779 g (right: 0.2333 g, 8.3 mm × 7.0

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