SHORT COMMUNICATIONS

The Condor 98:832–836

BREEDING BEHAVIOR, SOCIAL ORGANIZATION AND MORPHOLOGY OF RED-SHOULDERED (*AGELAIUS ASSIMILIS*) AND TAWNY-SHOULDERED (*A. HUMERALIS*) BLACKBIRDS[1]

LINDA A. WHITTINGHAM[2]
Department of Biology, Queen's University, Kingston, Ontario, K7L 3N6 Canada

ARTURO KIRKCONNELL
Museo Nacional de Historia Natural, Capitolio Nacional, La Habana, Cuba

LAURENE M. RATCLIFFE
Department of Biology, Queen's University, Kingston, Ontario, K7L 3N6 Canada

Key words: Red-shouldered Blackbirds; Agelaius assimilis; *Tawny-shouldered Blackbirds;* Agelaius humeralis; *breeding; territoriality; sexual dichromatism.*

The New World Blackbirds (Icterinae) have been the focus of many studies including recent investigations of the evolution of sexual dichromatism (Irwin 1994) and sexual dimorphism (Webster 1992) in relation to mating system. Such comprehensive studies are possible because of the extensive literature available on the breeding behavior and social organization for many species. The genus *Agelaius* is of particular interest because mating systems, parental care patterns and sexual dimorphism vary among species (Orians 1980, Webster 1992, Irwin 1994). Within this genus, the Red-winged Blackbird (*A. phoeniceus*) and the Tricolored Blackbird (*A. tricolor*) have been the focus of many studies and as a result their habits are known best (Orians 1961, Payne 1969, Searcy and Yasukawa 1995). In contrast, other members of this genus, such as the Red-shouldered (*A. assimilis;* formerly *A. phoeniceus assimilis,* see below) and Tawny-shouldered (*A. humeralis*) Blackbirds, have been studied very little and are relatively unknown.

In this paper we describe the breeding behavior of these two Caribbean species. Both of these species are non-migratory permanent residents with restricted distributions. The Red-shouldered Blackbird breeds exclusively in the marshes and swamps of western Cuba and the Isle of Pines, whereas the Tawny-shouldered Blackbird breeds in the open lowland country of Cuba and Haiti (Bond 1971). The Red-shouldered Blackbird was previously considered a race of the Red-winged Blackbird but recently has been considered as a separate species (Garrido and Kirkconnell 1996, AOU 1997). We have shown previously that these species differ dramatically in their vocal behavior (Whittingham et al. 1992). Here we show that these species also differ in several aspects of their breeding behavior and the plumage of nestlings. In many of the traits that we examined the Red-shouldered Blackbird is more similar to the Tawny-shouldered and Yellow-shouldered Blackbirds (*Agelaius xanthomus*) than to the Red-winged Blackbird or other species of *Agelaius.*

METHODS

We studied Red-shouldered and Tawny-shouldered Blackbirds at Guama, Cuba. Guama is located in the Zapata Swamp, approximately 162 km southeast of Havana. Guama consists of 12 small islands near the edge of Treasure Lake. We observed the breeding behavior of both species during the nesting period (25 May–4 June, 17–18 June and 1–2 July) in 1993. Observation periods during the nest-building, incubation and nestling periods were 30–240 min each day. Birds were watched continuously while their activities were recorded on cassette tapes which were later transcribed.

We caught 50 Red-shouldered Blackbirds (in 1992) and 20 Tawny-shouldered Blackbirds (in 1993) in mist nets and all birds were banded with a unique combination of colored leg bands. For each bird the following measurements were taken: (1) bill length, depth and width, (2) tarsus, wing and tail length, (3) length and width of epaulet, and (4) body mass. During the nesting period, egg mass and nestling body mass also were recorded at nests which were accessible. Means are presented with their standard errors.

RESULTS

MATING SYSTEM

Throughout the nest building, incubation and nestling periods we observed birds only in pairs for both spe-

[1] Received 11 October 1995. Accepted 12 July 1996.
[2] Present address: Department of Biological Sciences, Lapham Hall, University of Wisconsin-Milwaukee, P.O. Box 413, Milwaukee WI 53201.

cies. Thus, both Red-shouldered and Tawny-shouldered Blackbirds appeared to be socially monogamous. In addition, we observed Red-shouldered Blackbirds singing and foraging only in pairs during the pre-nesting period (Whittingham et al., unpubl. data).

TERRITORIES, NEST SITES AND NEST BUILDING

We observed six pairs of Red-shouldered Blackbirds on their breeding territories at Guama. Territories were established in the vegetation (primarily *Typha spp.*, *Phragmites spp.* and *Sagittaria lancifolia*) along the periphery of Treasure Lake and nests were built approximately 20 cm above the water. Territories were 700 ± 128 m² with a 200–250 m edge along the lake. The six pairs we observed held adjacent territories; other breeding pairs were distant even though there appeared to be abundant suitable habitat nearby. There were only two nests with completed clutches during our observations of the six pairs. Nest (n = 2) measurements were as follows: outside diameter of nests at top = 92, 105 mm, inside diameter at top = 72, 70 mm and depth = 53, 66 mm. Nests were built solely by the female from material collected exclusively within the boundaries of the territory. Clutch size was two or three eggs which had the following measurements: length 24.6 ± 0.2 mm, width 17.5 ± 0.2 mm and mass 4.0 ± 0.1 g (n = 5 eggs).

We observed eight additional pairs of Red-shouldered Blackbirds at Los Canneles approximately 30 km from Guama in the Zapata Swamp. Territories (n = 8) were larger (900 ± 50 m²) than those at Guama probably because there was more water and less vegetation within the territory. As with the Red-shouldered Blackbirds at Guama, only one female was associated with each male on the territory, birds foraged only within territorial boundaries and territorial interactions were rare. Unfortunately, access to this area was limited and we were only able to observe these birds for one day. Thus, further discussion of Red-shouldered Blackbirds refers only to the birds observed at Guama.

At Guama, Tawny-shouldered Blackbirds did not defend territories but did defend the area immediately around the nest. Nests were built in *Eucalyptus* (spp.) trees up to 50 m high and in branches overhanging water. Nests were also built in conical shaped outdoor lamps (in which the light bulbs had burned out) on the islands at Guama. Overall, nests were 8–25m apart (n = 11 nests). Nests were built primarily by the female, although two males were observed occasionally carrying nesting material. Clutch size was either three or four (3.5 ± 0.3; n = 5 nests) and eggs had the following measurements: length 22.2 ± 0.4 mm, width 16.6 ± 0.2 mm and mass 3.7 ± 0.3 g (n = 7 eggs). All five nests had completed clutches; however, eggs were measured from only two nests.

INCUBATION AND BROODING

In both species, only the female incubated eggs and brooded nestlings. Female Red-shouldered Blackbirds (n = 2) spent an average of 28.6 ± 3 min/hr^{-1} incubating eggs, while Tawny-shouldered females (n = 5) spent 44.5 ± 3 min/hr^{-1} incubating eggs. During the nestling period females of both species often perched over the nestlings with their wings open, thus, shading nestlings from the sun rather than brooding them.

PROVISIONING NESTLINGS

In both Red-shouldered and Tawny-shouldered Blackbirds males and females fed nestlings at similar rates. For Red-shouldered Blackbirds only two nests hatched successfully and we made provisioning rate observations during 6 periods (60–240 min each) over 2 days (1–2 July) when nestlings were 1 and 2 or 8 and 9 days old (0 = hatching). Over this time period both male and female fed nestlings at a similar rate (male: 3.9 ± 1.5; female: 2.7 ± 0.3 feeding visits/ hr^{-1}).

For Tawny-shouldered Blackbirds we were able to observe five nests and observe each nest when nestlings were 1–2, 3–4, and 7–8 days old (25 May–4 June and 17–18 June). Males (9.5 ± 1.8 feeding visits/hr^{-1}) and females (8.4 ± 1.4 feeding visits/hr^{-1}) fed nestlings at similar rates (U = 63, n_1 = 5, n_2 = 5, P = 0.8). Male and female provisioning rates increased only slightly as nestlings grew older (male: r_s = 0.34, P = 0.3; female: r_s = 0.48, P = 0.1). During all observation periods brood size was three at all nests.

NESTLING MORPHOLOGY

The feather sheaths of nestlings broke when nestlings were 5–6 days old. Nestling plumage was dull black except the lesser wing coverts (epaulet) which were reddish-brown. This was the case for all Tawny-shouldered Blackbird nestlings we observed (n = 5 nests) and for one of two Red-shouldered Blackbird nestlings, presumably a male. In contrast, the plumage of the other Red-shouldered Blackbird nestling was entirely dull black lacking any coloration in the lesser wing converts, presumably a female. Thus, nestlings developed plumage coloration similar to the adults, including the presence of epaulets, prior to fledging and did not show the streaked brown plumage characteristic of nestling Red-winged Blackbirds. One 8-day old Red-shouldered Blackbird nestling had the following measurements: wing chord 53.0 mm, tail 11.0 mm, tarsus 22.7 mm, bill length 14.4 mm, epaulet 21 × 24 mm, mass 25.0 g. Two Tawny-shouldered Blackbird nestlings were measured at 12 days of age: wing chord 58.0, 57.5 mm, tail length 20.0, 19.9 mm, tarsus 22.3, 21.9 mm, bill length 11.2, 11.2 mm, mass 24.0, 23.5 g. The epaulet measured 28 × 30 mm for one nestling and 18 × 8 mm for the second nestling; presumably these were male and female respectively.

ADULT MORPHOLOGY IN RELATION TO SEX AND AGE

In both Red-shouldered and Tawny-shouldered Blackbirds males are significantly larger than females in all measurements of bill morphology, tarsus, wing, tail, and body mass (Tables 1 and 2).

In Red-shouldered Blackbirds male plumage was entirely jet black except for the epaulet, which differed between males in their second calendar year of life (SY) and males in at least their third calendar year of life (ASY) (Pyle et al. 1987). ASY males had entirely red-orange epaulets which were larger (length 46.9 ± 0.3 mm, width 25.3 ± 0.4 mm) than the epaulets of SY males (length 43.0 ± 0.6 mm, width 20.1 ± 1.0 mm;

TABLE 1. Morphological measurements ($\bar{x} \pm$ SE) of male and female Red-shouldered Blackbirds.

Variable	ASY males	ASY females	SY males	SY females	t[1]	$P <$
Bill length (mm)	23.84 ± 0.3	20.74 ± 0.3	22.73 ± 0.3	20.82 ± 0.2	10.25	0.001
Bill depth (mm)	10.40 ± 0.1	9.65 ± 0.2	10.05 ± 0.2	10.15 ± 0.2	4.86	0.001
Bill width (mm)	7.54 ± 0.1	6.68 ± 0.3	7.85 ± 0.2	7.00 ± 0.2	3.32	0.002
Tarsus (mm)	28.90 ± 0.5	27.37 ± 0.5	28.56 ± 0.4	27.02 ± 0.7	2.12	0.04
Wing (mm)	110.48 ± 0.3	96.40 ± 0.3	105.20 ± 0.9	94.86 ± 0.5	34.42	0.001
Tail (mm)	83.91 ± 0.5	73.30 ± 0.6	80.00 ± 1.0	72.28 ± 0.8	12.66	0.001
Body mass (g)	54.39 ± 0.5	41.80 ± 0.9	50.60 ± 1.3	41.57 ± 0.8	12.74	0.001
n	23	9	10	8		

[1] t-test; comparison between ASY males and ASY females.

$t = 6.28$ $P < 0.001$, $t = 5.64$, $P < 0.001$, respectively). For SY males the epaulet was more orange than red in color and had black interspersed among the orange. SY males had an average of 37.5 ± 5.7% orange in the epaulet but this varied considerably (10–60% orange). ASY males had a yellow band (8.1 ± 0.2 mm wide) along the entire lower edge of the epaulet (similar to the Red-winged Blackbird) which was not present in the SY males. In contrast, females were entirely jet black and lacked the epaulet. SY females had olivaceous feathers at the base of the lower mandible and whitish edges on the greater and middle wing coverts as well as the under tail coverts.

In Tawny-shouldered Blackbirds both males and females had rust colored epaulets; however, male epaulets were considerably larger (length 36.2 ± 1.1 mm, width 30.4 ± 0.7 mm) than female epaulets (length 28.2 ± 1.3 mm, width 22.5 ± 0.9 mm; $t = 4.66$, $P < 0.001$, $t = 6.93$, $P < 0.001$ respectively). ASY males had a cream-colored band (2.2 ± 0.1 mm) along the lower edge of the epaulet which was not present in SY males. SY males had uniformly rust colored epaulets lacking black feather tips that were present in SY Red-shouldered Blackbirds and the epaulets of nestlings in both species.

COMPARISON TO OTHER SPECIES OF *AGELAIUS*

We compared seven species of *Agelaius* for which information on breeding behavior, social organization and territoriality were available (Table 3). In all species only the female incubates and builds the nest, with the exception of the Yellow-hooded Blackbird (*A. icterocephalus*) in which only the male builds the nest. Red-shouldered and Tawny-shouldered Blackbirds are (1) similar to Yellow-shouldered Blackbirds (*A. xanthomus*) in mating system, all levels of parental care and the extent of plumage dichromatism, (2) similar to Yellow-winged Blackbirds (*A. thilius*) only in mating system and female nest building and incubation, but differ considerably in the male's contribution to feeding nestlings as well as the extent of plumage dichromatism, (3) different from Yellow-hooded, Tricolored (*A. tricolor*) and Red-winged Blackbirds in mating system, the male's contribution to feeding nestlings and the extent of plumage dichromatism. Spacing during the breeding period varies extensively and does not appear to be correlated with any of the other variables examined.

DISCUSSION

Our data suggest that the Red-shouldered and Tawny-shouldered Blackbirds are more similar behaviorally to each other and to the Yellow-shouldered Blackbird than to other species of *Agelaius*. Furthermore, Red-shouldered and Tawny-shouldered Blackbirds share little in common with the Red-winged Blackbird in terms of mating system, patterns of parental care and sexual dichromatism. These differences provide further support for the status of the Red-shouldered Blackbird (*A. assimilis*) as a separate species from the Red-winged Blackbird (*A. phoeniceus*).

The development of nestling plumage suggests additional similarity between Red-shouldered, Tawny-shouldered and Yellow-shouldered Blackbirds and dis-

TABLE 2. Morphological measurements ($\bar{x} \pm$ SE) of male and female Tawny-shouldered Blackbirds.

Variable	ASY males	Females[2]	SY males	t[1]	$P <$
Bill length (mm)	17.90 ± 0.1	16.65 ± 0.2	17.73 (17.73–17.74)	5.57	0.001
Bill depth (mm)	7.66 ± 0.1	7.34 ± 0.3	7.72	2.84	0.01
Bill width (mm)	5.87 ± 0.1	5.47 ± 0.1	5.89 (5.20–6.58)	3.09	0.007
Tarsus (mm)	23.36 ± 0.2	21.85 ± 0.5	22.54 (22.20–22.88)	3.01	0.008
Wing (mm)	103.70 ± 0.6	95.75 ± 0.9	102.5 (102–103)	7.42	0.001
Tail (mm)	80.00 ± 0.6	75.5 ± 0.8	78.5 (78–79)	4.82	0.001
Body mass (g)	38.30 ± 0.6	34.45 ± 0.6	35.0 (33–37)	4.44	0.001
n	10	8	2		

[1] t-test; comparisons between ASY males and females.
[2] All females were included because age classes were not known.

TABLE 3. Breeding biology and sexual differences for seven species of *Agelaius*. Mating system is described as either polygynous (P) or monogamous (M). Parental care includes information on which sex (M = male, F = female) builds the nest (NB) and incubates (I), and the relative amount that each sex feeds nestlings (FN). Sexual difference in size is presented as the numerator of the ratio of male to female wing chord or tarsus length. Sexual difference in plumage is represented as an index of dichromatism (Irwin 1994). Higher numbers represent greater differences in plumage between the sexes over the seven body regions scored (Irwin 1994). Spacing indicates whether breeding birds defend territories (T), defend only the area immediately around the nest site (N), or breed colonially in dense (D) or loose (L) aggregations (after Orians 1985).

Species	Mating system	Parental care			Sexual differences			Spacing	Source
		NB	I	FN	Wing	Tarsus	Plumage[d]		
Red-winged Blackbird (*Agelaius phoeniceus*)	P	F	F	F > M	1.22[a]	1.10[a]	14	T	Nero 1956
Tricolored Blackbird (*Agelaius tricolor*)	P	F	F	F > M	1.14[b]	1.13[b]	14	T, D	Payne 1969
Yellow-hooded Blackbird (*Agelaius icterocephalus*)	P	M	F	F > M	1.11[c]	1.06[c]	13	T, L	Wiley and Wiley 1980
Yellow-winged Blackbird (*Agelaius thilius*)	M	F	F	F > M	1.08[c]	1.03[c]	10	N, L	Orians 1980
Yellow-shouldered Blackbird (*Agelaius xanthomus*)	M	F	F	F = M	1.12[b]	1.01[b]	0	N, L	Post 1981
Tawny-shouldered Blackbird (*Agelaius humeralis*)	M	F	F	F = M	1.08	1.07	0	N	this study
Red-shouldered Blackbird (*Agelaius assimilis*)	M	F	F	F = M	1.15	1.05	2	T	this study

[a] Whittingham et al. (1992).
[b] Measurements from Ridgway (1902).
[c] Specimens from the Louisiana State University Museum of Natural Science measured by LAW.
[d] All values from Irwin (1994) except *A. humeralis* which was calculated by LAW following the method of Irwin (1994).

similarity with Red-winged Blackbirds. Both Red-shouldered and Tawny-shouldered Blackbird nestlings exhibited adult-like black plumage with colored epaulets. This is similar to the plumage of nestling Yellow-shouldered Blackbirds which is uniformly dull black except the lesser wing coverts which are buffy yellow (Ridgway 1902). The plumage of these nestlings is in sharp contrast to the plumage of nestling Red-winged and Tricolored Blackbirds which is entirely streaked brown in both sexes, similar to the adult female (Ridgway 1902).

Within *Agelaius,* a high degree of sexual dichromatism and relatively little male assistance with feeding nestlings is associated with a polygynous mating system, whereas little sexual dichromatism and equal effort by both sexes feeding nestlings is associated with social monogamy (Table 3). The exception to this pattern is the Yellow-winged Blackbird in which the sexes are highly dichromatic and males provide relatively little parental care similar to polygynous species, yet they pair monogamously.

The similarity between the sexes in Red-shouldered, Tawny-shouldered and Yellow-shouldered Blackbirds occurs because the female is black and therefore more similar to the male (Irwin 1994) than in the other *Agelaius* species in which males are black and females are generally olive-brown (Yellow-hooded Blackbird) or streaked brown (Red-winged, Yellow-winged and Tricolored Blackbirds). Among the Icterinae, greater plumage dichromatism is associated with sexual selection on males, whereas reduced dichromatism is most likely the result of natural selection on females for brighter plumage (Irwin 1994). Thus, it is not surprising that we found relatively monochromatic Red-shouldered and Tawny-shouldered Blackbirds in socially monogamous pairs.

The extent of sexual size dimorphism appears to be greater in polygynous species than in monogamous species. Webster (1992) found a positive relationship between size dimorphism and harem size among the Icterinae and within five species of *Agelaius.* Our data seem to support this trend as Red-shouldered and Tawny-shouldered Blackbirds showed relatively little size dimorphism and males were only observed with one mate.

Lanyon (1994) recently examined the phylogenetic relationship of nine species of *Agelaius* (*A. assimilis* was not included). His data suggested that the genus was not monophyletic and that the species separate rather neatly into three distinct clades: North American (*A. phoeniceus, A. tricolor*), South American (*A. icterocephalus, A. thilius, A. ruficapillus, A. cyanopus, A. xanthophthalmus*) and Caribbean (*A. xanthomus, A. humeralis*). Our data on breeding behavior, morphology and social organization suggest that the Red-shouldered Blackbird may be more closely aligned with the Caribbean clade than with the North American clade. Alternatively, these similarities may have occurred through convergent evolution. Further work on these species will be necessary to resolve these relationships.

We thank P. Dunn, J. V. Remsen Jr. and F. Sheldon for comments on the manuscript. A Queen's Advisory Research Committee Award and an NSERC operating grant to LMR provided financial support for this project. We extend special thanks to the many helpful people at Guama who made our work possible.

LITERATURE CITED

American Ornithologists' Union. 1997. Forty-first supplement to the American Ornithologists' Union check-list of North American Birds. Auk in press.

Bond, J. 1971. Birds of the West Indies. Houghton Mifflin, Boston.

Garrido, O., and A. Kirkconnell. 1996. Taxonomic status of the Cuban form of the Red-winged Blackbird. Wilson Bull. 108: 372–374.

Irwin, R. E. 1994. The evolution of plumage dichromatism in the New World blackbirds: social selection on female brightness? Am. Nat. 144: 890–907.

Lanyon, S. M. 1994. Polyphyly of the blackbird genus *Agelaius* and the importance of assumptions of monophyly in comparative studies. Evolution 48: 679–693.

Nero, R. W. 1956. A behavior study of the Red-winged Blackbird. I. Mating and nesting activities. Wilson Bull. 68: 4–37.

Orians, G. H. 1961. The ecology of blackbird (*Agelaius*) social systems. Ecol. Monogr. 31: 285–312.

Orians, G. H. 1980. Some adaptations of marsh-nesting blackbirds. Princeton Univ. Press, Princeton, NJ.

Orians, G. H. 1985. Blackbirds of the Americas. Univ. of Washington Press, Seattle.

Payne, R. B. 1969. Breeding seasons and reproductive physiology of Tricolored Blackbirds and Redwinged Blackbirds. Univ. Calif. Publ. Zool. 90: 1–115.

Post, W. 1981. Biology of the Yellow-shouldered Blackbird—*Agelaius* on a tropical island. Bull. Florida State Mus. Biol. Sci. 26: 125–202.

Pyle, P., S. N. G. Howell, R. P. Yunick, and D. F. DeSante. 1987. Identification guide to North American passerines. Slate Creek Press, Bolinas, CA.

Ridgway, R. 1902. The birds of Middle and North America, Part II. Government Printing Office, Washington, DC.

Searcy, W., and K. Yasukawa. 1995. Polygyny and sexual selection in Red-winged Blackbirds. Princeton Univ. Press, Princeton, NJ.

Webster, M. S. 1992. Sexual dimorphism, mating system and body size in New World blackbirds (Icterinae). Evolution 46: 1621–1641.

Whittingham, L. A., A. Kirkconnell, and L. M. Ratcliffe. 1992. Differences in song and sexual dimorphism between Cuban and North American Red-winged Blackbirds (*Agelaius phoeniceus*). Auk 109: 928–933.

Wiley, R. H., and M. S. Wiley. 1980. Spacing and timing in the nesting ecology of a tropical blackbird: comparison of populations in different environments. Ecol. Monogr. 50: 153–178.