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Tricolored Blackbird
Agelaius tricolor
Order
PASSERIFORMES
– Family
ICTERIDAE
Issue No. 423
Authors: Beedy, Edward C., and William J. Hamilton, Iii

Introduction

Enlarge Tricolored Blackbird, male; Kern Co., CA; May

Enlarge Figure 1. Distribution of the Tricolored Blackbird.

Enlarge Tricolored Blackbird, female; Kern Co., CA; May

Tricolored Blackbirds are largely native to California (which is home to more than 99% of the

population). The geographic range of the Tricolored Blackbird is restricted to the Central Valley and surrounding foothills, throughout coastal and some inland localities in southern California, and scattered sites in Oregon, western Nevada, central Washington, and western coastal Baja California (Fig. 1). They are sexually dimorphic in size, plumage, and behavior. Males are larger than females, possess striking red, white, and black plumage, and display conspicuously when breeding. They are sympatric with Red-winged Blackbirds (*Agelaius phoeniceus*). Unlike Red-winged Blackbirds, however, Tricolored Blackbirds breed in dense colonies and may travel several kilometers to secure food for their nestlings; males defend small territories within colonies and mate with 1 to 4 females.

The Tricolored Blackbird forms the largest colonies of any North American passerine bird. Breeding colonies may attract thousands of birds to a single site. In the 1930s, 1 colony was estimated to include more than 200,000 nests. Colonies require nearby water, a suitable nesting substrate, and open-range foraging habitat of natural grassland, woodland, or agricultural cropland. In winter, they often form single-species, and sometimes single-sex, flocks, but they also flock with other blackbird species. They often change their nesting locations from year to year. These changes may be an adaptation to exploit rapidly changing environments in ephemeral habitats, providing secure nesting sites and plentiful insect food supplies. They are itinerant breeders, nesting more than once at different locations during the breeding season.

The status of the Tricolored Blackbird is of concern because its population has declined and its colonial nesting behavior makes it vulnerable to nesting failures affecting thousands of nests at large colonies. Studies in the 1970s reported that the overall population was greatly reduced from that observed during the 1930s. A decline of 37% between 1994 and 1997 was identified by intensive population surveys. Historically, this species was killed to control damage to rice and grain crops. Currently considered a Species of Concern by the U.S. Fish and Wildlife Service and a Species of Special Concern by the California Department of Fish and Game, Tricolored Blackbirds experience large annual losses of reproductive effort to crop-harvesting activities and suffer habitat losses to land conversions from rangeland to vineyards, orchards, and urban development.

Key studies include those covering socioecology (Orians 1961a, 1961b, Collier 1968), vocalizations and behavior (Collier 1968, Orians and Christman 1968), reproductive biology and physiology (Payne 1969), population trends (DeHaven et al. 1975a, Hamilton et al. 1995), and distribu-tion and migration (Neff 1937, 1942, DeHaven et al. 1975b). Recent population censuses (Beedy and Hamilton 1997) and itinerant breeding considerations (Hamilton 1998) indicate that continuing population declines warrant active management of this species and its breeding, foraging habitats, and possibly its unstudied winter range.

Distinguishing Characteristics

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Articles

Distinguishing Characteristics

Enlarge Tricolored Blackbird, male; Kern Co., CA; May

Enlarge Tricolored Blackbird, female; Kern Co., CA; May

Medium-sized, sexually dimorphic blackbird. Total length 18–24 cm. Body mass 40–70 g, depending on sex and season.

Definitive Basic (adult) male entirely black, glossed bluish (in full sunlight), with bright brownish-red lesser wing-coverts forming reddish patch on wing shoulder (epaulets) and median-coverts buffy white (Aug–Feb) to pure white (Feb–Jul) (Mailliard 1910, DeHaven 1975). Adult female mostly black, with distinct grayish streaks; relatively whitish chin and throat, rarely with faint pinkish or peach wash; and small but distinct reddish shoulder-patch (DeHaven 1975). Immature male similar to adult male, but plumage duller black and mottled with gray (Aug–Mar), becoming almost entirely dull black (Apr–Jul), and with shoulder-patch mixed with black (Aug–Mar only). Immature female similar to adult female, except wing lacks reddish patch. Immatures of both sexes usually retain some brownish or grayish underwing-coverts, which contrast with newer adjacent black feathers. Juveniles of both sexes (Apr–Aug) are similar to adult female, but much paler gray and buff (Pyle 1997).

In North America, most similar to Red-winged Blackbird. Besides limited range, both sexes of Tricolored are distinguished from Red-winged Blackbird by bill shape, tail shape, and primary feathering formula (Payne 1969, Pyle 1997). P9 (outermost primary) is longer than P6 in Tricolored Blackbird, shorter in Red-winged Blackbird (Mailliard 1910, Payne 1969). Greater length of outer primaries of Tricolored Blackbird creates narrower and more pointed wing shape (Tables 1 and 2), which is conspicuous enough for experienced observers to distinguish them from other blackbirds (Mailliard 1910, Orians 1961a). Bill of Tricolored is

longer and narrower than that of Red-winged Blackbird, so ratio of bill length to bill depth is greater in Tricolored Blackbird (see Table 11 in Pyle 1997: 627). Tail of Tricolored Blackbird is squarish, tail of Red-winged Blackbird is more graduated (Pyle 1997).

In the field, median wing-coverts of adult male Tricolored Blackbird are whiter (buffy white to white) than those of Red-winged Blackbird (buffy white to yellow), while female Tricolored Blackbird has blacker plumage than female Red-winged Blackbird, nape and/or central back-feathers lack chestnut edgings, chin and throat have little or no pinkish wash, and undertail-coverts usually have distinct gray edgings (Pyle 1997). However, female not always safely distinguished from female of most races of Red-winged Blackbird in the field, especially in Basic I plumage and closely resembles the California race of Red-winged Blackbird (*A. p. californicus*) at all ages (DeHaven 1975). Immatures and both sexes in nonbreeding plumage show grayish brown feather edgings. When present in California Red-winged Blackbirds, these edgings are always rusty or rufous (Mailliard 1910).

Flight of Tricolored Blackbird is characterized by long, shallow undulations (Hoffman 1955), and flocks tend to be compact (Orians and Christman 1968). Often silent in flight, but Flight Call is a distinctive *wuk* (Collier 1968); much lower in frequency than flight call of Red-winged Blackbird (Orians and Christman 1968).

Distribution Introduction

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Distribution

Enlarge Figure 1.
Distribution of the Tricolored Blackbird.

Enlarge Figure 2.
Tricolored Blackbird colonies in CA.

The Americas

Breeding Range

Figure 1 . *California.* Since 1980, active breeding colonies observed in 46 California

counties (see Fig. 2) and most of the largest colonies are in the Central Valley. Breeds locally west of Cascade Range, Sierra Nevada, and southeastern deserts from Humboldt and Shasta Cos. south to extreme sw. San Bernardino Co., w. Riverside Co., and w. and s. San Diego Co. In central California, breeding extends east into foothills of Sierra Nevada. Also breeds in marshes of Klamath Basin in Siskiyou and Modoc Cos. and Honey Lake Basin in Lassen Co. in ne. California. Historically, most California colonies have been located in Sacramento and San Joaquin Valleys, but habitat loss has reduced breeding considerably in this area in recent years (Hamilton et al. 1995, Beedy and Hamilton 1997).

Oregon. Breeds locally in s. Klamath and s. Jackson Cos. and at several isolated locations, including ne. Portland, Multnomah Co.; near Clarno and Wamic, Wasco Co.; John Day Fossil Beds National Monument, Wheeler Co.; and near Stanfield, Umatilla Co., in n.-central Oregon, as well as at Summer Lake, Lake Co., in s. Oregon. Scattered summer reports have occurred elsewhere in Oregon, including Willamette Valley (Gilligan et al. 1994).

Washington. A small colony nested in Grant Co. in 1998, the state's first documented breeding record.

Nevada. Small colonies near Minden, Douglas Co. in 1996 and 1997 (G. Chisholm pers. comm.)

Baja California. Formerly bred in central and western portion of Baja California Norte south to El Rosario (Wilbur 1987), but now local within this area (Howell and Webb 1995).

Winter Range

During winter, withdraws from Oregon (only a few remain in Jackson and Klamath Cos. or in central Oregon; Gilligan et al. 1994), portions of n. California outside of Central Valley, and Nevada. Also withdraws from Santa Barbara Co. and e. San Diego Co., and from Baja California. Resident within remainder of breeding range, but largely withdraws in winter from s. San Joaquin Valley and n. Sacramento Valley (rare in Sacramento Valley north of Sacramento Co.), concentrating in and around Sacramento–San Joaquin River Delta and coastal areas, including Monterey and Marin Cos. Small flocks may appear at other coastal locations from Sonoma Co. south to Santa Cruz Co. and sporadically north to Del Norte Co. (Beedy and Hamilton 1997).

Outside The Americas

Not recorded.

Historical Changes

Surveys indicate that overall range of species is little changed since the mid-1930s (Neff 1937, DeHaven et al. 1975a, Beedy et al. 1991, Hamilton 1998). Neff (1937) reported breeding colonies from sea level in San Diego and Santa Cruz Cos. to about 1,280 m at Klamath Lake, OR. High-elevation colonies in California at 1,158 m near Tehachapi, Kern Co. (Collier 1968), and at 1,219 m near Susanville, Lassen Co. (DeHaven et al. 1975a). Historical breeding colonies in Jackson and Klamath Cos., OR (Neff 1933, Richardson 1961). Since 1980, confirmed breeding in Klamath, Multnomah, and Umatilla Cos., OR (Beedy et al. 1991). Eggs collected near Minden, Douglas Co., NV, in 1928 (Western Foundation of Vertebrate Zoology), and small colonies observed near there in 1996 and 1997 (G. Chisholm pers. comm.). Formerly common in marshes of nw. Baja California (Bryant 1889), but observed rarely by Thayer and Bangs (1907) and Huey (1926); nesting not confirmed. Now described as "local" in Baja California by Howell and Webb (1995); only a few breeding colonies in 1990s (D. Anderson pers. comm.). Elsewhere, as for example, in Yolo Co., numbers greatly reduced, from >100,000 in 1960 (Orians 1961a) to only about 1,200 in 1998 (WJH). First documented breeding record for Washington occurred in 1998 in Grant Co.

Fossil History

Not reported.

Systematics Distinguishing Characteristics

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Articles

Systematics

Geographic Variation; Subspecies

No subspecies recognized (Am. Ornithol. Union 1957, Pyle 1997). Banding studies by Neff (1942), DeHaven et al. (1975b), and DeHaven and Neff (1973) indicated that banding returns from populations breeding in s. California from Santa Barbara Co. south to Baja California and east to the Sonoran desert were not from outside this area. Songs of male Tricolored Blackbirds are not regionally distinguishable, unlike those of some Red-winged Blackbird populations in California (Collier 1968).

Related Species

Study of mitochondrial DNA (cytochrome *b*) sequences suggested that the 9 *Agelaius* species are a polyphyletic assemblage of ecologically similar species (Lanyon 1994). Red-winged and Tricolored blackbirds were found to be sister taxa; in turn these species are sister to Tawny-shouldered Blackbird (*A. humeralis*) and Yellow-shouldered Blackbird (*A. xanthomus*) found in Caribbean. Systematics of genus *Agelaius* and origin of Tricolored Blackbird require further study.

Migration Distribution

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Migration

Nature Of Migration In The Species

Banding studies (Neff 1942, DeHaven and Neff 1973) and observations of unbanded birds (Payne 1969, R. Payne pers. comm.) demonstrated that some Tricolored Blackbirds reside in Central Valley throughout year. Individuals may occupy and breed at several sites during breeding season (Hamilton 1998).

Breeding-Season Movements

During breeding season, exhibits itinerant breeding (Hamilton 1998). Individuals move after first nesting efforts (Mar–Apr) in San Joaquin Valley and Sacramento Co. north to Sacramento Valley, ne. California, and rarely s. Oregon (Beedy and Hamilton 1997). Although later nesting is typical in northern range, small colonies may form Apr–Jun throughout geographic distribution (Hamilton 1998).

Postbreeding-Season Movements

Banding studies demonstrated major postbreeding-season movement into Sacramento Valley (DeHaven et al. 1975b). At least 1 bird from 18 of 21 Central Valley colonies where nestlings were banded was recovered near a postbreeding season roost on Colusa National Wildlife Refuge, Colusa Co. Large postbreeding roosts continue to develop in Sacramento Valley from Aug into fall near abundant food supplies (rice [*Oryza sativa*] and water grass [*Echinochloa crusgalli*]) and presence of roost sites at managed wildlife refuges and other marshes.

Winter Movements

In winter, numbers decline in Sacramento Valley and increase in Sacramento–San Joaquin River delta and n. San Joaquin Valley (Neff 1937, Orians 1961b, Payne 1969, DeHaven et al. 1975b). Large foraging flocks occur in pasturelands in s. Solano Co. by late Oct (ECB). Winter-ing flocks numbering 12,000–14,000 assemble near dairies on Point Reyes Peninsula, Marin Co., by mid-Oct (R. Stallcup pers. comm.). Some individuals also winter in central and s. San Joaquin Valley (D. Woolington pers. comm., G. Zahm pers. comm., ECB). Nonbreeding flocks of >15,000 individuals may gather at one location and disperse to foraging sites. Sometimes these flocks consist of only Tricolored Blackbirds, either mixed-sex or single-sex; sometimes they are in mixed-species blackbird flocks. Birds from one large winter roost in Sacramento Co. foraged over an area 32 km in diameter (Neff 1937). Marked individuals at persisting winter roost sites in s. San Joaquin Valley were gone in <3 wk, indicating winter turnover and mobility (Collier 1968). Winter distribution and movements need further study.

Spring Movements From Wintering Areas

Vacates wintering areas in Sacramento–San Joaquin River Delta and along coastal California. Arrives at breeding locations in Sacramento Co. and throughout San Joaquin Valley in early Mar–early Apr (DeHaven et al. 1975b). Smaller colonies at foothill locations and in San Joaquin Valley are often settled by late Mar, but sometimes not until as late as

end of May (WJH). In s. California and Baja California, may nest anytime throughout Apr–May. In Sacramento Valley, largest colonies are settled during May and early Jun (WJH).

Control And Physiology

Seasonal changes in amount of fat on Tricolored Blackbirds and resident California Red-winged Blackbirds parallel those of other resident species rather than those of migrants (Payne 1969). Tricolored Blackbirds on nesting grounds in early spring have less fat than those initiating nesting a month later. Seasonal gonadal development and sexual activity of Tricolored Blackbirds probably are regulated, like those of Red-winged Blackbirds, by increasing daylength of late winter and early spring, and possibly by other factors, such as abundance of insect food and rainfall (Payne 1969).

During autumn breeding, gonads enlarge again after having collapsed following vernal breeding and the subsequent Prebasic molt (Orians 1960, 1963, Payne 1969). Field observations in late 1950s and early 1960s suggested that autumn breeding was associated with grasshoppers, rain, and/or Sep–Oct abundance of rice. Breeding response to rain and abundance of food in Central Valley at this time may have mimicked conditions under which autumn breeding of Tricolored resulted (Payne 1969).

Habitat Systematics

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Habitat

Breeding Range

Almost 93% of 252 breeding colonies observed in Sacramento Valley, from 1931 to 1936, were in freshwater marshes dominated by cattails (*Typha* spp.) or bulrushes (*Schoenoplectus* spp.); remaining colonies were in willows (*Salix* spp.), blackberries (*Rubus* spp.), thistles (*Cirsium* and *Centaurea* spp.), and nettles (*Urtica* sp.; Neff 1937). In contrast, only 53% of colonies reported in Sacramento and San Joaquin Valleys during 1970s were in cattails and bulrushes (DeHaven et al. 1975a). Breeding habitat now includes diverse upland and agricultural areas (DeHaven et al. 1975a, Beedy et al. 1991, Cook 1996). Nests in larger marshes and selects denser vegetation than Red-winged Blackbird (Payne 1969).

In recent decades, many colonies have been reported in Himalayan blackberries (*Rubus discolor*). Some of the largest colonies are in silage and grainfields in San Joaquin Valley (Collier 1968, Cook 1996). Other nesting substrates include giant cane (*Arundo donax*); safflower (*Carthamus tinctorius*); mustard (*Brassica nigra*; Orians 1961a, DeHaven et al. 1975a); stinging nettles (*Urtica dioica*); tamarisk (*Tamarix* spp.); riparian scrublands and forests (e.g., willows [*Salix* spp.], Fremont cottonwood [*Populus fremontii*], California ash [*Fraxinus latifolia*]); mule fat (*Baccharis salicifolia*); a desert olive (*Forestiera neomexicana*) grove; and spiny field plants, such as wheat (*Triticum* spp.), barley (*Hordeum* spp.), and thistles; and a lemon (*Citrus limon*) orchard (*American Birds* file data 1960–1989; Beedy et al. 1991, Hamilton et al. 1995).

Dairies and feedlots are components of many Tricolored Blackbird habitats (Hamilton et al. 1995). This association was not mentioned in earlier species accounts (e.g., Neff 1937, Orians 1961a, 1961b, Payne 1969, DeHaven et al. 1975a). In 1994, 55% of all observed nests were associated with dairies (Hamilton et al. 1995). In some places, nesting substrate, water source, and foraging habitat are all contained on a single, large dairy operation.

Some small breeding colonies at private and public lakes, reservoirs, and parks are surrounded by shopping centers, subdivisions, and other urban development. Adults from such colonies forage in undeveloped uplands nearby. These small, urban wetlands and upland foraging habitats may continue to accommodate Tricolored Blackbirds unless they also are eliminated entirely by development.

Foraging Range

Usually only part of the area within commuting range from breeding colony provides suitable foraging. Low-quality foraging habitats, such as cultivated row crops, orchards, vineyards, and heavily grazed rangelands, usually are present in association with high-quality foraging areas, such as irrigated pastures, lightly grazed rangelands, dry seasonal pools, mowed alfalfa (*Medicago sativa*) fields, feedlots, and dairies. May forage in various scrub plant associations (Beedy and Hamilton 1997).

Nonbreeding Range

Forms large roosts, sometimes in association with other species, such as Red-winged Blackbirds, Brewer's Blackbirds (*Euphagus cyanocephalus*), and European Starlings (*Sturnus vulgaris*; Collier 1968, Payne 1969). Preferred roost sites include cattail and bulrush marshes near suitable foraging areas in pasturelands and croplands.

Food Habits Migration

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Food Habits

Feeding

Main Foods Taken

Characterized by Orians (1961b) and Payne (1969) as a grasshopper (Orthoptera) follower, the counterpart of Old World locust-dependent starlings. When later observations failed to confirm this relationship, Crase and DeHaven (1977) suggested that the decline in abundance of Tricolored Blackbirds they observed (for 1968–1972 interval, compared with Neff's 1930s observations) might reflect loss of California grasslands and grasshoppers. Opportunistic foragers, Tricolored Blackbirds consume any locally abundant insect resource, including grasshoppers (Collier 1968), grains (maturing and ripe seeds), snails (Martin et al. 1951), and small clams (Skorupa et al. 1980). Often exploits concentrated agricultural food resources (Skorupa et al. 1980).

Microhabitat For Foraging

See Habitat: foraging range, above.

Foraging Distance

Breeding individuals forage away from their nest sites, often well out of sight of colony. Most forage within 5 km of colony sites (Orians 1961a), but may commute to 13 km one way (WJH). Short-distance foraging (i.e., within sight of colony) for nestling provisioning also common (Cook 1996). At smaller colonies (<1,000 adults) outward flights are pulsed; at large colonies (>40,000 adults), departures may form continuous and persistent streams from colony to food resource or outward flights may scatter even in largest colonies.

Food Capture And Consumption

Like other blackbirds, Tricolored Blackbird gapes, opening bill forcibly against resistance to expose insect prey in leaves of agricultural plants, aquatic plants and under tilled soil, sticks, and rocks (Orians 1985). Picks seeds and insect prey from ground, gleans vegetation, and occasionally fly-catches near and above breeding colonies, sometimes to 30 m high. Often forages deep in grass, where not observable. At all seasons, attracted to foraging flocks of other blackbirds.

Diet

Foraging and food differences between Tricolored Blackbirds and Red-winged Blackbirds appear to be based primarily on sociality and choice of foraging locations, not on specific foods.

Breeding Season

In s. California, Collier (1968) concluded that diet of Tricolored Blackbird in breeding season is no more specialized than that of Red-winged Blackbird. Foods delivered to Tricolored nestlings include grasshoppers, beetles and weevils (Coleoptera), caddis fly larvae (Trichoptera), moth and butterfly larvae (Lepidoptera; Mailliard 1914, Orians 1961a, Collier

1968, Payne 1969, Crase and DeHaven 1977, Skorupa et al. 1980), and, especially in current (1998) rice-growing areas, dragonfly larvae (Odonata; WJH). One large 1997 colony (>50,000) fed almost exclusively on lakeshore midges (Diptera; WJH). Quantitative analysis of esophagus contents of birds shot returning to a breeding colony showed that animal matter accounts for 91% (*n* = 95) of food volume for nestlings and fledglings, 56% (*n* = 107) for adult females, 28% (*n* = 27) for adult males (Skorupa et al. 1980). Collier (1968) found noctuid moth (Noctuidae) larvae and beetles the most prominent items taken by breeding adults.

Immediately before and during nesting, adults attracted to vicinity of dairies may take high-energy livestock foods (Collier 1968). Adults with access to livestock feed, such as cracked corn, may begin delivering it to chicks when they are about 10 d old (WJH). Long history of crop depredation (Tyler 1907), including newly sprouted rice (WJH), ripening oats (*Avena sativa*; Skorupa et al. 1980), and milk-stage barley (WJH). May offer considerable benefit as agent of insect control (Mailliard 1914, Skorupa et al. 1980), especially to organic and seed crop operations.

Nonbreeding Season

On the basis of winter food habits in Sacramento Valley , >88% (*n* = 37) of winter diet is plant material, primarily seeds of rice, other grains, and weeds (Crase and DeHaven 1978).

Food Selection And Storage

Does not store food. Selects grains as they ripen (milk stage).

Nutrition And Energetics

No information.

Metabolism And Temperature Regulation

Chicks in exposed nests avoid direct sun by crowding shaded edge of nest, pointing body and bill toward sun. Female shades nest and is reluct-ant to flush from eggs and nestlings at ambient temperature >42°C (WJH). Early observations of mass nestling losses due to high ambient temperatures in summer (Neff 1937) have not been documented subsequently, and no egg or nestling mortality observed following >43°C shade temperature (WJH).

Drinking And Defecation

Drinks by dipping bill in water, closing bill, raising head, and swallowing. Older nestlings defecate at one place at nest edge. Fledgling latrines leave a distinctive whitewash near colony edges, especially visible in Himalayan blackberry colonies.

Sounds Habitat

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Sounds

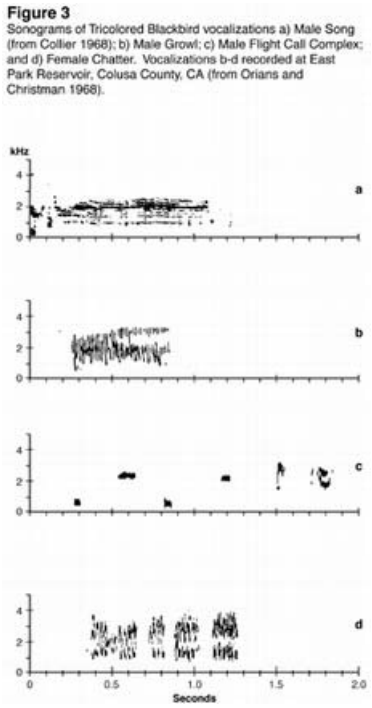
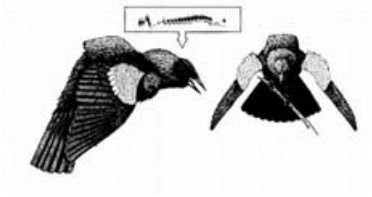


Figure 3
Sonograms of Tricolored Blackbird vocalizations a) Male Song (from Collier 1968); b) Male Growl; c) Male Flight Call Complex; and d) Female Chatter. Vocalizations b-d recorded at East Park Reservoir, Colusa County, CA (from Orians and Christman 1968).

Enlarge

Figure 3. Vocalizations of the Tricolored Blackbird.



Enlarge

Figure 4. Song spread of male Tricolored Blackbird

Vocalizations

Development

No vocalization noted before hatching. Begging Calls develop soon after hatching and change to loud, shrill calls at about 10 d after hatching (WJH). No information on vocal learning. Vocal imitation not reported.

Vocal Array

Collier (1968) and Orians and Christman (1968) provide the only detailed descriptions of the vocalizations of this species, as well as comparisons with vocalizations of Red-winged Blackbird. Both male and female have characteristic array of calls, some shared by both

sexes. Calls are relatively short and simple, often with broad frequency ranges. In contrast to Red-winged Blackbird, Tricolored Blackbird's lack of geographic variation in song or song types is interpreted as suiting their rapid integration into wandering flocks and effective breeding groups (Collier 1968).

Flight Calls. *Wuk* or *kuk*, given by both sexes in flight to and from foraging grounds. Measured at 1.3 kHz, compared to Red-winged Blackbird flight call at 2.5 kHz (Collier 1968).

Distress and Alarm Calls. Distress Call given by both sexes: *chu-raah* . Gives at high intensity when mobbing snakes (Collier 1968) or Common Ravens (*Corvus corax*; WJH).

The *chuck* or *chur* Alarm Calls of Tricolored Blackbird are similar to those of Red-winged Blackbird, but lower in pitch. Other less common calls include *prit*, *check*, and *haah-uh*; gives *check* usually with plumage sleeked, epaulets covered, and tail flicked. Alarm Calls are typically given when flocking, may function to keep birds together (Orians and Christman 1968). In contrast to Red-winged Blackbird, Tricolored Blackbird does not give hawk Alarm Calls (Orians and Christman 1968). In response to Northern Harriers (*Circus cyaneus*), a common disturbance at large Central Valley colonies, they become suddenly silent and remain in place, or fly up and circle in tight formation (WJH).

Both sexes give Scream when handled by humans or caught by predators, and when chasing potential predators: loud, long, squalling note, similar to that of Red-winged Blackbird draws other Tricolored Blackbirds (Orians and Christman 1968).

Courtship Calls. When female settles on territory, male gives guttural Nest Invitation Call (*wugup*) as prelude to nest initiation and attracting female to nest site (Collier 1968). Associated with male Nest Invitation Display (see Behavior: sexual behavior, below).

Precopulatory Calls. Given by both sexes: repeated *ti ti ti* . Female call similar to that of Red-winged Blackbird, but fainter. Used for only about a week, usually before copulation. In addition to primary Precopulatory Call, commonly gives other notes, including *kee*, *chee*, *seetuck*, and *keow*, but their significance is unknown (Orians and Christman 1968). Male reported to give repeated Precoition Call (*gleep*) when pursuing female to nest site (Collier 1968).

Male Song. Long, growl— *ker-aaah*, *ker-ah-ooow*, or *ker-ay-rooow* —given for about 1.25–1.5 s; song frequency of fundamental range about 1.5–2.25 kHz (Collier 1968, Orians and Christman 1968). Typical Male Song (see Fig. 3A) recorded in Ventura Co., CA (Collier 1968). During territory defense, Male Song usually accompanied by Song-Spread Displays (see Behavior: sexual behavior, below) of varying intensity and frequency, and often accompanied by several *kwik*, *cup*, and *cheewit* calls. Given to females when they enter colony, and to adjacent males. Induces overflying individuals of both sexes to join colonies; does not attract Red-winged Blackbirds (Collier 1968). When unaccompanied by displays, Male Song usually evokes only singing response from other territorial males. Male Song occurs throughout year, but in nonbreeding season it is restricted to periods of resting, preening, and roosting (Orians and Christman 1968) and is not accompanied by Song-Spread Display.

Growl. Given only by males (see Fig. 3B). Characteristic sound of settling and egg-laying colonies is *haah-uh* call of territorial males (Orians and Christman 1968). Gives threatening, buzzing Growl (*kraah*) to displace territorial intruders (Collier 1968). Sometimes heard at nonbreeding roosts accompanied by rush toward other males, especially when territories are being established; can approach physical combat (Collier 1968).

Flight-Call Complex. Long, complex calls given only by male flying from territory (Orians and Christman 1968) during periods of territory establishment and feeding of young; most conspicuous during colony establishment. Flight-Call Complex begins with low, clear note followed by higher notes; often repeats introductory note one or more times. Lower in pitch than flight-call complex of Red-winged Blackbird (Fig. 3C). *Keet* and *kwik* often are part of Flight-Call Complex; several other calls, including *t-deechick*, *weet*, and *chet*, have been recorded but are rare and have unknown significance (Orians and Christman 1968). Male also reported to give distinctive Nest Departure Call (*chu-laak*) when leaving colony. Male Red-winged Blackbird utters similar, but higher-pitched calls both when leaving and when returning to territory (Collier 1968, Orians and Christman 1968).

Female Chatter. The only call given exclusively by female; considered functional equivalent of Male Song (Orians and Christman 1968). Consists of rapidly repeated notes— *tree-tree-tree* —with wide frequency range (Fig. 3D), similar to chatter of female Red-winged Blackbird. Females chatter only when leaving or returning to a nest being built or containing eggs. This call reportedly is not heard before nest-building or after eggs hatch (Orians and Christman 1968), but Collier (1968) indicated that it could be heard throughout nesting cycle. Usually directed at mate during Nest-Site Appeasement Display (Collier 1968; see Behavior: sexual behavior, below).

Phenology

Male gives loud, distinctive song throughout year; in breeding season, Male Song functions in territorial defense and attracting females. Female has no loud song. Gives many vocalizations for only short period of year, at specific stages of nesting season (Collier 1968, Orians and Christman 1968).

Daily Pattern

Male Song is most frequent early in morning and at dusk, but also is heard as a droning chorus at breeding colonies throughout day. Male Song also is given at dawn and dusk at roost sites in nonbreeding season (ECB).

Places Of Vocalizing

Male sings from exposed perches within territory, usually the highest emergent vegetation or other nesting substrate. Then shifts to deep vegetation at or near nest. Some vocalizations, including most female sounds, occur near nest site. In nonbreeding season, vocalizes at roost sites, mostly in cattail marshes.

Nonvocal Sounds

Heerman (1859: 53) and Baird et al. (1874: 166) noted a “dull rushing, roaring noise” from massed birds in flight.

Behavior Food Habits

Recommended Citation
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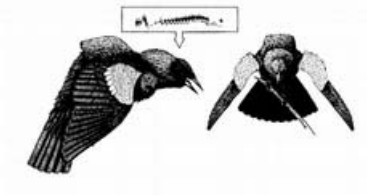
Tricolored Blackbird
Agelaius tricolor
Order
PASSERIFORMES
– Family
ICTERIDAE
Issue No. 423
Authors: Beedy, Edward C., and William J. Hamilton, Iii

Behavior



Enlarge Figure 4. Song spread of male Tricolored Blackbird

Locomotion

Walking, Hopping, Climbing, Etc
Usually forages on ground. Well coordinated when hopping among stems of emergent vegetation.

Flight
Strong, agile. Direct flight with long, shallow undulations (Hoffman 1955); often flies in relatively compact flocks (Orians and Christman 1968). Carries more weight per unit of wing surface than does Red-winged Blackbird (Orians 1961a; see Table 3). At breeding colonies, may fly alone, in pulses of flocks, or in continuous lines to distant foraging sites. In flight, holds head and tail directly out from body, epaulets conspicuous from above. Flight speed 40–48 km/h in still air (WJH).

Self-Maintenance

Preening, Head-Scratching, Stretching, Bathing, Anting, Etc
Often preens and scratches head at breeding colonies. Anting not observed.

Daily Time Budget
Male devotes about half his time to territory establishment and defense during week when nests are built and eggs laid, about twice as much time in territorial defense as male Red-winged Blackbird during that period (Orians 1961a). Throughout rest of breeding season, male expends little energy on territorial defense and substantially more energy provisioning nestlings because of long flights to distant foraging sites; Red-winged Blackbird both defends and forages on territory (Orians 1961a).

Agonistic Behavior

Physical Interactions
Fighting said to be rare (Orians and Christman 1968), but actual occurrence not described. Bill-Up, a classical ictericd agonistic display (see Territorial Boundary Display, below; Orians and Christman 1968), not associated with overt fighting as in Red-winged Blackbird (Collier 1968).

Communicative Interactions

Flight Displays. Unlike Red-winged Blackbird, male Tricolored Blackbird does not perform aerial flight displays because territories are too small to permit these displays within their boundaries (Orians and Christman 1968). Occasionally male returning to territory assumes incipient Flight-Song postures. Supplant-ing flights are regular among Tricolored and other blackbirds most of the year, but no specific displays have been described; further study is needed (Orians and Christman 1968).

Aggressive Rush. Intimidation display used by males in territorial defense. Given with threatening Growl (see Sounds: vocalizations, above); territorial male may erect plumage while rushing intruders (Collier 1968).

Territorial Boundary Display. Given by both sexes. Male directs this perched display toward opponent. Points bill up in rigid posture with beak and head pointed, neck stretched, contour feathers sleeked, epaulets exposed and slightly flared (Collier 1968). Female occasionally directs this display towards male, including her mate (Orians and Christman 1968) and uses it more frequently than do female Red-winged Blackbirds.

Spacing

Territoriality

Males defend only immediate nesting area. Male territory size ranges from 1.8 m^2(Lack and Emlen 1939) to 3.25 m^2(Orians 1961a). Average size of recently established territories of 6 banded males at 2 different colonies was 3.25 m^2(range 2.6–4.6); volumetric territories in willows calculated to be 8.5–11.3 m^3(Collier 1968). Some Himalayan blackberry colonies have nesting densities up to 6 nests/m^2(L. Cook pers. comm., WJH). After week of nest-building and egg-laying, males may cease territory defense (Orians 1961a). However, Collier (1968) observed resumption of territorial defense at hatching when males return to colony to participate in provisioning young. Because nests are usually started on first day of territory establishment, females spend almost no time in aggressive behavior (Orians 1961a).

Individual Distance

Not reported.

Sexual Behavior

Mating System And Sex Ratio

Female constructs nest within small territory of male (Lack and Emlen 1939). Sometimes polygynous; 1–4 females/male (Payne 1969). Some colonies have nearly equal numbers of males and females (Hamilton et al. 1995). Because males make fewer trips than females per unit time, sex ratios of provisioning Tricolored Blackbirds cannot be used to estimate mating sex ratios (Collier 1968). The measure of seasonal reproductive success is complicated by itinerant breeding because Tricolored Blackbirds, unlike Red-winged Blackbirds, nest at more than one location during their annual breeding cycle (Hamilton 1988; see Migration: breeding-season movements, above).

Polygyny studies of Tricolored Blackbird (Orians 1961a, Collier 1968, Payne 1969) were based on small sample sizes and lack precision of more recent studies of polygyny in Red-winged Blackbird (Searcy and Yasukawa 1995, Beletsky 1996, Beletsky and Orians 1996). Collier (1968) reported 2–3 females/territorial male and concluded that Red-winged Blackbird is more highly polygnous. Polygny in Red-winged Blackbirds is measured by number of mates per season at a given locality. Comparable seasonal matings of Tricolored Blackbird would need to measure the collective association of individual males with females at all locations throughout a breeding season or, more realistically, the number of times both sexes breed and where they do so in a breeding season.

Pair Bond

Prospecting males arrive before females at colony sites, but sometimes by <1 d (WJH). At sites where nonbreeding roosts precede colony settlement, both sexes are present throughout colony establishment (Collier 1968). Dense concentrations of birds gather at alternative sites in marshes, then suddenly fly to another place (Orians 1961a). Prospectors mass and chorus at alternative breeding sites, changing locations frequently in synchronous displaylike flights as if not foraging seriously, then return to potential nest sites. Prospecting behavior may continue for several days before colony becomes established (Orians 1961a),

and it persists until nesting begins (Collier 1968). Males on territories simultaneously disappear when females pass over. Males may spend half their time below vegetation canopy performing Nest-Site Demonstration Display (see Sexual behavior, courtship displays, below; Orians and Christman 1968).

Courtship Dsplays. Sexual Chasing rare for Tricolored Blackbird but a common Red-winged Blackbird behavior. Reported only during early courtship and nest-building, when male occasionally pursues female up to about 200 m from colony to areas where nesting materials are gathered (Collier 1968). Male flies to perch site, sings, preens, shifts positions, and repeats the performance (Orians 1961a). Aerial courtship displays are absent in Tricolored Blackbird (see Agonistic behavior: communicative interactions, above); may be related to colonial behavior with small nesting territories that do not accommodate flight displays within their boundaries (Orians and Christman 1968).

Song-Spread Display accompanies Male Song (see Sounds: vocalizations, above). Most common and conspicuous display of territorial male; restricted to breeding season (Orians and Christman 1968). Tail and wings depressed and spread, neck-feathers erect (similar to but more pronounced than in male Red-winged Blackbird), greatly increasing apparent size of male (Orians and Christman 1968). Viewed frontally, appears as 3 superimposed discs formed by head, puffed arched neck, and wings and trunk (Fig. 4); accentuated by bluish luster of shiny male plumage (Collier 1968). Song-Spread Display is male-male feature of prospecting period and prelude to interactions with female. Continues throughout male presence at colony until egg-laying is completed (Collier 1968).

Nest-Site Selection Display follows Song-Spread Display. Male follows female to potential nest site, which may have bent vegetation from which he displays (Orians and Christman 1968). This behavior occurs under dense emergent vegetation, Himalayan blackberry brambles, and thistle thickets.

In Nest Invitation Display, male moves toward nest site seeking female; usually associated with Nest Invitation Call (see Sounds: vocalizations, above). While moving toward nest site, arches wings, wags head, and erects plumage. Frequent, but limited to 2–3 d of settlement (Collier 1968).

Nest-Site Demonstration Display begins with male perched on display platform. After sighting female, male gives Song-Spread Display, elevates wings to V-shape, lowers and spreads tail, and moves into vegetation. Working through vegetation with female following, male continues to display, including pointing bill at prospective nest site, moving bill back and forth rapidly, and occasionally picking up nesting material. Female may pick up nesting material and display with male (Orians and Christman 1968).

Copulation; Pre- and Postcopulatory Displays. Copulation usually is initiated by solicitation by female (Orians and Christman 1968). Both sexes raise and lower wings and tail as preliminaries to copulation. Mutual mating responses, includ-ing coition, usually start 2 d (Orians 1961a) or 3 d (Collier 1968) before egg-laying and continue to initiation of incubation. Postcopulatory Display, in which male points bill downward and tail upward, has been observed several times, but it is not known if this is a typical behavior (Orians and Christman 1968). Association of mated individuals in successive nesting efforts is unstudied.

Nest-Site Appeasement Display is given during incubation. Female arches wings upward or horizontally; usually directed at mate and accompanied by Female Chatter (see Sounds: vocalizations, above; Collier 1968, Orians and Christman 1968).

Extra-Pair Copulations
Not determined.

Social And Interspecific Behavior

Degree Of Sociality
Highly colonial (Heermann 1853, Mailliard 1900, 1914, Tyler 1907, Dawson 1923, Evermann 1919, Neff 1937, Lack and Emlen 1939). Figure 5 illustrates a freshwater-marsh breeding colony. In the 1930s, 1 colony contained >200,000 nests spread over about 24 ha of cattail marsh (Neff 1937). As many as 100,000 nests were reported in cattail marshes of 4 ha (Orians 1961b, 1980), and a Los Angeles Co., colony in giant cane contained 2,500 adults

in a cross-sectional area of 3.9 x 12.7 m; nests arranged vertically (DeHaven et al. 1975a). After nest predation and other causes of nest losses, colonies sometimes contain only a few active nests (Payne 1969). Areas peripheral to year-round range in Central Valley usually support small colonies (<1,000, often <100, adults; Beedy and Hamilton 1997).

Social in nonbreeding season; forages and roosts in large flocks, sometimes in association with Red-winged Blackbirds and Brewer's Blackbirds (Orians 1961a, Payne 1969). Roost sites in Sacramento and San Joaquin Valleys may contain hundreds of thousands of birds, including Red-winged Blackbirds, Brewer's Blackbirds, Brown-headed Cowbirds (*Molothrus ater*), and European Starlings. Preferred roosting sites are large, heavily vegetated freshwater marshes. One Colusa Co., roost attracted birds foraging from Sacramento River west to foothills of Coast Ranges and for at least 16 km to north and south (Orians 1961a). Arrival at roost closely follows local sunset; lasts about 1.5 h. Morning exodus from roost site starts about 0.5 h before sunrise and lasts from 0.5 h (Orians 1961a) to 1.0 h (ECB).

Play

Not reported.

Nonpredatory Interspecific Interactions

When Tricolored Blackbirds arrive at a marsh, previously established breeding Red-winged and Yellow-headed (*Xanthocephalus xanthocephalus*) blackbirds may be excluded from territories by overwhelming numbers of Tricolored Blackbirds (Orians and Collier 1963, Payne 1969). Male Red-winged Blackbirds whose territories are invaded are initially aggressive toward male Tricolored Blackbirds. Settling birds normally exhibit no interspecific aggression; any male chased by a male Red-winged Blackbird flies short distance until chased again (Orians and Collier 1963). Aggression gradually subsides, and nesting Red-winged Blackbirds may leave central portions of nesting colony, becoming restricted to less heavily vegetated fringes of marshes and nearby upland locations where they continue aggression toward and are ignored by male and female Tricolored Blackbird (Payne 1969). Red-winged Blackbirds effectively maintain territories only if colony numbers of Tricolored Blackbirds are reduced for other reasons (Collier 1959, Orians and Collier 1963), or if they are tending older nestlings when Tricolored Blackbirds arrive (WJH). Roosting of European Starlings is associated with desertion of Tricolored Blackbird colonies (Payne 1969). Flocks of nonbreeding Tricolored Blackbirds and other marsh-roosting birds may descend on active colonies during day and evening (WJH).

Predation

Relationship Of Habitat To Predation

Nesting sites are protected from terrestrial predators by flooded or spiny vegetation. Numerous flooded plant species may serve as nesting sites, especially cattails, bulrushes, and willows. Aquatic sites are subject to increased predation if they become dry during breeding season (Neff 1937). Peripheral nests at both aquatic and terrestrial nesting sites are subject to higher rates of predation and are occupied after interior portions of colony (WJH).

Kinds Of Predators; Manner Of Predation

Diverse predators have been reported at nesting colonies, including wolves (*Canis lupus*) and gray foxes (*Urocyon cinereoargenteus*; Heermann 1853), raccoons (*Procyon lotor*; Cooper 1875), Swainson's Hawks (*Buteo swainsoni*) and Black-crowned Night-Herons (*Nycticorax nycticorax*; Mailliard 1900), skunks (*Mephitis* spp.) and opossums (*Didelphis virginiana*; Evermann 1919), Cooper's Hawks (*Accipiter cooperii*), Burrowing Owls (*Athene cunicularia*), American Crows (*Corvus brachyrhynchos*), and mink (*Mustela vison*; Neff 1937). Other predators are feral cats (*Felis catus*), Northern Harriers, Barn Owls (*Tyto alba*), Short-eared Owls (*Asio flammeus*), and Yellow-billed Magpies (*Pica nuttalli*). Garter snakes (*Thamnophis elegans*), gopher snakes (*Pituophis catenifer*), and western rattlesnakes (*Crotalus viridis*) have been observed in colonies and are suspected predators of nestlings (Payne 1969). King snake (*Lampropeltis getulus*) observed devouring a brood (WJH). Merlins (*Falco columbarius*) are associated with wintering flocks; prey on adults (T. Manolis pers. comm., J. Winter pers. comm.). Observations document losses of nest contents of entire colonies (up to 100% of nests) to Black-crowned Night-Herons and Common Ravens; some large colonies (to 100,000 adults) may lose > 50% of nests to coyotes (*Canis latrans*; WJH).

Response To Predators

The response of a colony of Tricolored Blackbirds to predators, especially American Crows, Common Ravens, and Northern Harriers, is to sit silently. This contrasts strikingly with Red-winged Blackbirds in the same marshes which fly up to attack these predators (Orians and Christman 1968). Mob snakes and humans handling eggs and chicks (Collier 1968); also mob Common Ravens, and Burrowing Owls (WJH). Humans who enter active colonies cause waves of nesting adults to leave colony until older nestlings (6–8 d) are present. Then individuals and sometimes flocks mob intruders (ECB, WJH).

Breeding Sounds

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Tricolored Blackbird
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PASSERIFORMES
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Authors: Beedy, Edward C., and William J. Hamilton, Iii

Breeding

Phenology

Pair And Colony Formation

Males begin singing as early as late Feb; this behavior is correlated with sperm development (Payne 1969). Males sometimes arrive at breeding sites before females, but at some sites both sexes arrive and initiate breeding the same day. Overflight activity during colony settlement phase is mostly by males not on established nesting territories. Males on breeding territories remain out of view below canopy (WJH).

Individual pairs in breeding colonies may initiate nesting synchronously. Even in colonies of up to 50,000–100,000 nests, all first eggs may be laid within 1 wk (Orians 1961a). Some colonies, however, grow through peripheral initiation of nesting over a period of days or weeks at established colonies. Phenology may vary in different parts of colony (Orians 1961a, Collier 1968). Most initial nesting occurs from late Mar to Apr; by late Apr, most birds are associated with breeding colonies, some probably renesting (Fig. 6).

Colonies can occur throughout known range in early Apr, but nesting may be initiated in late Mar in San Joaquin Valley (WJH); May–Jun in rice-growing region of Sacramento Valley and foothill areas (Orians 1961a). Later colonies established north of Sacramento Co. probably are second or later nesting attempts (Hamilton 1998). All breeding usually is completed by late Jul–early Aug (WJH). Autumnal (Sep –Nov) breeding was documented at several different sites between 1959 and 1964, often hatching but seldom fledging young (Orians 1960, Payne 1969). No 1965–1998 observations of fall breeding in Central Valley, but some reported on Point Reyes Peninsula, Marin Co., in 1980s and 1990s (R. Stallcup pers. comm.) where most breeding colonies are established in May or Jun (Shuford 1993).

Nest-Building

Most adults at colony site initiate nesting 12–17 d after prospecting begins (Collier 1968). As colonization of breeding site proceeds, area occupied by nests expands (Tyler 1907) gradually or in synchronous pulses (Collier 1968). At some colonies, expansion ends before all suitable nesting habitat is occupied; at others all suitable habitat is used for nesting (WJH). Additional breeding birds may be recruited to established colony (Orians 1960, 1961b, Payne 1969); later nests may be initiated where advanced, active nests are already present (Orians 1961a).

First Brood Per Season

Egg-laying can begin as early as second day after nest initiation, but typically starts about 4 d after settlement at breeding sites (Collier 1968, Payne 1969). First eggs can be laid at early colonies by mid-Mar, but at most colonies first eggs are laid in late Mar or early Apr (see Fig. 6). One egg laid/d; clutch typically contains 3–4 eggs, but may contain as few as 1–2 or as many as 5 (Payne 1969). In Tulare Co., first egg 19 Mar 1997, 23 Mar 1998, 5 Apr 1999; in Yolo Co. in 1998, eggs hatched as late as 22 Jul, and the last breeding adult left the colony in mid-Aug (WJH). Estimated incubation period 11–12 d (Emlen 1941, Orians

1961b); 11–14 d for interval from laying of last egg to hatching of last hatching egg, 11–12 d (*n* = 12), 12 d (*n* = 10), 13 d (*n* = 5), 14 d (*n* = 1; Payne 1969). From laying of first egg to hatching of first egg, 11 d (*n* = 2), from laying of all marked eggs to their hatching, 11 d (*n* = 6), from laying of last egg to hatching of first egg, 9 d (*n* = 2; WJH).

Clutches take 9–11 d from hatching until oldest nestling will jump from a disturbed nest; undisturbed young fledged 12–14 d after hatching (Payne 1969). A successful nesting cycle for a reproductive pair is 41–45 d, about 10 d less than that of Red-winged Blackbird (Payne 1969). Colony with asynchronous nesting may remain active to >90 d (WJH).

Second/Later Broods Per Season

Nests "are started a day or two before the young of the first brood in that section of the colony leave their nests, and egg-laying begins about four days later" (Emlen 1941: 210). This statement implies an interval between successful broods of as little as 30 d. Such a schedule also was observed in a small, freshwater marsh bordering a rice field in Yolo Co., CA (Fig. 7). Here, 2 synchronized Tricolored Blackbird nesting events occurred with mean interval of 31 d between initiation of broods, compared to a single, relatively asynchronous breeding schedule for Red-winged Blackbirds there (WJH; see Migration: nature of migration in the species, above).

Nest Site

Selection Process

Males establish territories at breeding colonies; females may select nest sites. In marshes (Payne 1969) and weedy, fallow fields (WJH), male territories are established first in densest patches of vegetation. Later nests are built at periphery of first nests in sparser, less preferred nesting areas (Tyler 1907).

Site Characteristics

Requirements for breeding-colony sites are (1) accessible water, (2) protected nesting sites (flooded or surrounded by thorny or spiny vegetation), and (3) suitable foraging area providing adequate insect prey within a few kilometers of nesting colony (Beedy and Hamilton 1997). Nests are bound to upright plant stems from a few centimeters to about 1.5 m above water or ground, rarely on ground (Neff 1937). Nests up to >3 m high in willow canopies (Tyler 1907, ECB); also in valley oak saplings and canopies of small ashes (WJH; see Habitat: breeding range, above).

Nest

Construction Process

Nest construction, exclusively by female, may be initiated from arrival at breeding colony (Neff 1937, Lack and Emlen 1939, Orians and Collier 1963, Payne 1969). Nest construction averaged 4 d: 2–5 d for first nestings; 3–5 d for second (Emlen 1941). Collier (1968) reported 3 d, Payne (1969) 4–7 d. Typical 4-d period: Spends first day building and securing basal platform, second day rounding up sides, third day forming mud and wet vegetation, fourth day lining and completing nest (Emlen 1941).

Structure And Composition Matter

Constructs open-cup nests with lower and outer layers of long leaves (e.g., cattail thatch, annual grasses, entire forbs, stems and leaves) woven tightly around supporting stems. Forms middle layer from mud or algal fibers within shaped, outer structure (Emlen 1941). Anchors nest to several strong stems.

Dimensions

Outside dimensions and shape of nests vary greatly, depending on location and materials used to build nest (Tyler 1907). Outside measurements about 17.8 cm high x 12.7 cm wide, but vertical height may be much greater at cer-tain attachment sites; inside dimensions more uniform, about 7.6 cm high x 7.6 cm wide (Cooper 1875).

Microclimate

Usually situated under dense, overhanging vegetation, preventing most exposure to direct sunlight. Soaking of nests by rain causes mortality of nestlings <6 d old (WJH).

Maintenance Or Reuse Of Nests

Nests are said not to be maintained (Payne 1969), but sometimes are reused in subsequent nesting attempt during same year, not necessarily by same individual (Emlen 1941); most are replaced. In willows and especially nettles, limited number of suitable sites at a given locality sometimes results in nests from successive years being placed on top of nest residue from previous years (WJH).

Nonbreeding Nests
Not constructed.

Eggs

Shape
Typically oval; varies from short oval to long oval. Exceptionally large or small eggs are usually the first of clutch (Dawson 1923).

Size
Mean length 24.38 mm (range 21.38–26.54, *n* = 89 clutches), breadth 17.50 mm (range 16.34–19.00, *n* = 89 clutches; Western Foundation of Vertebrate Zoology [WFVZ]). Bendire (1895) reported means and ranges for 41 eggs, within WFVZ ranges.

Mass
Individual egg mass about 8% of female body mass. Following from WJH. Whole egg mass at 1 colony 2.4–5.0 g/egg (mean 4.25, *n* = 5 three-egg clutches); mean 4.09 (*n* = 16 four-egg clutches); elsewhere mean 3.35 (*n* = 8 four-egg clutches). Smallest total mass of clutches of 3 eggs is 7.0 g, for 4 eggs 11.6 g; largest mass for clutch of 3 eggs 14.6 g, for 4 eggs 18.2 g.

Color
Ground color pale blue to pale olive green, with brown, purple, or black splotches and scrawls, especially on large end (Tyler 1907, Dawson 1923). Amount of dark pigment is highly variable and may appear as wash over most of egg, giving buffy color (Dawson 1923). Egg color, pattern, glossiness, shape, and size usually are constant within clutches; vary among clutches (WJH). Similar to Red-winged Blackbird eggs.

Surface Texture
Smooth; glossiness varies strikingly among clutches (WJH).

Eggshell Thickness
Mean thickness of dried shells, including membranes, 0.11 mm ± 0.006 SD (*n* = 16 eggshells; Grau et al. 1987). Mean empty shell mass 0.21 g (range 0.17–0.29, *n* = 24 clutches, 89 eggshells; WFVZ).

Clutch Size
Clutches of 3–4 eggs predominate (Dawson 1923, Lack and Emlen 1939, Emlen 1941, Bent 1958, Orians 1961a, Payne 1969). Clutches of 2 and 5 eggs observed occasionally (Mailliard 1914, Emlen 1941). Dawson (1923) examined about 3,500 nests and observed a few nests with 6 eggs and 1 with 7 eggs. Clutches of 1 egg said to be incomplete (Payne 1969), but female may incubate a single fertile egg to hatching or near hatching (Payne 1969, WJH). Clutch size may be same throughout season or decline with second or later clutches (Collier 1968, WJH).

Egg-Laying
First egg usually laid the day after nest is completed, occasionally before; 1 egg laid/day for 1–5 d (Emlen 1941, 1985), within 1 h after sunrise (Payne 1969). Egg-laying begins as early as second day after nest initiation, but ordinarily starts on day 4 (Payne 1969). Determinate layer; eggs re-moved from nests are not replaced (Emlen 1941). No nest material added during laying (Payne 1969), or nest may be completed after initial laying (Dawson 1923).

Incubation

Onset Of Broodiness And Incubation In Relation To Laying
Only female broods and incubates (Orians 1961a); usually starts with laying of last egg or on following day (Emlen 1941).

Incubation Patch
Only female has incubation patch. Incubation patch indices, based on 4 subjective classes of dermal edema, were highest during egg-laying and incubation and dropped steeply to a low during nestling and fledgling stages; incubation patch nearly complete early in nest-building stage (Emlen 1985).

Incubation Period
See Phenology: first brood per season, above. All eggs hatch within 24 h (Payne 1969), or hatching may extend to 72 h for some 4-egg clutches (WJH).

Parental Behavior
Female on nest is silent during incubation; active colonies may appear largely deserted. Highly synchronous colonies are particularly inconspicuous; may be overlooked or underestimated during incubation. Close approach by observer induces female to leave nest. Incubating female sometimes flycatches during incubation; flies up to capture small insects 5–20 m above colony (WJH). During incubation, males are absent from colonies during days until eggs hatch, when they return and assist in feeding young (Emlen 1941); roost at colony during incubation (Collier 1968).

Hardiness Of Eggs Against Temperature Stress; Effect Of Egg Neglect
No data.

Hatching

Preliminary Events And Vocalizations
No data.

Shell-Breaking And Emergence
Average time from pipping to hatching in laboratory is about 0.5 h (range 0.25–4.0, n = 39 hatched eggs; Grau et al. 1987).

Parental Assistance And Disposal Of Eggshells
Parents do not assist in hatching. Female removes eggshell by carrying in bill and drops it a short distance from colony (ECB).

Young Birds

Condition At Hatching
Blind, largely naked, and poorly coordinated, but has strong gaping response; mean neonate mass 3.05 g (n = 23; Grau et al. 1987) to <2 g for some hatch-day chicks (WJH). Natal down darker and more grayish than that of Red-winged Blackbird; feathering on all major tracts. Skin orange to pinkish red. Mouth-lining of hatchling pink, with cream-colored commissure; mouth-lining of Red-winged Blackbird hatchling distinctively paler, with white commissure. Whitish egg tooth in Tricolored Blackbird persists for 4 d, embryonic membranes remain attached to umbilicus, which is visible for about 10 d after hatching, and orange yolk in yolk sac is visible through skin for 2 d (Payne 1969).

Growth And Development
From Payne 1969 . Nestlings open eyes on days 5 or 6. Feather follicles appear under skin on day after hatching, and many feather papillae project through skin on day 5. Primaries and secondaries break through sheath-tips on days 7 and 8. Early development is similar to that of Red-winged Blackbird. Detailed study of time of eruption and feather growth of all tracts in 130 Tricolored Blackbirds and 48 Red-winged Blackbirds revealed no species differences, but at $\geqslant$ 10 d, heads of Tricolored Blackbird nestlings are more completely feathered.

Nestlings that weigh <20 g at 8 d usually starve, but few nestlings are in this category (Payne 1969). In Tricolored Blackbird colonies, starving and well-fed nestlings often are together in same nests (Payne 1969). Many last-hatched chicks are never fed (WJH). Proportion of starving nestlings is usually higher than for Red-winged Black-birds (Payne 1969).

Parental Care

Brooding

No information.

Feeding
Both sexes feed nestling. After fledging, remain at colony. Adults continue to feed fledglings up to at least 3 km away from colony until independence. Most early feedings at nests are by female; young at 5 nests fed 9–18 times during 3 h (Payne 1969). Collier (1968) measured foraging trip duration at 4 colonies during 3 yr, found mean female foraging trip interval 15.9 min for 150 trips (range 5–52 min), male trip interval 33.7 min for 50 trips (range 10–107 min). But conditions of observations need consideration because males are notoriously more wary than females near nests. Whether individual male provides food at >1 nest is not known. Female continues to feed young until they fledge, occasionally assisted by male (Payne 1969; see Food habits: diet; Behavior: self-maintenance, above).

Nest Sanitation
Both sexes remove fecal sacs from nest (ECB).

Carrying Of Young
Female carries dead or dying chicks from nest and drops them a short distance from colony (ECB, WJH).

Cooperative Breeding

None.

Brood Parasitism

Brown-headed Cowbird is the only interspecific brood parasite. Nests of Tricolored Blackbird are rarely parasitized (R. Payne pers. comm., WJH), but brood reduction, if any, resulting from nest parasitism not reported. All of 23 cowbird eggs laid in nests of Tricolored Blackbird failed to hatch (Hamilton et al. 1995).

Fledgling Stage

Departure From Nest
Fledges at 11–14 d (Payne 1969), 13–14 d (WJH). Actively vocalize during fledgling stage. By 22 d, wings and tails of fledglings almost completely feathered, lores still featherless (Payne 1969).

Association With Parents Or Other Young
Fledglings from several nests flock together in nest vicinity in first week (Payne 1969). Parents may bait fledglings with grasshoppers and other large food items to induce cross-colony practice flights. Dispersal of fledglings from colonies to water and foraging areas is directed by adults; at times characterized by distinctive, whirling flight high over colonies (WJH). Sometimes long (>300 m) early flights by single individuals to water and associated vegetation accompanied by one or both parents (WJH). Form creches, between colonies and at favorable foraging areas, wherever there is sufficient cover. These assemblages often have the appearance of and have been reported as colonies.

Ability To Get Around, Feed, And Care For Self
Young independent at about 25 d (Payne 1969).

Growth
Mean mass of 3- to 4-wk-old males 46.7 g (range 37.0–54.8, *n* = 10); females of same age, 35.4 g (range 30.0–45.0, *n* = 7; Payne 1969).

Immature Stage

Juveniles roost with adults (Payne 1969). Dispersal reported from natal colony in San Joaquin Valley in first 80 d to large roost 224 km north in Sacramento Valley (DeHaven et al. 1975b).

Demography and Populations Behavior
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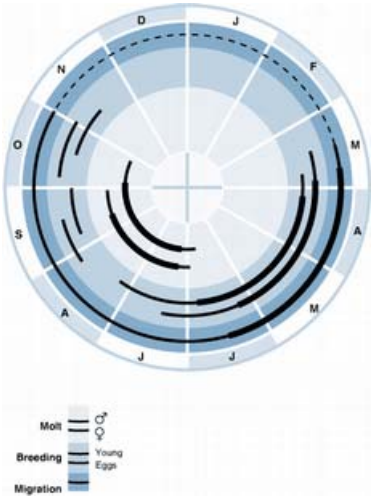
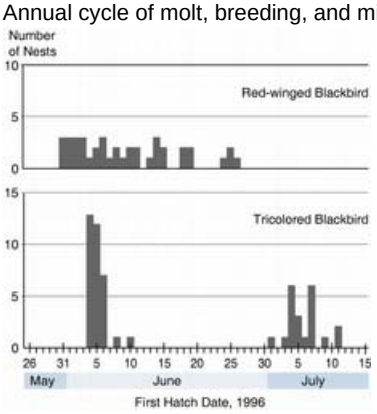
Demography and Populations



Enlarge Figure 6.
Annual cycle of molt, breeding, and migration of Tricolored Blackbird in Central Valley, CA.



Enlarge Figure 7.
Breeding schedules of Tricolored and Red-winged blackbirds

Measures Of Breeding Activity

Age At First Breeding; Intervals Between Breeding
Females breed in first year; males apparently defer breeding until at least 2 yr (Orians 1963, Payne 1969).

Clutch
See Breeding: eggs, above.

Annual And Lifetime Reproductive Success
These parameters cannot be determined without following marked individuals throughout

their lifetimes. There is no information about reproductive success at more than a single nest by any individual. The number of nestlings fledged, measured as number of nestlings present 8 d after the first chick hatched, ranged from 1 to 4 in successful nests. The mean number of young fledged in successful nests, per colony, for colonies sampled at 20 or more successful nests, ranged from 1.0 to 3.4 at 47 colonies. In addition, some colonies failed to fledge any chicks (WJH, L. Cook pers. comm.).

Number Of Broods Normally Reared Per Season

From Hamilton 1998 . May breed 2 or more times/yr. At some colonies a second wave of nesting follows fledging of the initial cohort, sometimes as great as the initial effort, but usually a minor fraction of it. On basis of schedule of breeding throughout range, additional nesting effort takes place at alternative geographic locations.

Life Span And Survivorship

Banding studies, summarized by Neff (1942) and DeHaven and Neff (1973), indicated life span to at least 12 yr; Kennard (1975) almost 13 yr. No annual survivorship studies; available banding data are inadequate to determine annual survivorship and evaluate conservation strategies.

Disease And Body Parasites

Diseases

None reported.

Body Parasites

In some years, many nestlings have mites (WJH).

Causes Of Mortality

Exposure

High nestling mortality reported after severe or prolonged storms (Cook 1996). Females occasionally shelter nests during rain; at a Colusa Co. colony in 1994, 17 of 2,040 nests examined postnesting contained a dead female covering her chicks or eggs (WJH). In 1998, a steady 66-km/h wind knocked down about 6% of all active nests at a large cattail marsh colony in Colusa Co. Rainfall can destroy from a few to all nests in a colony, depending on developmental stage of nestlings and severity of storms. Other effects of severe storms include blowdown of cattails, silage, and other plants supporting nests (WJH). Responses to drought include failure to breed (Collier 1968), abandonment of active colonies, and low reproductive success (Orians and Collier 1963).

Predation

Predation is a major cause of nest failures ; can be 100% for entire colonies in Central Valley, CA (Beedy and Hayworth 1992, Hamilton 1998; see Behavior: predation, above).

Starvation And Infanticide

In 5-yr study throughout California, most broods were reduced via starvation (Hamilton et al. 1995). Brood reduction by females includes infanticide (removal of living chicks from nests). Most eggs hatch, but >3 nestlings in nests uncommon before fledging, rarely 4 if abundant food available, but 1–3 is the usual fledging cohort (WJH).

Competition With Other Species

In recent years, Great-tailed Grackles (*Quiscalus mexicanus*) nested near and within several s. California colonies; they are aggressive toward nesting Tricolored Blackbirds and may be a serious future threat (WJH; see Behavior: social and interspecific behavior, above).

Range

Initial Dispersal From Natal Site

Of 33,058 birds banded as nestlings, 33 adults were recovered by shooting at breeding colonies. Only 39% of recoveries were within 16 km of natal colonies (DeHaven et al. 1975b).

Fidelity To Breeding Site And Winter Home Range

Itinerant breeding suggests that this species could be philopatric to >1 site (Hamilton 1998).

Breeding colonies may exhibit annual site fidelity if essential resources, including adequate nesting sites, water, and suitable foraging habitats, persist in subsequent years. Nineteen of 72 total colony locations (1991–1994) were active the following year (Hamilton et al. 1995). An additional 11 colonies (15% of total) located in 1994 were active at same site in either 1992 or 1993, but not both years. Of 75 colonies active in late Apr 1997, 19 were within 0.5 km of sites also active in 1994 (Beedy and Hamilton 1997).

Dispersal From Breeding Colony

See Migration: nature of migration in the species, above. Payne (1969) banded a female, probably initiating incubation, and recaptured her on 4 eggs at a nearby (1.4 km) colony 15 d later. From histological examination and brood patch characteristics he estimated that no more than 7 d elapsed between loss of her clutch and laying of the first egg in a new nest at another marsh.

Home Range

Range widely in flocks to >15 km from active colony sites (WJH).

Population Status

Numbers

Few nineteenth-century accounts exist of Tricolored Blackbirds in formerly extensive marshland and grassland habitats. Heermann (1859: 53) described fall flocks of thousands in Shasta region of California, and saw a wintering flock in Suisun Valley, Solano Co., “numbering so many thousands as to darken the sky for some distance by their masses.” Belding (1890) observed an “immense” colony near Stockton, San Joaquin Co. According to notes of J. G. Cooper, Tricolored Blackbirds were “the most abundant species near San Diego and Los Angeles, and not rare at Santa Barbara” (Baird 1870: 266, Baird et al. 1874: 166). Grinnell (1898) reported them present in “considerable numbers” throughout the year in Los Angeles Co.

Published and unpublished accounts of historical breeding summarized by Dawson (1923), Neff (1937), Grinnell and Miller (1944), and Beedy et al. (1991). Systematic, rangewide surveys of population status and distribution, conducted by Neff (1937, 1942), estimated >700,000 adults/year (1934) in just 8 counties. During 5-yr interval (1931–1936), breeding Tricolored Blackbirds were found in 26 California counties, including 1 colony in Glenn Co. containing >200,000 nests (about 300,000 adults) covering 24 ha, and several others in Sacramento and Butte Cos. containing >100,000 nests each (Neff 1937). Orians (1961a) observed colonies of up to 100,000 adults in both Colusa and Yolo Cos., but did not attempt to survey entire range of the species.

In 1994, 94% of all breeding adults observed in a California statewide survey were in Central Valley (Hamilton 1998). Combined results from population surveys conducted throughout California by Hamilton et al. (1995) and volunteers sponsored by U.S. Fish and Wildlife Service (USFWS), California Department of Fish and Game (CDFG), and National Audubon Society estimated the 1994 population at 370,000 (±15%) breeding adults. Survey of similar coverage and intensity, performed by same participants, estimated 1997 population at 233,000 (±15%) adults (Beedy and Hamilton 1997).

Activity during early stages of colony settlement may give erroneous impression of local nesting densities because more males are present at some colonies initially than remain to nest (WJH). Males on breeding territories may remain out of view below canopy. Number of active nests per unit area is far better indicator of local abundance than number of singing males (Neff 1937, Hamilton et al. 1995).

Trends

DeHaven et al. (1975a) conducted population surveys and banding studies in Central Valley from 1969 through 1972; the reported average of about 133,000 individuals/yr and estimated overall population had declined by >50% from Neff’s (1937) estimate.

Comparison of results from 1994 to 1997 indicated 37% decline in population during this 3-yr interval, with geographic range unchanged since 1930s (Beedy and Hamilton 1997). Population declines were most apparent in Central Valley. Although Tricolored Blackbirds were once abundant in s. California (Baird 1870), Willet (1933) described them as rare throughout this former range, except in some sections of San Diego Co. Recently (1997)

observed populations in s. California consist of about 43,000 breeding adults (Beedy and Hamilton 1997). More than half of all observed nesting efforts throughout the distribution of this species in 1990s occurred in a few, large colonies (>5,000 nests; Beedy and Hamilton 1997, Hamilton 1998).

Declines can be attributed to loss of nesting and foraging habitat throughout the breeding distribution of this species in the Central Valley of California and in s. California.

Population Regulation

Population regulation is determined by processes extending over range of species. Tricolored Blackbirds exhibit limited philopatry (DeHaven et al. 1975b), and entire population north of s. California probably is a single metapopulation (Hamilton 1998), freely exchanging individuals throughout alternative colony sites in n. California portion of their geographic range. Hence, number of individuals in this metapopulation depends on survival of fledglings and adults throughout the region. Reproductive success is low in most large cattail marshes because of predation, and many agricultural field colonies are lost during harvesting (WJH); reproductive success is high in Himalayan blackberry habitats and isolated cattail marshes, but varies greatly across these habitats (Hamilton et al. 1995, Cook 1996). Those upland habitats that consistently support high reproductive success (Cook 1996) are currently (1999) being lost at alarming rates as tens of thousands of acres are converted to vineyards, orchards, and urban development throughout the Central Valley.

Orians (1961a) and Payne (1969) considered possible regulation of number of breeding birds in colonies by social behavior. Great variation in numbers of breeding birds in different colonies suggested no upper or lower limit to local population size. At colony settlement, far more males than will successfully breed often arrive at colony sites (Orians 1961a, Payne 1969). Departure of some settlers was interpreted as response to local relative abundance of insect food, as determined by frequent prospecting flights to foraging fields (Orians 1961a). However, male territorial behavior affects density within breeding colonies, and males at periphery of colonies may be excluded from breeding opportunities because no females settle there (WJH). At some colonies, all suitable nest sites may be occupied (Collier 1968, WJH); at others, large areas of similar habitat are not colonized. Subsequent waves of settlement in areas where nests are already established may result in 2 or more waves of fledging. At some Himalayan blackberry and giant-cane colonies, settlements become highly compressed; DeHaven et al. (1975a) found 2,500 birds nesting in a space 12.8 x 3.9 m at Del Sur, Los Angeles Co.

Conservation and Management Breeding

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Conservation and Management

Effects Of Human Activity

Degradation Of Habitat

Greatest effects of human activity are related to habitat loss and alteration. Virtually all suitable habitats in the form of perennial grasslands, marshlands, and riparian woodlands in Central Valley once supported foraging and nesting Tricolored Blackbirds. Most of Central Valley has been converted by agriculture and urbanization (Frayer et al. 1989, Wilen and Frayer 1990, Kreissman 1991). In some places, most historical breeding and foraging habitats have been eliminated, and currently there is little or no breeding where large colonies once existed (Orians 1961a, Beedy et al. 1991, Beedy and Hamilton 1997).

Harvesting, Plowing, And Burning

Nests and nest contents in cereal crops and silage often are destroyed by agricultural operations (Bent 1958, Collier 1968, Hamilton et al. 1995). Harvesting of silage and plowing of weedy fields currently are the most common reasons for destruction of nesting colonies. Large colonies (>50,000 nests) in San Joaquin Valley have been lost in 1990s (WJH). Spring burning and disking of marshes at Central Valley ranches and duck clubs decreases number of suitable early-spring breeding sites, resulting in temporary loss of habitat in some areas (Collier 1968, Payne 1969).

Shooting, Trapping, And Poisoning

From nineteenth century until 1930s, market hunting was a major mortality factor; >300,000 Tricolored and Red-winged blackbirds were marketed from Sacramento Valley during a 5-yr interval (Neff 1937). McCabe (1932) described strychnine poisoning of 30,000 breeding Tricolored Blackbirds. Poisoning to regulate numbers of blackbirds preying on Central Valley crops, especially rice, was a major source of adult mortality (Neff 1942). This practice continued until 1960s. Improved harvesting methods, earlier-ripening rice varieties, and reduced blackbird populations resulted in fewer reports of crop damage by blackbirds. No control programs currently are operating (J. Clark pers. comm.).

Pesticides And Other Contaminants/Toxics

During 1986, Beedy and Hayworth (1992) observed almost complete nesting failure of large colony (about 47,000 adults) at Kesterson Reservoir, Merced Co., an area contaminated by selenium deposited from agricultural drainage water. At a Kern Co. colony, all eggs sprayed with mosquito abatement oil failed to hatch (WJH). Hosea (1986) attributed loss of at least 2 colonies to aerial herbicide applications.

Direct Human/Research Impacts

Periodic, cautious entry into colonies does not cause abandonment (WJH). In a colony of >40,000 nests, 22 of 23 nests successfully fledged following daily weighing for 8 d at each nest of all nestlings (R. Bowen pers. comm.). Beedy and Hayworth (1992) observed localized abandonment of active nests in Himalayan blackberries and cattails when colonies were entered for several hours to collect eggs.

Management

Conservation Status

Formerly candidate (cate-gory 2) for federal listing as either Threatened or Endangered by USFWS (59 Federal Register [219]: 58990). Now included on informal list of Species of Concern (USFWS 1995). Considered Bird Species of Special Concern in California by CDFG (K. Hunting pers. comm.).

Measures Proposed And Taken

In 1991, Yolo Audubon Society petitioned CDFG to list this species as Endangered under state Endangered Species Act, on basis of findings of Beedy et al. (1991). Petition was withdrawn in 1992 after 2 breeding seasons of intensive fieldwork, revis-ing estimates of current breeding population upward.

USFWS and CDFG recently supported preparation of management guidelines (Beedy and Hamilton 1997). Management objectives include maintaining a viable, self-sustaining population throughout current geographic range, avoiding losses of colonies and their associated habitats, increasing breeding population on suitable public and private lands managed for this species, and enhancing public awareness and support for protection of habitat and active colonies. Tricolored Blackbird should be considered in regional USFWS Habitat Conservation Plans, other multispecies conservation plans, and ongoing private land habitat conservation programs.

Effectiveness Of Measures

In 1993 and 1994, CDFG and USFWS purchased portions of crops to preserve several large colonies in Kings, Fresno, and Tulare Cos. These actions and participation by landowners (e.g., delaying harvest to protect active nesting colonies) resulted in addition of an estimated 37,000 and 44,000 first-year adults to 1994 and 1995 breeding seasons, respectively (WJH).

Appearance Demography and Populations

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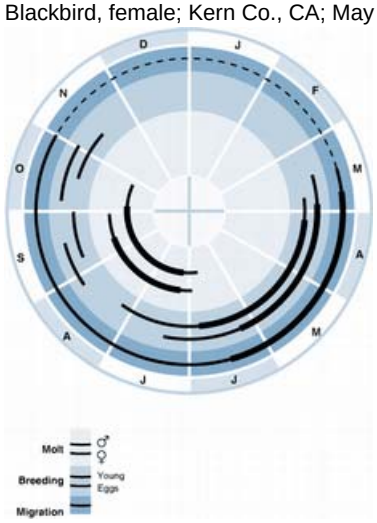
Articles

Appearance

Enlarge Tricolored Blackbird, male; Kern Co., CA; May

Enlarge Tricolored Blackbird, female; Kern Co., CA; May



Enlarge Figure 6. Annual cycle of molt, breeding, and migration of Tricolored Blackbird in Central Valley, CA.

Molts And Plumages

Because of wide variation of nesting times within range of Tricolored Blackbird, molting schedules vary considerably from south to north (DeHaven 1975). Molt patterns are similar to those of Red-winged Blackbird (Payne 1969, Meanley and Bond 1970, Yasukawa and

Searcy 1995).

Hatchlings
Recently hatched birds largely naked, but with a sparse covering of grayish down; feathering on all major feather tracts (Payne 1969).

Juvenal Plumage
Early development similar to that of Red-winged Blackbird. Feather follicles appear under skin on day after hatching, and many feather papillae project through skin on day 5. Primaries and secondaries break through sheath-tips on days 7 and 8. For additional information Prejuvenal molt see Payne (1969).

Juvenal plumage (Apr–Aug) resembles Basic I female, but much paler gray and buff. Sexes simi-lar (Pyle 1997).

Basic I Plumage
Prebasic I (Postjuvenal) molt is incomplete to complete; usually includes all contour feathers and all flight-feathers except possibly some to all greater underwing-coverts, and possibly a few middle secondaries (among S3–S6). Species occasionally attempts breeding in fall, and fledglings from such attempts might retain flight-feathers until second Prebasic molt (DeHaven 1975, Pyle 1997). Molt usually begins early Jul and lasts 60–70 d. Alar and ventral tracts usually molt first; caudal and capital tracts are among the last contour feathers to molt (DeHaven 1975).

Male. Pale black to grayish overall. Crown-, nape-, and back-feathers heavily tipped with smoke gray; breast-feathers heavily tipped with buffy brown. Lesser upper wing-coverts often dark scarlet orange, but may be pale scarlet orange or brownish red in some individuals, usually moderately flecked with black feathers, or may be nearly all black or lacking almost any trace of black. Median upper wing-coverts also variable; mixture of cream and black feathers with cream tips is most common, but a few males (especially those with brownish-red epaulets) have mostly cream feathers. Upper portions of greater upper wing-coverts tipped with smoke gray. Occasionally, outer 3 or 4 primaries are strongly edged with smoke gray (DeHaven 1975, Pyle 1997).

Female. Molt sequence similar to that of male. Overall body color of female is dark blackish gray above, dark gray below. Feathers of back, nape, and crown heavily tipped with buffy brown. Median-and greater upper wing-coverts tipped with smoke gray, creating 2 indistinct wing-bars. Throat-feathers strongly edged with light pale gray, fading to smoke gray on upper abdomen. Females may show brownish red on lesser upper wing-coverts. Some or all underwing-coverts often pale brownish (retained Juvenal feathers), contrasting markedly with adjacent dark-brown feathers (DeHaven 1975, Pyle 1997).

Alternate I Plumage
Prealternate I molt partial and limited, includes some or all lesser coverts, but not greater coverts or flight feathers (Pyle 1997).

Male. By spring, feathers of head, nape, back, and breast usually worn, and most birds appear uniformly dark blackish gray; a few feathers retain smoke-gray or buffy-brown tips. Tips of primaries and rectrices also worn in this plumage, fading from dark fuscous of fall to a browner fuscous that shows best when wings are folded against body. Lesser upper wing-coverts similar to fall aspect, but may appear brighter when contrasted with body-feathers that have lost most of their streaking. Median upper wing-coverts fade from cream to shades of white or pale gray. Underwing is same as in Basic I plumage, uniformly light blackish gray and contrasting with darker, more evenly colored upper wings and body (DeHaven 1975). Male usually does not breed in this plumage.

Female. Compared to Basic I plumage, most pale edgings of back-feathers, greater and median upper wing-coverts are lost during this time, making birds a uniform, blackish gray. Crown and nape retain much brown on feather-tips. As in male, tips of primaries and some rectrices appear browner than in fall. Breast-feathers often lose some pale tipping and appear uniformly blackish gray-fuscous (DeHaven 1975). Female usually breeds in spring of second calendar year.

Definitive Basic Plumage

Definitive Prebasic molt complete; usually begins in mid-Jun, lasts 60–70 d, usually complete by mid-Sep; extremes mid-Jun–early Oct (Payne 1969). Male and female initiate molt on same schedule, but more males than females are in molt through Sep; molt delayed in late-season breeders (Payne 1969; Fig. 6).

Male. Plumage entirely black (except for wing), with bluish hue; feathers edged light gray when fresh (Aug–Mar). Lesser upperwing-coverts dark brownish red to buffy orange, and without black flecks. Median upper wing-coverts buffy whitish (Aug–Feb) without black flecks (Pyle 1997). Body sheen of older birds is somewhat more bluish than Alternate I plumage (DeHaven 1975).

Female. Female in Definitive Basic plumage is marginally distinguishable from blackish-gray immature female in Basic I plumage; older birds usually have more brownish-red feathers or feather edgings mixed with smoke gray on median upper wing-coverts (DeHaven 1975). Lesser upper wing-coverts with reddish brown (little or no reddish on hatch-year or second-year females); underwing-coverts blackish brown, with little or no contrast to adjacent feathers (Pyle 1997). When present in fall, feather edgings are various shades of smoke gray or buffy brown. Undertail-coverts are very dark, usually with distinct pale-gray edgings with diffuse streaking blending to black; central back- and nape-feathers lack chestnut edgings.

Definitive Alternate Plumage

Definitive Prealternate molt presumably includes lesser upper wing-coverts as in Prealternate I molt, but may be absent or very limited; occurs Jan–Apr (Pyle 1997).

Male. Similar to Definitive Basic plumage but worn contour feathers uniformly black (Apr–Jul), and median upper wing-coverts are white (Feb–Jul) without black flecks (DeHaven 1975, Pyle 1997). By spring, primary-tips wear to various shades of brownish, but less distinctive than those of males in Alternate I plumage.

Female. Similar to Definitive Basic plumage. Most females retain reddish-brown tips on lesser upper wing-coverts into spring, forming small, but distinct shoulder-patch (DeHaven 1975).

Bare Parts

Bill And Gape

Male in Definitive Basic plumage has black bill. Male in Basic I plumage has bill similar to that of female: dark brown above and lighter brown below. Gape bright red.

Iris

Dark brown in both sexes; not known to change with age.

Legs And Feet

Black on male; dark brown or dusky on female.

Measurements Conservation and Management

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Measurements

Linear

Bill Length And Depth
Overall, bill significantly longer and narrower than those of most Red-winged Blackbird subspecies (Orians 1961a, Pyle 1997); however, Kern Red-winged Blackbirds (*A. p. aciculatus*) have longer, deeper bills than Tricolored Blackbirds. Measurements are given in Table 3 .

Wing Length
In Tricolored Blackbirds P9 (outermost) is always longer than P6 and in Red-winged Blackbirds P9 is always shorter than P6. This difference in wing structure occurs in juveniles and adults of both sexes (Mailliard 1910, Payne 1969, Pyle 1997).

Tail Length
See Table 3 .

Tarsus Length
See Table 3 .

Mass

Adult male mass shows little seasonal variation between Jan and Jun (range 66–69 g, *n* = 139); no significant changes in spring breeding season, but significantly lower during Oct breeding than in preceding 2 mo (Payne 1969). In Jul, when birds are in early stages of molt, mean mass significantly lower than in Feb. Slight increase in Aug, when feeding on new crop of rice. Deposition and loss of subcutaneous fat from season to season accounts for some of gain and loss of mass, averaging heavier in winter than during breeding season (Payne 1969).

Adult female annual cycle of mass similar to that of male between Jan and Jun (range 43–48 g, *n* = 129; Payne 1969). Mean mass highest in Jan; declines before breeding season. Higher mass in Apr–May reflects increased mass of ovaries and oviducts of laying birds. Nesting-female mass showed sig-nificant downward trend from nest-building to fledging (49–43 g, *n* = 80); most mass loss occurred during nestling and fledgling stage (Emlen 1985).

Priorities for Future Research Appearance

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Priorities for Future Research

Many basic aspects of Tricolored Blackbird biology are unknown. No study has evaluated the use and depletion of food resources near breeding colonies nor are there measures of the extent and character of foraging habitats near colonies. Habitat selection mechanisms and the relative value of alternative foraging habitats to breeding birds requires further study. Such information is essential for establishing management guidelines.

Annual adult and first-year survival remain unmeasured. Long-term studies with marked individuals from several breeding colonies could develop a greater understanding of survivorship and individual fidelity to breeding sites. Survivorship data are essential for interpreting reproductive success and for developing life tables to examine population trends.

The breeding biology of males is largely unknown. Estimates of the degree of polygyny range from 1 to 4 females/male. These estimates are based on 12 banded birds. Males may provision only a single nest or all nests in their territories. Participation of first-year males in breeding is uncertain, and their locations during the breeding season have not been studied. The relationship of territoriality to the breeding density of males and females is known only in a preliminary manner; female territoriality is unstudied.

Other key unreported information includes (1) the taxonomic status of the southern California population, (2) the site fidelity and philopatric status of coastal and other small breeding populations in peripheral portions of the range, (3) the relationship of itinerant breeding to annual reproductive success, (4) social organization and behavior when high-density settlements occur and when subsequent waves of settlers enter already active colonies, (5) analysis of brood reduction mechanisms and their relationship to food, (6) the effects of land-use characteristics on reproductive success within colonies, (7) individual behavior and population responses to predators, and (8) the distribution, resource utilization, and survival of wintering birds.

Acknowledgments Measurements

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Acknowledgments

We are deeply indebted to the earlier serious investigators of Tricolored Blackbirds: Johnson Neff (1931–1936), Gerald Collier (1953–1959), Gordon Orians (1957–1960), Robert Payne (1961–1965), and Richard DeHaven (1965–1975). We thank Donald Kroodsma, Robert Payne, Alan Poole, and Susan Sanders for valuable insights and comments. Keith Russell revised the sections on Distinguishing Characteristics, Distribution, and Appearance. Rhys Bowen, Lizette Cook, and Lily Starling contributed important data and observations. Kevin Hunting (California Department of Fish and Game) and Tara Zimmerman (U.S. Fish and Wildlife Service) provided financial support for field studies. Anne Forcella assisted with data analysis and provided editorial assistance. Susan E. Davis also edited the manuscript. Graphics were prepared by Timothy Messick and Christy Anderson. Tim Manolis created the artwork. Photo by Arnold Small.

About the Author(s) Priorities for Future Research

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About the Author(s)

Edward C. (Ted) Beedy received his B.S., M.S., and Ph.D. from the University of California, Davis. He has studied Tricolored Blackbirds in the Central Valley for more than 10 years. He has been active in efforts to conserve this species and Central Valley wetland habitats for this unique species and other wildlife. He is currently a Senior Wildlife Biologist and Associate Principal at the environmental firm of Jones & Stokes Associates. Current address: Jones & Stokes Associates, Inc., 2600 V Street, Sacramento, CA 95818-1914. E-mail: tbeedy@jps.net.

William J. Hamilton III received his B.S. at Cornell University and his Ph.D. at the University of California, Berkeley. He is an Emeritus Professor of ecology at the University of California, Davis. He has spent the last 7 spring and summer seasons evaluating factors influencing the distribution and abundance of breeding Tricolored Blackbirds, especially in agricultural areas of the Central Valley. He has worked actively with Beedy on Tricolored Blackbird conservation issues. Current address: P. O. Box 927, Winters, CA 95694. E-mail: wjhamilton@ucdavis.edu.

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Figure Gallery

Figure 1. Distribution of the Tricolored Blackbird.

Figure 2. Tricolored Blackbird colonies in CA.

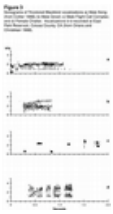
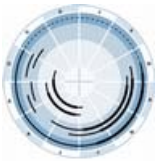


Figure 3. Vocalizations of the Tricolored Blackbird.

Figure 4. Song spread of male Tricolored Blackbird

Figure 5. Tricolored Blackbird breeding colony at a freshwater marsh.



Enlarge

Figure 6. Annual cycle of molt, breeding, and migration of Tricolored Blackbird in Central Valley, CA.

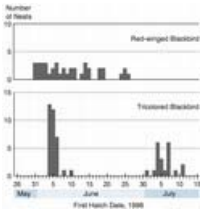


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Figure 7. Breeding schedules of Tricolored and Red-winged blackbirds

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Data Tables and Appendices

Table 1.

Wing measurements (cm) and wing areas (cm2) of Tricolored Blackbirds compared with Red-winged Blackbirds (Orians 1961a). Sample sizes courtesy G. H. Orians. Data shown as mean ± SD (n).

Table 2.

Wing loading of Tricolored Blackbird and Red-winged Blackbird in grams/cm2 of wing surface. This table also provides some weight information (Orians 1961a). Sample size courtesy G. H. Orians.

Table 3.

Linear measurements (mm) of Tricolored Blackbird morphological characteristics, from Orians (1961a). Sample sizes provided courtesy G. H. Orians. Data shown as mean ± SD (range, n).

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	Tricolored Blackbird	Red-winged Blackbird
Wing spread		
Male	38.4 ± 0.48 (46)	39.1 ± 0.76 (32)
Female	33.5 ± 0.69 (33)	33.5 ± 0.58 (13)
Wing width		
Male	8.9 ± 0.25 (46)	9.9 ± 0.28 (32)
Female	7.9 ± 0.30 (33)	8.1 ± 0.25 (13)
Wing area		
Male	254.2 ± 13.22 (31)	293.6 ± 13.23 (22)
Female	191.0 ± 8.45 (22)	202.6 ± 7.23 (12)

Tricolored Blackbird

***Agelaius tricolor* | *Order* PASSERIFORMES – *Family* ICTERIDAE**

Table 1.

Wing measurements (cm) and wing areas (cm2) of Tricolored Blackbirds compared with Red-winged Blackbirds (Orians 1961a). Sample sizes courtesy G. H. Orians. Data shown as mean ± SD (n).

- Orians 1961a

Close

	Sample size	Wing area cm ^{2}	Mean mass (g)	Wing load grams/cm ^{2}
Tricolored Blackbird				
Male	31	254.2	63.3	0.25
Female	23	191.0	46.5	0.24
Redwinged Blackbird				
Male	22	293.5	66.1	0.23
Female	12	202.6	42.4	0.21

Tricolored Blackbird

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Table 2.

Wing loading of Tricolored Blackbird and Red-winged Blackbird in grams/cm2 of wing surface. This table also provides some weight information (Orians 1961a). Sample size courtesy G. H. Orians.

- Orians 1961a

Close

Culmen	
Male	24.5 ± 1.0 (22.4–27.3, 41)
Female	21.8 ± 1.0 (19.8–24.5, 46)
Bill depth	
Male	8.0 ± 0.3 (7.5–8.5, 41)
Female	6.9 ± 0.8 (6.3–8.0, 46)
Wing	
Male	120.8 ± 2.1 (115.5–125.2, 41)
Female	105.2 ± 2.1 (102.2–111.2, 46)
Tail	
Male	81.1 ± 3.1 (75.4–89.7, 41)
Female	68.9 ± 2.3 (64.0–78.6, 46)
Tarsus	
Male	28.1 ± 1.0 (26.6–30.4, 41)
Female	25.2 ± 0.8 (23.1–26.8, 46)

Tricolored Blackbird

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Table 3.

Linear measurements (mm) of Tricolored Blackbird morphological characteristics, from Orians (1961a). Sample sizes provided courtesy G. H. Orians. Data shown as mean ± SD (range, n).

- 1961a

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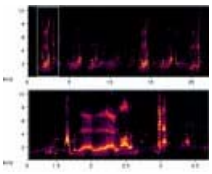

"Kwik," "cup," "cheewit," and male song ("ker-aaah, ker-ah-oow") of a Tricolored Blackbird.

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Photo Gallery

Tricolored Blackbird, male; Kern Co., CA; May

Tricolored Blackbird, female; Kern Co., CA; May

Adult male Tricolored Blackbird, Moonglow Dairy Farm, Monterey, California, 1 April 2007.

Adult male Tricolored Blackbird, Moonglow Dairy Farm, Monterey, California, 1 April 2007.

Adult female Tricolored Blackbird, Moonglow Dairy Farm, Monterey, California, 1 April

2007.

Presumed juvenile Tricolored Blackbird, Moonglow Dairy Farm, Monterey, California, 2 July 2007.

Presumed juvenile Tricolored Blackbird, Moonglow Dairy Farm, Monterey, California, 2 July 2007.

Adult male Tricolored Blackbird, Moonglow Dairy Farm, Monterey, California, 14 September 2007.

Adult male Tricolored Blackbird, Moonglow Dairy Farm, Monterey, California, 14 September 2007.

Presumed juvenile Tricolored Blackbird molting, Moonglow Dairy Farm, Monterey, California 8 August 2007.

Presumed juvenile Tricolored Blackbird molting, Moonglow Dairy Farm, Monterey, California 8 August 2007.

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