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BIOLOGY OF THE YELLOW-SHOULDERED BLACKBIRD—*AGELAIUS* ON A TROPICAL ISLAND

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BIOLOGY OF THE YELLOW-SHOULDERED BLACKBIRD—*AGELAIUS* ON A TROPICAL ISLAND

William Post[1]

Synopsis: The Yellow-shouldered Blackbird (*Agelaius xanthomus*) nests in mangroves, scattered trees in pastures, and in suburbs. In the most frequently used habitat, mangroves, birds use isolated cays or scattered trees in salt pans. Nests are either open cups placed on branches or are built in cavities.

The breeding season starts with the spring rains in April and May. These rains stimulate new vegetative growth, which may result in an increase in the numbers of insects on which the blackbirds feed. Most young are in the nest during the relatively dry summer period and fledge before the fall rains begin in September or October.

Pairs form 6-10 weeks before egg laying within groups of birds that visit nesting areas of previous years. During the mate acquisition period males display at old nest sites, which the females visit. Males follow and guard females. The extended period of affiliation before mating may be advantageous to the female if it assures male loyalty, as male parental care is important in a species with such widely separated feeding and nesting sites. All males and females studied during a 2-year period were monogamous.

The average clutch is three eggs. The incubation period is 12.5 days, and hatching is asynchronous. Only females incubate and brood, but some males deliver food to their incubating mates. Males guard the nest when the female is away. Both sexes deliver food at the same rate. Delivery rates are like those of North Temperate icterids. The growth pattern of *A. xanthomus* is the same as that of Red-winged Blackbirds (*A. phoeniceus*). After fledging, young follow adults for at least 24 days.

Nest success (proportion of nests producing at least one young) was 46% (54 nests). Nests on offshore cays had higher success than those in adjacent mainland areas, because they were parasitized less by Shiny Cowbirds (*Molothrus bonariensis*). Pairs nesting in cavities fledged about three times as many young per nest as did those nesting in the open. Mortality during the egg stage outweighed that during the nestling stage, mainly because of disruption by cowbirds.

The average distance between nests in colonies was 16 m. Two pairs occasionally nested in the same tree. Nesting aggregations seemed to result from active attraction among birds, rather than common response to limited nest sites. Communal mobbing was a conspicuous behavior of the nesting groups. The space around the nest consistently defended against conspecifics and other species was small, extending 3 m in any direction. Males defended the nest vicinity more often than females.

The species forages mainly in the upper strata of trees, obtaining arthropods by probing and gleaning epiphytes, leaf clusters, and the surfaces of branches and trunks. This use of foraging behaviors more typical of orioles and woodpeckers may reflect the scarcity of competitors in habitats where the blackbirds are common, in combination with lack of suitable ground-foraging sites (marshes) in Puerto Rico. Most food brought to nestlings is gathered up to 2 km from nests, but commuting pairs do not follow each other to scattered foraging sites.

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The Yellow-shouldered Blackbird feeds on the ground as do other *Agelaius*, but unlike its marsh-dwelling congeners, when ground-feeding it gathers mostly vegetable material rather than arthropods. When delivering to nests, adults carry more than one item in their beaks. They also regurgitate both plant material and arthropods to young.

The sex ratio is equal, although winter feeding flocks often held significantly larger proportions of one sex. This difference is due to the greater feeding site specialization of females, perhaps related to male dominance at some feeding stations.

Annual survival of adults was 82.4%, and of juveniles 65.5%. No difference was found between the annual survival of males and females. The individuals considered were permanent residents in the study area, although they occupied large home ranges, with an average distance of 1.5 km between successive recaptures.

The species uses at least 26 distinct displays and vocalizations, a larger repertoire than described for other monogamous icterids. Unlike polygamous icterids, *A. xanthomus* has few intersexual differences in the quantity or quality of its displays. Each sex has only one unique display, and the remaining displays and vocalizations are shared by both. Structural characteristics of the action patterns and sounds of *A. xanthomus* make them useful for transmitting information over short distances, in competition with the displays of close neighbors.

SINOPSIS: La mariquita o tordo de espaldas amarillas (*Agelaius xanthomus*) anida en manglares, árboles aislados, en pastizales y en zonas suburbanas. Los manglares son su habitat preferido y ahí estos pájaros utilizan cayos aislados dispersos en bandejones de sal. Los nidos pueden ser copas abiertas colocadas sobre ramas o pueden ser contenidos dentro cavidades.

La estación de reproducción comienza con las lluvias de primavera en Abril y Mayo. Estas lluvias estimulan nuevo crecimiento vegetativo, que puede resultar en un aumento en el numero de insectos que constituyen alimento para los tordos. La mayoría de los jovenes permanecen en el nido durante el período relativamente seco del verano y obtienen su plumaje adulto antes de las lluvias de otoño en Septiembre u Octubre.

Las parejas se forman entre 6 a 10 semanas antes de la puesta de huevos, entre grupos de pájaros que visitan las áreas de anidaje de años anteriores. Durante el período de adquisición de parejas los machos se exhiben en los antiguos sitios de anidación, que las hembras visitaron. Los machos siguen y cuidan de las hembras. El extenso período de afiliación antes del apareamiento podría ser ventajoso para la hembra si se asegura la lealtad del macho, ya que el cuidado por parte del macho parental as importante en especies con lugares de alimentación y de anidación tan ampliamente separados. Todos los machos y hembras estudiados en un periodo de 2 años fueron monógamos.

La camada promedio es de 3 huevos. El periodo de incubaciónes 12.5 días y el rompimiento del cascarón es asincrónico. Sólo hembras incuban y cuidan la camada pero algunos machos llevan alimento a su pareja mientras ésta incuba. Los machos cuidan el nido cuando la hembra no está. Ambos sexos acarrean alimento en la misma proporción. La taza de entrega de alimento es como en ictéridos de Zonas Temperadas del Norte. El patrón de crecimiento de *A. xanthomus* es el mismo que el del tordo de alas rojas (*A. phoeniceus*). Después de abandonar el nido los jovenes siguen a los adultos a lo menos 24 días.

El éxito del nido (proporción de nidos que producen por lo menos un joven) fue 46% (54 nidos). Los nidos en los cayos cercanos a la playa tuvieron un éxito mayor que aquellos de tierras firmes adyacentes ya que fueron menos parasitados por el pájaro vaquero (*Molothrus bonariensis*). Parejas anidando en cavidades produjeron cerca de 3 veces mas jovenes por nido que aquellos anidando en áreas abiertas. La mortalidad durante el período de huevo fue mayor que la durante el período de cría, principalmente a interferencia producida por el pájaro vaquero.

La distancia promedio entre los nidos en las colonias fue 16 m. Ocasionalmente dos parejas anidaron en el mismo árbol. El agrupamiento de nidos parece ser el resultado de atracción activa entre los pájaros más que una respuesta a un número limitado de sitios de anidación. La conducta ataque o rechazo en forma colectiva fue un comportamiento conspícuo en los grupos de anidación. El espacio cercano al nido, que fue constantemente defendido contra conespecíficos y otras especies, fue pequeño, extendiéndose 3 m en toda dirección. Los machos defendieron las cercanias del nido más a menudo que las hembras.

La especie se alimenta principalmente en la estrata superior de los árboles, obteniendo artrópodos a partir de un cuidadoso sondeo de epífitas, grupos de hojas y superficies de ramas y troncos. Esta conducta de forrageo, representativa de orioles y pájaros carpinteros, podria reflejar la falta de competidores en un habitat donde los tordos son más comunes, en combinación con la carencia de adecuados sitios de forrageo en el suelo (pantanos) en Puerto Rico. La mayoria del alimento llevado a los polluelos es colectada hasta 2 km de los nidos. Parejas cercanas no se siguen hasta los esparcidos lugares de forrageo. La mariquita se alimenta en el suelo como lo hacen otros *Agelaius*, pero a diferencia de sus congéneres habitando pantanos, cuando se alimenta en el suelo su alimento consiste principalmente de material vegetal en vez de artrópodos. Cuando acarrean alimento a los nidos, los adultos llevan mas de un item en sus picos. Ellos además regurgitan para el joven tanto material vegetal como artrópodos.

La razón de sexos es igual, a pesar que en el invierno las bandadas representan a menudo proporciones significativamente mayores de un solo sexo. Esta diferencia es debida a la mayor especialización de las hembras por lugares de alimentación, tal vez relacionada a una dominancia del macho en algunos sitios de alimentación.

La sobrevivencia anual fue de 82.4% en adultos y 65.5% en jovenes. No se encontró diferencia en la sobrevivencia anual entre machos y hembras. Los individuos considerados fueron residentes permanentes en el área de estudio, aunque ellos ocupaban extensos ámbitos de hogar, con una distancia promedio de 1.5 Km entre recapturas sucesivas.

La especie utiliza por lo menos 26 distintas conductas de exhibición y vocalización, un repertorio mayor que el descrito para otros ictéridos monógamos. A diferencia de ictéridos polígamos, *A. xanthomus* tiene pocas diferencias intersexuales en la cantidad y calidad de sus exhibiciones. Cada sexo tiene sólo una conducta de exhibición siendo las restantes conductas de exhibición y vocalización compartidas por ambos. Las características estructurales de los patrones de acción y sonidos de *A. xanthomus* hace que ellos sean muy útiles para la transmisión de información a distancias cortas, especialmente cuando compite con sus vecinos mas cercanos utilizando conductas exhibicionistas.

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INTRODUCTION

The recognition that social systems are integrated complexes of adaptations sensitive to variations in environmental conditions (Orians 1961; Crook 1964, 1965) has generated interest in understanding the evolutionary, ecological, and behavioral diversity of these systems. Theories relating the social organizations of animals to ecological factors may be examined by comparing the behavior of the same or related species existing under different conditions. The blackbird genus *Agelaius*, with nine species, is well suited to this approach. Seven of the nine breed mainly in the emergent vegetation of freshwater marshes. Two North Temperate species, the Red-winged Blackbird (*A. phoeniceus*) and the Tricolored Blackbird (*A. tricolor*), have been studied intensively in most of their ranges. A tropical species, the Yellow-hooded Blackbird (*A. icterocephalus*) has been studied recently (Wiley and Wiley 1980; T. Manolis, pers. comm.). A fourth marsh dweller, the Yellow-winged Blackbird (*A. thilius*), a South Temperate Zone species, has been studied recently (Orians 1980). The biology of the other three marsh *Agelaius*, all South American species, is still poorly known.

The remaining species, the Yellow-shouldered Blackbird (*A. xanthomus*) and the Tawny-shouldered Blackbird (*A. humeralis*), both of the Greater Antilles, depart from the prevalent pattern of the genus in being occupants of savannah and mangrove habitats rather than marshes. This paper examines the biology of one of these insular forms, the Yellow-shouldered Blackbird, to examine a hypothesis based on socioecological theory, that the social system of a species may be explained in large part as a product of two selective forces: (1) the nature and distribution of its food, and (2) the pattern and intensity of predation. These selective forces are believed mainly to account for the response in sociality of the species in question.

A. xanthomus includes two subspecies. *A. x. xanthomus* is restricted to Puerto Rico and has not been recorded on any of the nearby islands except Vieques. *A. x. monensis* occurs on Mona and Monita Islands only. Once common throughout lowland Puerto Rico (Wetmore 1916), the Yellow-shouldered Blackbird is now mainly confined to three restricted coastal regions: Mona Island, E Puerto Rico in the vicinity of Ceiba, and SW Puerto Rico in a narrow coastal zone from Guánica to Boquerón. The total population is probably less than 3000, of which about 2000 are in SW Puerto Rico, and the remainder equally divided between Mona Island and E Puerto Rico, including Vieques. Details of the species' status and distribution are given elsewhere (Post and Wiley 1976).

The plumage of males and females is similar. Except for the humeral patch, which is close to spectrum yellow (Smithe 1974), the feathers of adults are predominately blackish neutral gray (Smithe 1974), and in the sunlight have a faint bluish green reflection (Ridgway 1902). The humeral patch is usually edged with a narrow white margin, and under the wing the humeral feathers are occasionally tinged with orange. When they appear in nestlings, the feathers of the humeral tract are buff-yellow to spectrum yellow, tipped with dark grayish brown. Most juveniles retain their dark tipped humeral feathers until the first postnuptial molt (in the fall of the year after hatching). Other regions of the nestling and juvenal plumage are dark grayish brown. Males have wings 1.1 times as long as those of females (102.8 ± [S.D.] 2.0 mm for 366 males and 93.3 ± 2.0 mm for 216 females), and weigh 1.17 as much (41.4 ± [S.D.] 2.3 g for 270 males and 35.5 ± 2.8 g for 157 females).

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METHODS OF STUDY

The study ran from December 1972 to February 1976. I averaged about 2 days per week in the field during the blackbirds' nonbreeding season (October-April), and 5 days per week during their breeding season.

I captured birds either with mist nets placed around feeding stations where birds gathered to eat the food of domestic animals, or with manually operated wire drop traps or treadle traps placed on feeding shelves baited with rice, sugar, or bananas. The birds were marked with three color bands and one numbered aluminum band. During the breeding season I determined the sex of captured birds by looking for the female's brood patch, or for the male's cloacal protuberance. After I accumulated a sufficient sample of wing measurements of birds sexed by these criteria, I sexed the birds by wing length alone.

To gather information on marked birds, I made monthly censuses of flocks feeding at seven stations around La Parguera. During the three years of study I caught 505 Yellow-shoulders, recaptured 114, and made 4034 sightings of color-marked individuals.

I watched low nests from burlap blinds, usually from 5 m away. I watched higher nests from blinds placed on platforms so that my eyes were about the same level as the nest, and observed birds that nested in tall palms through a telescope from a distance. I watched feeding flocks from towers, houses, or other vantage points that allowed examination of all flock members through a telescope.

To study nesting activities, I divided the day into six equal-length intervals and apportioned observations equally through the day. This method also permitted comparisons between samples collected on days of different length (Verner 1965). I visited nests at least once every other day, examining inaccessible nests by means of a mirror attached to a pole. Calculations of nesting success are not corrected for exposure (Mayfield 1961). I collected weight data for nestlings between 0900 and 1000. Before banding at about six days of age, young were nail-clipped for identification. I collected food from young birds by placing a tight-fitting pipe cleaner around their necks (Orians 1966) and extracting one hour's accumulation of food with forceps. Young that were used for food samples were not weighed.

To measure foraging behavior, I walked slowly through habitats used as feeding sites and recorded the following information on an individual's foraging behavior: height, position in vegetational strata (e.g. inner canopy, outer subcanopy), and the nature of five consecutive foraging maneuvers (e.g. probing epiphyte, flycatching). After these data were collected for one bird, I searched for the next subject. As most individuals were color-marked, I was able to avoid studying the same bird more than once per day. I determined the rates and durations of displays by analyzing film sequences.

The statistical measure of dispersion used in this paper is standard deviation, unless otherwise indicated.

DESCRIPTION OF STUDY AREA

The study site was in southwestern Puerto Rico along the Caribbean coast near La Parguera (17°58'N). It included and extended 5 km SW from the town of La Parguera (Fig. 1). Most of this area is composed of mangrove forest, with several scrub-covered islands, mangrove cays, pastures with scattered deciduous trees, and small settlements. With the exception of some older red mangrove (*Rhizophora mangle*) stands, most of the area at one time was cut over or burned. The principal vegetation of this coastal zone is red mangrove, bordered on its landward edge by extensive stands of black mangrove (*Avicennia germinans*). The black mangroves are often intermingled with open mud flats and salinas. Slightly farther inland the mangrove edge grades into dry coastal scrub, with trees such as corcho (*Pisonia albida*), mesquite (*Prosopis juliflora*), gumbo-limbo (*Bursera simaruba*), pigeon-berry (*Bourreria succulenta*), such shrubs as *Lantana involucrata*, *Bumelia* spp., *Comocladium dodonea*, and cacti such as *Cephalocereus royenii* and *Opuntia rubescens*. Farther inland the mangroves or coastal scrub border lowland pastures,

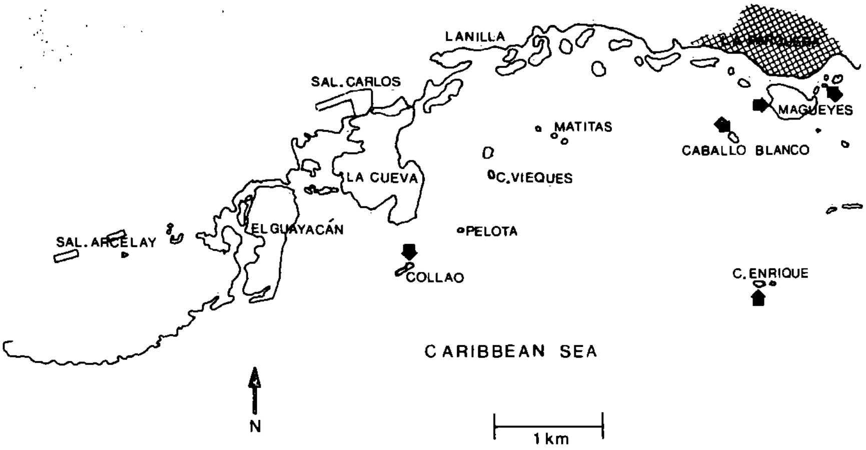

FIGURE 1.—Main study site in SW Puerto Rico, extending WSW from La Parguera to Salinas Arcelay. Abbreviations: Sal. = salinas; C. = cayo. Arrows indicate roost locations.

dotted with large deciduous trees such as black olive (*Bucida buceras*). These savannah-like pastures, intermingled with tracts of scrub, rise gradually toward the Sierra Bermeja, a system of hills (maximum altitude about 92 m) that parallels the coast. Further details of the vegetation cover of the region are given by Gleason and Cook (1926).

Offshore lie two islands (Fig. 1), El Guayacán (ca. 35 ha) and La Cueva (ca. 20 ha), where I did much of my work. These islands are facilities of the Caribbean Primate Research Center and harbor about 1000 free-ranging rhesus macaques *Macaca mulatta*. The vegetation is mainly red and black mangrove and stunted coastal scrub, described elsewhere (Post 1978). Many small mangrove cays, usually less than 0.5 ha, lie between El Guayacán and La Parguera (Fig. 1). The smaller cays are composed entirely of red mangroves, while larger ones have black mangroves on their drier interiors. At the eastern edge of the study tract, the town of La Parguera, with a population of some 2000, covers about 75 ha.

The climate of this coastal zone is semi-arid, with an annual rainfall ranging from 56 cm on La Cueva Island (12 year average, 1962-1973) to 68 cm in La Parguera (6 year average, 1970-1975). Rainfall has two yearly peaks, most rain falling from August through October, with a lesser and more variable spring peak around May.

I also studied blackbirds at two inland localities in southwestern Puerto Rico. In the Lajas Valley I visited the agricultural experimental station of the University of Puerto Rico, where blackbirds fed around cattle barns and in cultivated fields. This site, 6.5 km N of La Cueva Island, has an annual rainfall of about 107 cm (6 year average, 1970-1975), falling mainly during August-October. Such trees as mangos (*Mangifera indica*) or royal palms (*Roystonea borinquena*) and irrigated crops such as sugar cane are widespread. The vegetation of this area is described by Danforth (1926). Still farther inland I visited the campus of Inter American University at San Germán where Yellow-shouldered Blackbirds nested in royal palms planted around the university buildings. This locality is 12 km N of La Parguera, and its climate is humid tropical, with an annual rainfall of 182 cm (2-year average, 1975-1977), concentrated during July-November. The San Germán site was characterized by large ornamental and fruiting trees, such as mangos, avocados, and royal palms, and by lawns, parking lots, stadia, and other typical university structures.

RESULTS AND DISCUSSION

BREEDING BIOLOGY

NESTING HABITATS AND NEST CHARACTERISTICS.—Nesting blackbirds used a variety of habitats. In the 1975 breeding season I searched as equally as possible those parts of the main study area where I had seen blackbirds during the previous two years. I found 36 nests in mangrove salinas, 7 in groves of trees in pastures, 6 on islands and 1 in a town. This does not include five nests found in suburban habitat at San Germán in 1975.

The most important habitat, salinas (salt pans), lies 3-5 km SW of La Parguera, near La Cueva and El Guayacán Islands (photographs in Post and Wiley 1976). Natural salinas are created in mangrove forests when tidal circulation is impeded, and salt concentrations build up as the water evaporates. High concentrations of salt kill the trees, usually black mangroves, over tracts as large as 4 ha (Holdridge 1940). Salt manufacturers also create salinas by diking mangrove areas and removing trees. At La Parguera salt processing was practiced until about 1960, but since then most salinas have been abandoned. With the dikes broken and normal water circulation restored, the salinas are recolonized by mangroves. Salinas Arcelay, W of El Guayacán (Fig. 1), is such a site. Natural salinas, and the edges of the man-made salinas, often have scattered dead trees and stumps, intermingled with recolonizing shrubs and small tree-sized mangroves. The water level in the salinas is slight, usually less than 10 cm at high tide, and the area may dry out entirely at low tide.

Yellow-shoulders nested in scattered mangroves as well as in cavities in the dead trees and stumps (photographs in Post and Wiley 1976). Birds built open nests on main branches or on crotches of the mangroves. The average height of 10 of these nests in the salinas near La Parguera was

0.9 ± 0.7 m, and the average height of eight trees that held nests was 1.8 ± 0.9 m. Birds nested in red mangroves most often (13 cases), followed by black mangrove (10) and white mangrove (*Laguncularia racemosa*)(2).

Yellow-shoulders used two types of cavities, holes in the sides of dead trees and holes in the tops of stumps or stubs. Two nests were in cavities in the sides of trees. The entrance of one of these was 4 x 8 cm, and the cavity depth was 17 cm, while the eggs were 15 cm below the entrance. The other was in a cavity whose circular entrance was 8 cm in diameter. The eggs were also 15 cm below the entrance. The five other cavity nests were in the tops of hollow stumps or dead tree stubs. The openings to these nest sites ranged in size from 8 to 19 cm in diameter, and the distance of the eggs below the entrance ranged from 5 to 30 cm. For all seven cavity nests, the average above-water height of the eggs was 0.61 ± 0.32 m, while the average substrate height was 1.6 ± 1.2 m.

Yellow-shoulders also nested in large (11-14 m) deciduous trees, mainly black olives, scattered through pastures along the edge of the mangroves (Fig. 2). Nine nests were placed on main branches or crotches

FIGURE 2.—Pasture with scattered trees near La Parguera. Yellow-shouldered Blackbirds nested in the outer branches of these trees, mainly black olives.

FIGURE 3.—Mangrove cay (W Matita), offshore La Cueva Island. Groups of Yellow-shouldered Blackbirds nested in the red mangroves composing the cay.

at an average height of 5.6 m, range 4.3-7.6 m. Three nests were 3, 4, and 1.5 m from the main trunk. Nests were usually screened from above by surrounding leaves, but were visible from below. Yellow-shoulders do not build pensile (oriole-like) nests when they nest in trees, as do Red-winged Blackbirds in these circumstances (Bent 1958). Danforth (1926) also reported *A. xanthomus* nesting in deciduous trees around Cartagena lagoon, and this habitat resembles the pastures around La Parguera.

The mangrove cays where the birds nested ranged in size from 10 m^2 to 1.3 ha (Fig. 3). The average distance to the mainland mangroves of 21 offshore nests was 1153 ± 269 m, range 880-1460 m, and the average distance of these same nests to feeding grounds on La Cueva was 813 ± 393 m, range 380-1340 m. The minimum distance that some birds, namely those nesting on E Matita, had to fly to mainland (including La Cueva) feeding grounds was 1340 m.

The characteristics shared in common by the nesting cays were small size, total coverage by red mangroves, and freedom from rats. The relatively small cays used by *A. xanthomus* had only red mangroves. As sediments accumulate under the red mangroves, the cays become drier and black mangroves begin to colonize the interiors, while the red mangroves there die. These older cays are larger, harbor rats, and usually lack nesting passerines.

On the islands Yellow-shoulder usually placed their nests on main branches or crotches. One nest was built on a red mangrove root 0.8 m above the water. Fifteen nests averaged 2.14 ± 1.2 m above the water. The average height of eight trees used for nesting was 4.3 ± 2.7 m. Tides around La Parguera are usually less than 0.6 m, and no nest was flooded. Most offshore nests were at or near the edges of their islands, but several on W Matita were in the interiors. The average distance of 10 nests from the edge of the cays, as defined by the last mangrove root, was 4.3 ± 3.6 m.

Yellow-shoulders nested fairly high in royal palms planted on the grounds of Inter American University in San Germán. The estimated mean height of four nests was 15.3, range 10.7-19.8 m. The nests were on the midribs of palm leaves, 1-2 m from the axil. The nest material was woven under the leaf rib and around the leaflets that extended up on either side of the nest. One nest was woven into the top of a young palm leaf growing vertically from the top of a palm, and the nest was completely surrounded and partly covered over by leaflets. Palm nests were buffeted around by the wind, and in a strong wind the movements of one particular nest described an arc of about 1.5 m. In spite of their firm anchoring to these leaves, nests were occasionally blown down. I found such a nest with one dead young on 24 May 1975.

The open cup nests of *A. xanthomus* resemble those described for other species of *Agelaius*. Nest dimensions were as follows: inside width: 8.1 ± 1.1 cm (N = 9); outside width: 5.9 ± 1.6 cm (9); inside depth: 5.6 ± 2.5 cm (8); outside depth of cup only: 11.6 ± 3.1 cm (10); outside depth of nest, including material hanging below or draped above the nest: 25.0 ± 6.7 cm (8). All the nests I examined lacked domes, and the birds did not appear to manipulate the vegetation to improve cover over the nest. Surrounding foliage provided shade.

On the mainland birds nesting in the open made nest platforms of leaves, grass, cotton, and occasionally paper, string, plastic bags, and twine. Nest cups were made of grass leaves and stems and cotton, and were usually lined with fine grass leaves and stems. As I worked in the mainland nesting grounds only during the nesting season of 1975, I have no information on the extent to which nests or nest sites there were reused in succeeding years. Some cavity nests were used more than once during the same nesting season, and also repeatedly from year to year, as evidenced by the layers of old nest material beneath new nests. All seven cavity nests that I examined were lined with grass, but material from previous nests formed the platforms. All the hole nests were heavily infested with mites (Post 1981).

Nests on Cays were more bulky than those on the mainland, because they contained large quantities of sargassum. Composition of five nests averaged 70% sargassum (range 30-90%), 12% turtle grass (*Thalassia)* (5-30%), 13.6% miscellaneous wrack (plastic bags, nylon twine, bamboo roots, pelican feathers, burlap, 3-40%), and 4% fine grass (1 nest only, 20%). The offshore nests often had material hanging under them, and two nests had sargassum hanging on a branch above the nest, where the females had probably tangled the material during nest construction. The weight of one freshly collected nest was 123.4 g. The same nest weighed 99.3 g when dry. The dry weight of another nest was 118.5 g.

Sargassum was abundant on the mangrove roots of the Cays in the spring, but at other times nesting material may have been in short supply, and I saw females stealing material from each other's nests. Also, on two occasions pairs took over the deserted nests of other birds shortly after they were abandoned. Nests remaining from previous years were used again by the same or different pairs. In three cases the same nest site was reoccupied, although no nest material remained from the previous year.

BREEDING SEASON. — At La Parguera the start of pairing coincided with the spring rains. The timing of the spring rains themselves may be too variable to act as reliable cues for initiation of gonadal growth, but these rains stimulate vegetation growth as much as the heavier fall rains (Vandenbergh and Vessey 1968; Fig. 4), and proximate factors such as resurgence of vegetation and associated arthropod populations could serve as cues.

The spring growth of vegetation provides food for foliage-feeding insects, such as moths and crickets, which are the main arthropod foods of *A. xanthomus*, and more available protein may be necessary for females to form eggs (Jones and Ward 1976). Several studies (Fogden 1972; Wolda 1978) have correlated the growth of arthropod populations and new vegetation in tropical sites. The rate of leaf growth in red mangroves is highest during spring-summer (Onuf et al. 1977; J. G. Vandenbergh, unpubl. data). The larvae of a moth, *Ecdytolopha*, which feeds on the leaf buds of red mangroves, appear at the time of new leaf growth. This moth is a main food source for nestling Yellow-shoulders (see below, under Food and Foraging).

Nestlings were found throughout the summer dry period before the September rains began and stimulated vegetative growth again. The peak in new vegetation growth, and presumably in insect availability, was in October (Fig. 4), the period when young were becoming independent of their parents (Fig. 5). The peak in the fruit crop also occurred at this time,

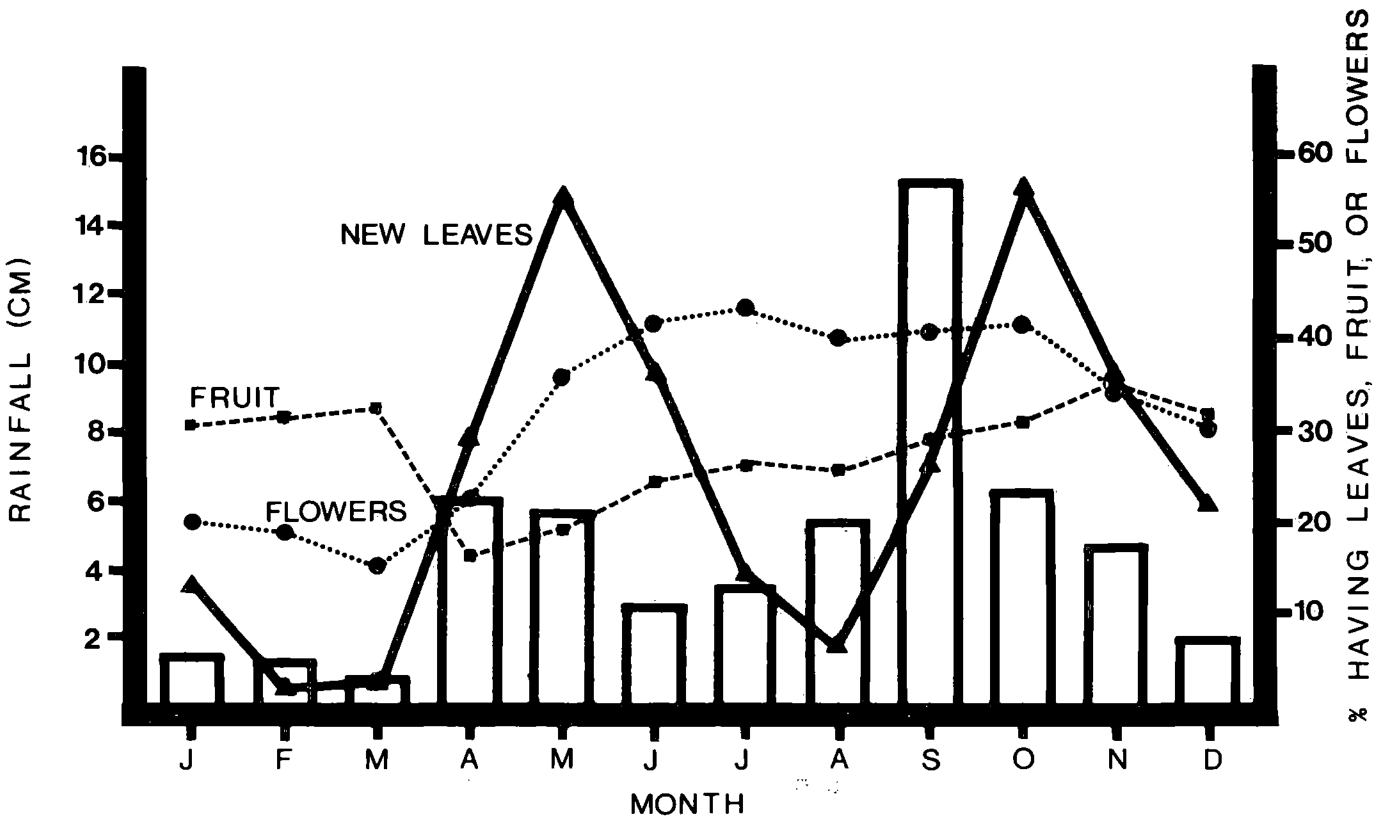

Figure 4.—Phenology of vegetation in relation to rainfall at La Parguera September 1963-August 1974. The left ordinate refers to amount of rainfall (cm) recorded per month, and indicated by heights of histograms. The right ordinate refers to the percentage of sample trees having the categories of foliage referred to. The vegetation data are from Vandenbergh and Vessey (1966) and J. G. Vandenbergh (unpubl. data).

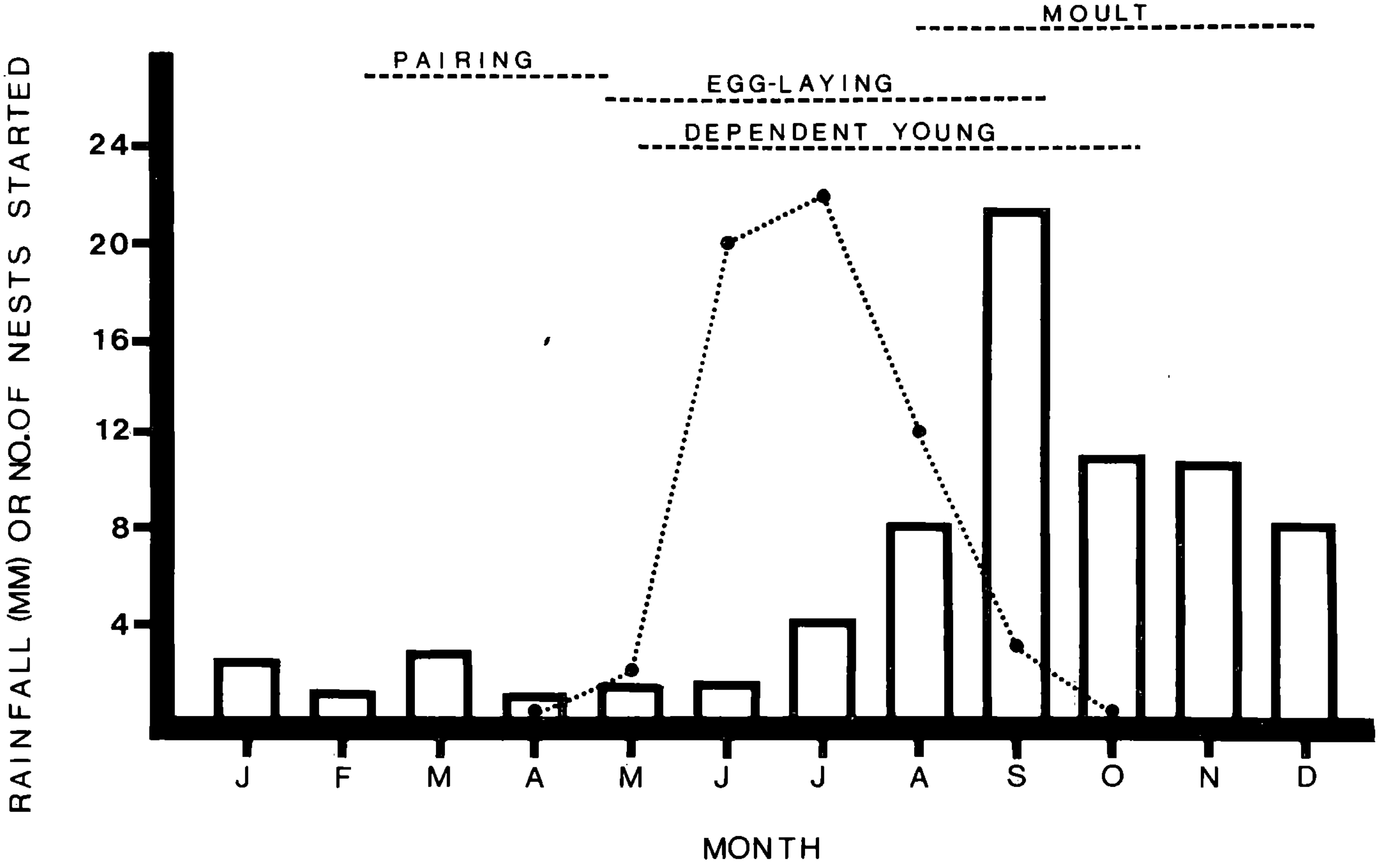

FIGURE 5.—Annual cycle of the Yellow-shouldered Blackbird in relation to rainfall, La Parguera, 1973-75. Rainfall: histograms; dotted line: number of nests with first egg.

and the young ate fruit after they left the nest. I saw adults feed bananas and granulated sugar to young that were following them.

Post-nuptial molt of Yellow-shouldered Blackbirds at La Parguera occurred after the fall rains started. I first saw replacement of remiges on 3 August, and the last molt of wing feathers on 20 December. Unfortunately, I was unable to follow the sequence of molt in my study populations in detail, but the few data from captures and from museum specimens show that molt is heaviest during October and November. Some birds that I caught in August were reproductively active and were also undergoing molt. For example, a female captured on El Guayacán on 9 August 1973 had a hard egg in her oviduct and was starting to replace her primaries (her two number one primaries were half grown). Another female caught on 16 August 1973 had a vascularized brood patch, while her primaries 1-2 were new.

MATE ACQUISITION. — Pairs established themselves in the nesting areas of previous years. Individuals and small groups of birds visited these localities all year, and some males began singing and sporadically defending sections of nest trees as early as late December. I saw no definite signs of heterosexual affiliation until late March (1975), about six weeks before eggs were first laid that year. In late March in scattered pasture trees at Lanilla groups of up to 15 birds gathered mornings after leaving the roost and stayed for about an hour every day before leaving for feeding grounds on El Guayacán. Similar groups gathered again in the evening on their way to roost. Birds arrived on the nesting grounds singly or in small groups, and not apparently as pairs. They often joined to form larger, but poorly integrated groups whose members alternated singing with bouts of foraging or resting. Pairs probably formed within these assemblages.

Pairing apparently depended on two behaviors: males displayed at specific sites and followed females persistently. Males visited the nest sites of previous years, usually standing in the nest or at its edge, alternately singing and jabbing or pulling at old nest material (nest advertisement display; see below). Nearby birds of either sex often sang within a short interval, probably in response to the first bird's displays. During this period of group visits to nesting grounds, the activities of individual males became more localized, and the male seemed to make the initial choice of a future nest site, which females then visited. Besides localizing their activities, males also began to follow females persistently around the nesting areas, and defended the females by singing, supplanting, and giving bill-up displays.

Persistent following and guarding lasted while birds were on the nesting grounds, but after leaving the males stopped following the females. For example in early April 1975 at Lanilla I watched a morning gathering of 15 birds composed of 4 pairs and 7 unassociated birds. I later

TABLE 1.—Histories of pairs nesting near La Parguera, 1974-1975.

					Distance Between (m):			
Male	Female	Nest locality	Date Nest Started	Nest Fate	Successive Nests	Nest and nearest communal feeding area	Nest and nearest communal roost	Comments
GABR	XARG	W Matita	24May74	deserted before completion	-	1260	2200	
		W Matita	8Jun74	deserted; contained 3 eggs	12	1260	2200	
		W Matita	11Aug74	deserted 24 Aug; contained 1 egg	9	1260	2200	
		E Matita	2Jun75	depredated 6 Jul; contained 1 young	275	1420	1600	male disappeared after nest failure; female moved to Collao, mated with AOOB
AOOB	RAYR	W Matita	19Jun74	depredated, contained 2 eggs	-	1260	2200	
		E Matita	26Jul74	deserted when partially built	280	1420	2000	
		Central Matita	29Jul74	nest completed, but deserted 7Aug	125	1340	2060	
AOOB	XARG	Collao	14Jul75	failure due to faulty nest construction; eggs in nest	male: 1950 female: 1945	480	3300	the former mate of AOOB disappeared after 23Jun75

RARG	A-	W Matita	5Jul74	young fledged 6 Aug	-	1260	2200	
		Collao	1 Sep74	young fledged 1 Oct	1950	480	50	
		Collao	4Jun75	young fledged 5 Jul	13	480	3300	
OAYY	BABX	Salinas Carlos	3Jun75	young fledged 3 Jul	-	720	3500	
			25Jul75	depredated 13Aug; contained eggs	110	720	3500	
YARB	ARBO	Salinas Carlos	31May75	depredated, contained young	-	720	3500	
		Salinas Carlos	6Jul75	fledged young 5 Aug	40	720	3500	young depredated after fledging?
		Salinas Carlos	12Aug75	nest deserted, contained eggs	52	720	3500	
AYGY	RYRA	W Matita	21Aug74	deserted?	-	1260	1780	
		Cayito Vieques	9Jul75	depredated; contained eggs	670	700	2280	after failure, pair moves to Collao
		Collao	Jul75	?	1250	480	3300	nest not found, but pair defending a territory

checked flocks containing these same color-marked individuals that were feeding on El Guayacán, and I saw no evidence of continued pair affiliation in the foraging flocks. In late April when the large winter feeding flocks began to break up, individuals associated as pairs more persistently, but even at the height of the nest-building period, males rarely defended the area around the female when the pair was away from the nesting grounds. Rather, the sexes maintained affiliation primarily by following each other.

NUMBER OF MATES ACQUIRED AND PERSISTENCE OF PAIR BOND.—The Yellow-shouldered Blackbirds I studied in SW Puerto Rico were monogamous. During 1974 and 1975 I watched 25 marked pairs involved in 43 nest attempts. I found no cases of polygamy, and only one instance of mate-switching during the breeding season, a case in which the mates of both birds had disappeared. I recorded 17 cases of renesting within the same year, 16 of which involved retention of the previous mate: 9 cases of one renesting and 4 cases of two renestings.

I have no evidence that Yellow-shouldered pairs are maintained during the nonbreeding season, but the birds' returning to their old nesting areas and nest sites increases the chances that they will pair again with their previous mates. The four pairs that I studied in 1974 all reformed in 1975 (Table 1), even though in two cases their last nestings of 1974 were failures.

Within the same nesting season pairs stayed together in spite of repeated failures, and in several instances the pair moved together to a new nesting locality, such as in the case of one pair that moved 1250 m from Cayito Vieques to Collao (AYGY and RYRA: Table 1).

AGE AT FIRST BREEDING.—Although I have no information on the age of first breeding of males, I found no evidence of a surplus population of unmated males, such as is characteristic of polygynous icterids (Orians 1969). Moreover the sex ratios among groups of birds that I captured at different times and places during the breeding season were close to unity.

I found no males nesting the first summer after their hatching year; some females bred the first summer. I color-marked 11 males and 29 females in juvenal plumage, most of them during their first summer and fall. For the first summer after hatching year I have information on the status of only two of these, both females. The first, ARYO, I caught 3 August 1974 on El Guayacán. In June 1975 she mated with a male I had banded as an adult in 1973. This pair nested successfully in a cavity on the mainland opposite El Guayacán. The second juvenile female was ARRO, captured on 6 July 1974 on El Guayacán. On 13 July 1975 I found her defending a nest in Salinas Carlos containing three Yellow-shoulder and four cowbird eggs. Her mate was an unmarked adult. The nest and eggs were deserted 22 July.

PATTERN OF PARENTAL CARE. — The average clutch of 30 undisturbed nests at La Parguera was 3.03 ± 0.32. There was no significant difference in the average clutch sizes of birds nesting on islands and on the mainland, nor between those using cavity or open nests. The distribution of clutch sizes was: 2 eggs, 1 nest; 3 eggs, 27 nests; 4 eggs, 2 nests. Because of the small variation in this sample, and because of the presence of cowbird young, I have no way of judging whether one blackbird clutch size was more successful than another. The average combined clutch size of 22 nests with cowbird and blackbird eggs was 5.59 ± 1.33. The most cowbird eggs contained in any Yellow-shoulder nest was six, in a nest with three blackbird eggs. All nine of these eggs hatched, the nest fledging two blackbirds and three cowbirds.

Incubation began after the second egg was laid, and hatching was asynchronous. I have information on the length of the incubation period for only one nest, which contained three blackbird and two cowbird eggs. One blackbird egg hatched 13 days after it was laid, or 12 days after incubation began, and another hatched 13 days after it was laid and after its incubation began.

Only females incubated and brooded. Females also stayed on the eggs at night while males usually left the nest sites to join communal roosts. One female at San Germán spent 77% of the daylight period incubating, while another nesting offshore La Parguera incubated 72% of the daylight period (Tables 2-3). The average duration of 37 daytime incubation bouts was 23.5 ± 16.7 min, range, 2.5-99.5 min (two nests). The average time that the two females spent off their nests during these same periods was 9.6 ± 8 min, range 1-36 min (N = 32). The longest continuous incubation time, 99.5 min, was recorded for a female on 19 July 1974 between 11:16 hrs and 12:55 hrs. Her eggs hatched on 21 July. I detected no diurnal variation in time spent on the nest nor in the length of incubation bouts. At San Germán the maximum percentage of any diurnal interval that was spent incubating was 86% (diurnal interval 5; 1433-1644 hrs), while the minimum percentage was 57% (diurnal interval 3; 1011-1222 hrs). There may have been a slight reduction in time spent incubating during midday, but this probably depended on the degree of shading surrounding vegetation afforded the eggs.

At one nest in San Germán the female brooded her young (less than three days old) 45% of the daylight period, while at another nest offshore La Parguera the female brooded young of the same age 16% of the daylight period. The difference in these brooding times may be related to the fact that the San Germán nest was more exposed to sunlight, and I noted that the female in San Germán sat on the nest more in the middle of the day than at other times.

I saw females regularly brooding young through day five (counting

TABLE 2.—Time budgets of a pair of Yellow-shouldered Blackbirds in the nest vicinity at San Germán, Puerto Rico.[1]

	Percentage of day[2] spent in various activities during:			
	Incubation period[3] by:		Nestling period[4] by:	
Activity	Male	Female	Male	Female
At nest	1.1	0.6	6.0	10.0
Incubate or brood	0	76.6	0	45.1
Forage	10.5	1.6	11.1	0.3
Rest	20.3	2.8	3.3	0.8
Body maintenance	11.5	0.9	0.1	0
Aggression	1.6	0.3	4.6	0.1
Flight	1.7	0.5	3.2	2.9
Gone	53.3	16.7	71.7	40.8

[1] Nest No. 175, located in royal palm on campus of Inter-American University.
[2] Samples, each at least 1 hr long, were spread equally through day.
[3] Observations conducted 20-27 May 1975. Male was watched 11.0 hr; female 10.3 hr.
[4] Observations conducted 2-6 June 1975, when young were less than 5 days old. Male and female were watched 5.7 hr each.

TABLE 3.—Time budgets of a pair of Yellow-shouldered Blackbirds in nest vicinity in La Parguera, Puerto Rico.[1]

	Percentage of day[2] spent in various activities during:					
	Incubation[3] period by:		Early nestling[4] period by:		Late nestling period[5] by:	
Activity	Male	Female	Male	Female	Male	Female
At nest	0	0.2	3.1	10.4	2.6	8.2
Incubate or brood	0	71.7	0	15.5	0	5.5
Forage	0	0	1.8	0	2.9	2.6
Rest	20.0	2.0	4.0	0.9	12.8	6.8
Body Maintenance	6.5	2.8	1.1	0.1	0.8	1.5
Aggression	0	0.7	0.9	0	1.1	3.0
Flight	5.5	1.3	12.8	4.9	11.7	6.5
Gone	68.0	21.3	76.3	68.2	68.1	65.9

[1] Nest 1B74, located on an offshore island (W Matita).
[2] Samples were spread equally through day.
[3] Observations conducted 14-19 July 1974. Male watched 2.2 hr; female 12.2 hr.
[4] Observations conducted 23-25 July 1974, when nest contained 2-3 young, 1-4 days old. Male watched 1.7 hr; female 5.3 hr.
[5] Observations conducted 26 July-5 August 1974, when nest contained 2 young, 6-15 days old. Male watched 7.7 hr; female 7.5 hr.

the day of hatching as day 0). For example, on 27 June 1975 a female on Collao brooded her three young (five days old) six times in 1 hr 16 min, for a total of 11.5 min. The next day, during the same diurnal interval and under the same weather conditions, she did not brood during a 1 hr observation period.

At about the same time that females stopped brooding regularly during the day, they began leaving the nest sites at night, flying with the males to communal roosts. A pair nesting on W Matita in 1974 left their single (7-8 day old) young to go to the communal roost on Caballo Blanco at 3 min before sunset on 25 June, and at 22 min before sunset on 26 June.

Both sexes delivered food at equal rates (Table 4). The average rate of delivery per nest per hr for all nests that I watched (11 nests; 65 samples, 73 hr) was 12.7 ± 5.8. The average delivery rate per young per hr was 5.4 ± 2.0. These delivery rates are about the same as reported for temperate zone blackbirds in which both males and females feed the young equally (cf. Willson 1966). I found no significant diurnal variation in food delivery rates (Table 5), but I did detect a difference between the rate of delivery to mainland and to offshore nests. This difference was possibly related to the fewer Yellow-shoulder and cowbird young in the offshore nests, as the number of deliveries per young per hr was the same for the two habitats.

Males and females both cleaned the nest cup. When standing on the nest rims, adults often pecked at their legs and nest surface, probably to remove mites. I saw both sexes preen feathers of the young, and they were apparently effective in keeping them free of ectoparasites. I found no warble flies (*Philornis*) on any of the 17 young (from seven nests) that I examined closely. In Puerto Rico, larvae of warble flies burrow under the skin of other species, such as the Pearly-eyed Thrasher (N. Snyder, pers. comm.). Both males and females removed fecal sacs (Table 4), carrying them off or eating them.

The average nestling period was 14.6 ± 1.3 days, range 13-16 (N = 10 young in five nests). The initial growth pattern of nestlings of both sexes is similar to that of comparable Red-winged Blackbird nestlings, and the growth pattern of both species is best described by the logistic curve. The growth rate (K; Ricklefs 1967) of the Yellow-shoulder young that I weighed was 0.458, while the time required for the young to grow from 10% to 90% of asymptotic weight (28.5 g) was 9.6 days. In comparison, the growth rate of a sample of Red-winged Blackbirds (Holcomb and Twiest 1971) was slightly higher ($K = 0.484$; $t_{10\text{-}90} = 9.1$). Red-winged Blackbirds leave the nest sooner than do Yellow-shoulders; the average nestling period for Red-winged Blackbirds is 10.5 days (Beer and Tibbitts 1950). The main difference between the growth of Yellow-shouldered and Red-winged Blackbirds is in the upper portion of their curves (Fig. 6).

TABLE 4. – Comparative reproductive efforts of males and females when young were in the nest.

Nest No.	Total Observation time (hr)	No. of food deliveries to nest		No. of distant feeding flights		No. of nest inspections		No. of fecal sac removals	
		Male	Female	Male	Female	Male	Female	Male	Female
1B74[1]	13.2	46	60	15	8	5	17	7	5
374[1]	12.1	32	35	9	11	12	22	0	0
174[2]	5.1	34	35	-	-	-	-	1	1
275[2]	2.2	10	9	3	4	2	2	0	2
775	6.7	51	58	52	57	0	5	6	14
875	6.0	53	57	52	56	0	2	3	8
975	6.6	73	44	54	25	2	0	7	4
1575[1]	8.1	62	78	6	3	2	2	12	18
33B75	3.0	18	11	1	1	0	1	2	0
4575	4.2	25	28	1	2	0	1	1	2
Total	67.2	404	415	193	167	23	52	39	54

[1] Nests on offshore islands, La Parguera.
[2] Nests at San Germán. All others in salinas at La Parguera.

TABLE 5.—Food delivery rates to nests, 1974-1975.

	Diurnal Interval						Average[1]
	1	2	3	4	5	6	for day
Deliveries per nest per hr							
offshore nests (N[2] = 32; 39hr)	14.6	12.6	13.6	10.9	8.3	7.9	11.3
							*[3]
mainland nests (N = 33; 34hr)	18.9	15.1	14.8	13.5	11.7	17.3	15.2
Deliveries per young per hr							
offshore nests (N = 32; 39hr)	5.2	5.2	6.0	5.1	5.0	5.1	5.2
mainland nests (N = 32; 33hr)	7.3	5.9	5.5	5.6	4.1	5.2	5.6

[1] Each diurnal interval was given equal weight in calculating the average for the day.

[2] N is number of sampling periods.

[3] * = $P < .05$ that averages were different due to chance alone (Student's *t* test).

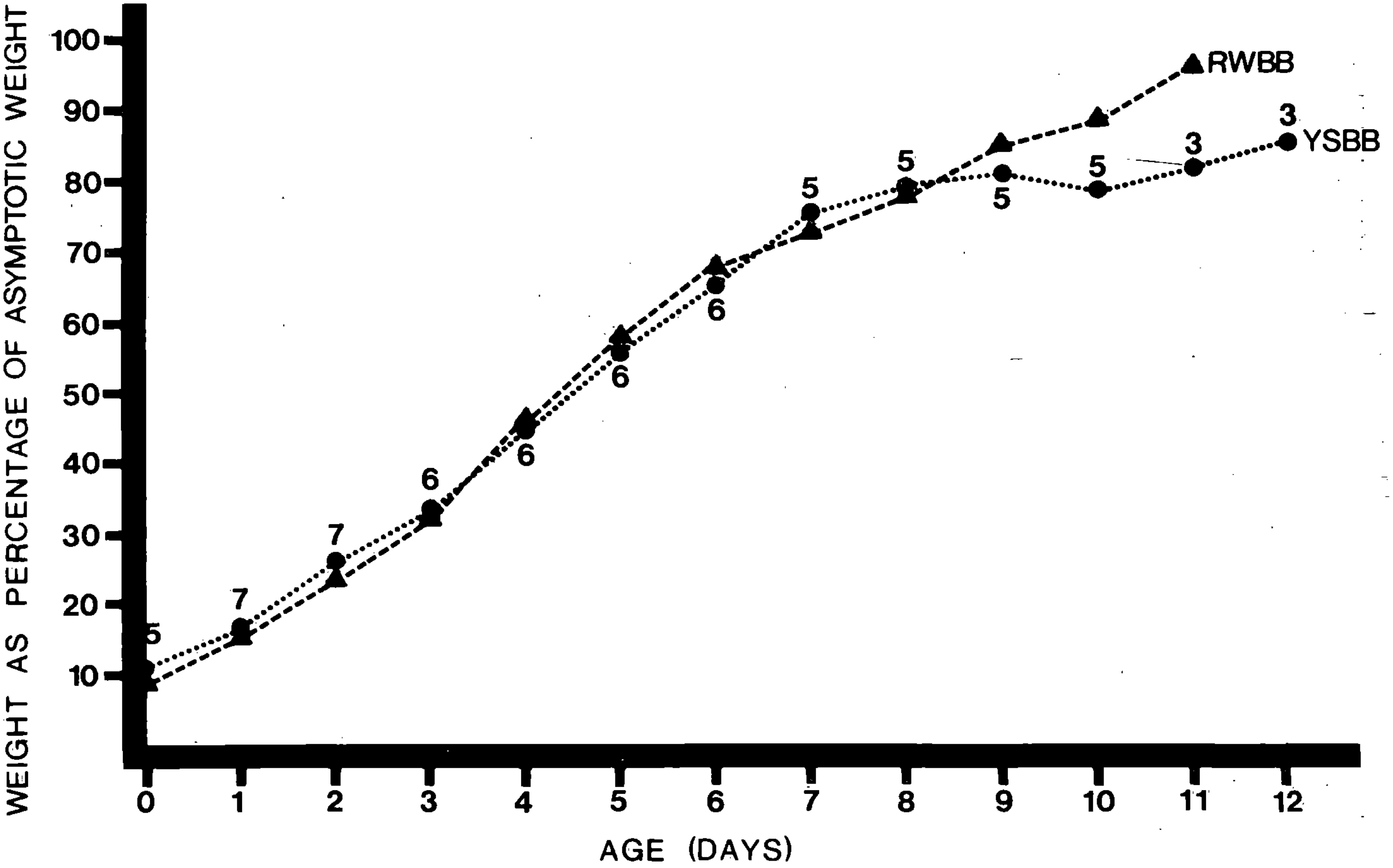

FIGURE 6.—Growth patterns of Yellow-shouldered and Red-winged Blackbirds. Solid circle is average daily weight of Yellow-shoulder nestlings. Number by each point is sample size. Dotted line connecting circles is growth curve of Yellow-shoulder, presented as percentage of asymptotic weight (28.5 g.). Dashed line is Redwing's growth pattern, as percentage of its asymptotic weight (37.0 g), based on data in Holcomb and Twiest (1971). Method for calculating asymptotic weight follows Ricklefs (1968).

Red-winged Blackbirds leave the nest soon after attaining asymptotic weight, while Yellow-shoulders remain 4-5 days after the growth rate falls off (days 7-8). The more sustained growth of Red-winged Blackbird nestlings when they are larger is perhaps made possible by the high productivity of temperate zone marshes, and has been selected for in the context of higher predation rates.

Species of the humid tropics have lower average growth rates than temperate zone species, and Ricklefs (1976) discussed the possible reasons for this difference. In comparison to other tropical species, the Yellow-shoulder has a higher growth rate. For example, 30 species of the humid tropics that weigh less than 100 g have an average growth rate of 0.387 (Ricklefs 1976). The growth rate of Yellow-shoulders is thus closer to that of temperate zone species of comparable size ($K = 0.502$; $N = 51$ species; Ricklefs 1976). No data are available on growth rates of passerines in the arid or semiarid tropics, but it may be found that other species nesting in such environments also exhibit growth characteristics more similar to temperate zone species than to species of the humid tropics.

After fledging, young remained in the nest vicinity for extended periods, and both parents continued to deliver food to them. Two young in one nest on W Matita fledged on 6 August 1975; both were still 5-6 m from the nest on 15 August, and one was still on the island within 50 m of the nest on 20 August. Both young had left the nesting island by 21 August.

After they left the nest vicinities, young followed their parents, giving begging vocalizations and a contact call, *pink*, while flying. The adults also used the *pink* call (see below). In the late summer and early fall I often saw one or two juveniles flying after adults as they visited monkey feeders. Adults fed these young monkey chow as well as other carbohydrate material such as bananas. Adults continued to feed the young for relatively long periods after they left the nest. Two young birds that fledged on 1 October 1974 were still following and being fed by their father, RARG, on 25 October.

As in most other monogamous passerines, males spend considerable time in parental care, either directly (feeding young and female, nest sanitation) or indirectly (territory defense, warning for predators). During the initial stages of nesting, females invest more time in reproduction, but after the young hatch, males probably spend about the same amount of time as females. (1) Females build the nest alone, but they are occasionally accompanied by males on trips to gather material. For one nest at San Germán, the female made 18 trips with nest material in 0.5 hr. In this case the male did not accompany her, but at the time he was engaged in mobbing. The one-way distances flown by this female were 60 m (16 trips), 140 m (1 trip), 240 m (1 trip), for a total of 2680 m/hr. (2) Only females incubate, and at two nests the females spent 72-77% of their time in this activity (Tables 2-3). Also, females alone brood, and at the same two nests they devoted 16-45% of their time to brooding. While females are on the nest, males may deliver food to them, although this behavior was variable, occurring in only two of the four pairs that I watched closely during the incubation period. At San Germán the male of one nest began delivering food to his female when she started incubating, about 12 days before the first egg hatched. This male delivered food to her at regular intervals, but infrequently: 18 deliveries in 12 hr. I did not see males feed incubating or brooding females at the nests I watched around La Parguera: in 17.5 hr of watching nest 1B74 during the incubation and early nestling period, I never saw the male deliver food to the female. Similarly, at 274, during 4.4 hr of observation, the male did not deliver food to the incubating female. (3) During the period the female was on the nest, males defended the nest area and engaged in mobbing predators (Table 6). When females were off the nest area, males were often present and they apparently guarded the nest. Also, during the rest of the nesting cycle males spent more time in nest defense than did females. (4) Males began feeding young at the same time as females, and the frequency of the male's visits to the nest in some cases exceeded that of the female's (Table 4). For two nests on W Matita I measured the minimum distances flown by the parents on foraging trips to the mainland opposite their nesting island: during the 2.5 hr observation period the females made 17 trips totalling 32 km while the males travelled 45 km (24 trips). (5) Both males and females feed the fledged young.

The male's investment in reproduction is high: although he neither incubates nor broods, he expends considerable time in nest defense. Males also feed females, which may be crucial in allowing them to stay on the nest when eggs or small young are threatened by weather or predators. After the young hatch, males make as many food deliveries as females. As some feeding sites are 2 km or more from the nests, the greater energy expenditure by males may be significant because of the high metabolic cost of flapping flight. Perhaps more significantly, males continued to feed young for long periods (at least 24 days) after they had left the nest. In this period the male's role may be not only important in providing food, but in protecting the naive young. Parental division of labor may be most crucial after the brood has dispersed (Smith 1978).

SPATIAL PATTERN OF NESTS AND AGONISTIC BEHAVIOR RELATED TO REPRODUCTION. — Yellow-shouldered Blackbirds usually nested in colonies. The average distance between 15 occupied nests in salinas habitat was 15.9 ± 7.6 m, range 5-35 m. The average distance between three offshore nests was 11.5 m, range 11-12.5 m. Pairs sometimes nested in the same tree: two nests in a pasture tree were 3 m apart, and two others in a

TABLE 6. —Nest attentiveness.

			Percentage of day[1] that:		
Nest number	Nest contents	Duration of sample (hr)	Male was away from nesting area	Female was away from nesting area	Nest was unguarded
1B74[2]	3 eggs	12.2	58.9	37.2	12.2
	2-3 young, 1-4 days old	5.3	75.5	68.1	50.6
	2 young, 6-15 days old	7.7	60.7	53.0	43.7
374[2]	1 young, 6-9 days old	11.9	67.6	69.9	56.3
775[3]	3-4 young, 6-11 days old	6.8	91.6	87.3	77.7
875[4]	2 young, 5-6 days old	6.1	80.6	86.4	69.3
975[4]	3 young, 9-10 days old	4.4	87.7	73.8	60.0

[1] Sample periods spread equally through day.
[2] Open nests on offshore island (Matita).
[3] Open nest in salinas.
[4] Cavity nest in salinas.

palm, 3.5 m apart. In 1977 two pairs nested simultaneously in different holes in the same dead tree at Salinas Arcelay (J. Wiley, pers. comm.). Adults defended only the immediate vicinity of the nest (Table 7) and spent long periods of time feeding away from the nesting area. Without experimentation it is difficult to determine to what extent the spacing of populations is influenced by social interaction or by common response to environmental factors. Birds settling to breed may use the presence of conspecifics as a cue to the suitability of a potential nesting area (Orians 1961), and such behavior would be advantageous to naive or unsuccessful breeders, especially if the displays of others and the presence of old nests indicated good nesting grounds. Alternatively, if suitable nest sites are limited, birds may be forced to settle close together. Such a patchy distribution of nest sites may be in part responsible for spatial contagion of Yellow-shoulders as well as for some populations of Brewer's Blackbirds (Horn 1968).

The following observations suggest that nesting aggregations of Yellow-shoulders resulted from active attraction among birds. (1) On different days groups composed of the same individuals gathered in the nesting areas and left together. (2) When disturbances occurred in a nesting area, all the nesting pairs deserted together, some relocating together at distant sites. In April 1975 my putting up blinds and markers on W Matita apparently disturbed the birds that were gathering there in the morning visiting old nesting sites. Members of this group, the same pairs that nested on W Matita in 1974, did not settle to nest there in 1975, but moved to other nearby islands (Table 1). (3) Birds visiting the nesting areas in early spring moved around together in loose groups composed mainly of pairs. Individuals and pairs displayed and answered each other frequently by singing. (4) Pairs whose nests failed or who were delayed in breeding stayed around the nesting colonies for long periods. (5) Although I did not sample vegetation, apparently suitable habitat around nesting groups remained unoccupied. Nests were close together and could have been spaced out more. All nesting pairs that I studied flew long distances to obtain food for themselves and their nestlings. For 750 deliveries to the nest, at least 48% of the food was obtained on distant feeding flights. In some years groups used certain nesting cays successfully but deserted others, while the same pairs used apparently identical cays nearby.

In salinas habitat shortage of suitable nest sites, particularly for hole nests, may have contributed to aggregation. But nests in pastures were close to each other, while surrounding apparently identical habitat was unoccupied. In San Germán royal palms were common, but pairs nested in adjacent trees or in the same palm, leaving many sites with palms unoccupied.

Birds in nesting groups responded in concert when mobbing such

TABLE 7. — Intraspecific nest defense by pairs of Yellow-shouldered Blackbirds.[1]

	Distance from Nest (m)									
Category of Behavior	0-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	Total
Number of Intrusions	25	20	15	12	16	11	7	0	4	110
Number of Intrusions at which Male was present	2	6	7	0	2	2	6	-	3	38
Number of Intrusions Challenged by Male	1	4	7	0	0	1	0	-	2	15 (54%)[2]
Number of Intrusions at which Female was present	10	6	15	11	13	9	7	-	4	75
Number of Intrusions Challenged by Female	1	1	3	4	3	0	0	-	0	12 (16.0%)[2]

[1] Data recorded for 3 adjacent nests on W Matita Island, La Parguera, 1975. Total observation time was 41 hr.

[2] A significantly larger number of intrusions was challenged by the male ($\chi^2 = 20.6$; $P < .005$; d.f. = 1).

predators as humans, Little Blue Herons (*Egretta caerulea)*, and Smooth-billed Anis (*Crotophaga ani)*. The mobbing response of individuals varied according to the stage of their nest. When colony members first spotted a predator, incubating females often stayed on the nest and gave occasional *check* calls. When the predator approached, they usually quietly flew off the nest, perched 10 m or more from it, and gave *checks*, *chwips*, or remained silent. The intensity of mobbing by both males and females increased as the young became older. I never saw adults diving at predators when their nests contained eggs, but they did so commonly when older young were in the nest. Non-nesters that frequented the nesting grounds also joined in communal mobbing. They, as well as neighboring nesting pairs, joined in mobbing within the defended area of the pair whose nest was threatened. In salinas habitat Yellow-shoulders may gain some predator protection from the proximity of Black-necked Stilts: I was often distracted by the constant calling and movements of the stilts when I was searching for blackbird nests. Interspecific nesting aggregation has been demonstrated to be advantageous in defense against predators (Göransson et al. 1975).

In March and April when pairs first formed, males showed rudimentary defense of the nest sites they visited as members of pairs or groups. About the same time, the males began defending females as they traveled around with them on the nesting grounds. But males did not defend females when they were away from the nesting sites, nor the females later in the nest cycle when they were away from the nest site itself. Such persistent defense would have been pointless: I noted that females were sexually receptive only in the vicinity of the nest and then only in the early stages of the nest cycle. As activities became more localized, the males' defense of females coincided increasingly with defense of nest site areas. If an old nest remained from the previous nesting season, the female showed signs of defending it from other Yellow-shoulders, but I most often saw site defense by females only after they had actually constructed or rebuilt a nest, and site-related intraspecific aggressiveness by females decreased after the young were 5-6 days old, about the time females stopped brooding.

Throughout the nesting cycle intraspecific defense of the nest site was primarily the males' role. The area regularly defended around the nest was small, extending about 3 m in any direction (Table 7). At the three offshore nests I watched, breeding and non-breeding Yellow-shoulders frequently entered the defended areas of nesting birds, and these intrusions were often left unchallenged, especially by the female (Table 7). Defense was most intense during the nest construction and egg-laying periods, probably because at these times neighboring pairs often stole each others' nest material. As only females incubated and brooded, they spent more time guarding the nest, but when they were off territory, males were usually near the nest. One nest containing eggs was left unguarded only 12% of the time, although the female was away from it 37% of her time (Table 6). After the eggs hatched, the nests were left unguarded 44-78% of the day. During periods when nests were unguarded, other Yellow-shoulders often visited them, inspecting their contents and sometimes even standing on their rims. Other than stealing of material, I saw no cases of interference with nests, nor did I see any assistance in the rearing of the young, as has been reported for some other icterids (Orians and Orians 1977).

Both sexes defended nest sites against the intrusions of other species, and as in intraspecific defense, males engaged in this activity significantly more often than females. For the island nests that I watched, the species that were challenged near the nest, Green Heron (*Butorides striatus*) and Yellow Warbler (*Dendroica petechia*), were the only others occupying the islands. GABR, a male nesting on W Matita in 1974, attacked Green Herons whenever they moved under his nest. Green Herons may have been predators of nests, but a pair on Collao in 1975 built their nest only 3 m from an occupied Green Heron nest. Yellow-shoulders at San Germán seldom invaded each other's defended areas, and I saw no intraspecific nest defense around the two nests that I watched. But other species commonly invaded the defended areas of the Yellow-shoulder nests, and in 14 hr at one nest I saw the Yellow-shoulders challenge Canary-winged Parakeets (*Brotogeris versicolurus*) 17 times (14 challenges by the male, 3 by the female), Shiny Cowbirds 13 times (all by the male), and Greater Antillean Grackles (*Quiscalus niger*) 5 times (4 by the male, 1 by the female). The pattern of interspecific nest defense (Table 8) reveals that many intrusions, particularly by Shiny Cowbirds, were ignored. While the male challenged only 28% of 46 Shiny Cowbird intrusions, he challenged 78% of the 18 Canary-winged Parakeet intrusions when he was present, a significant difference (Table 8). The different response of the male to two intruding species may have been due to the more surreptitious behavior of the cowbirds.

DISCUSSION.—The Yellow-shouldered Blackbird shows behavioral plasticity in its use of breeding habitats and nest sites. In addition to those situations enumerated above, the species also utilizes black mangrove forest in E Puerto Rico and cliffs on Mona Island (Post and Wiley 1976). Also on Mona, Barnés (1946) reported *A. xanthomus* nesting in cacti (*Selenicerus*) in scrub habitat.

At La Parguera I could detect no consistent pattern between the use of nesting habitats and feeding areas. Each habitat used for nesting was quite different, but the birds shared the same communal feeding sites (e.g. monkey feeders) or foraged independently in the same feeding

TABLE 8. — Response of a male Yellow-shouldered Blackbird to intruders near its nest.[1]

	Distance from Nest (m)										
Category of Behavior	0-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10	Total
Intrusions by Shiny Cowbirds	9	7	11	6	19	15	3	4	1	10	85
Number of Intrusions at which Male was Present	3	6	3	4	17	7	3	2	0	1	46
Number of Intrusions Challenged by male	3	2	1	3	2	1	0	0	0	1	13 (28%)[2]
Number of Intrusions by Canary-winged Parakeets	0	0	5	1	6	11	1	0	0	2	26
Number of Intrusions at which Male was present	-	-	4	1	4	8	1	-	-	0	18
Number of Intrusions Challenged by male	-	-	1	1	4	7	1	-	-	-	14 (78%)[2]

[1] Observations made in San Germán in 1975, totalled 14 hr. The nest contained eggs or young less than 5 da old.

[2] A significantly larger proportion of intrusions by Canary-winged Parakeets were challenged ($\chi^2 = 13.0$; $P < .005$; d.f. = 1).

habitats (e.g. pastures, mangrove-scrub edge). Only birds that nested in the savannah-like pastures commonly fed within the same habitat, but the pasture-nesting birds also flew long distances outside this habitat to gather food for nestlings at garbage dumps and monkey feeders.

The long distances that nesting birds flew to foraging sites may be a consequence of their preference for nest sites inaccessible to predators on small islands or isolated mangrove salinas. They probably expended relatively large amounts of energy on flights to feeding areas (see below, under Food and Foraging).

Birds that nested over water placed their nests lower than pairs nesting in terrestrial habitats such as pastures or suburbs, where they chose inaccessible sites, usually the high tips of branches or palm fronds. Other than those placed in cavities, nests in all habitats were readily visible. The relative scarcity of avian predators in coastal Puerto Rico may have encouraged this lack of crypticity. Thus the main selection pressure in molding habitat and nest site choice in *A. xanthomus* appears to come from ground predators, all of which are recent immigrants to Puerto Rico. It is difficult to envision what nesting habitats *A. xanthomus* might have used before the arrival of Europeans and the mammalian predators associated with their arrival. Possibly blackbirds nested closer to the ground in terrestrial habitats, such as scrub, or in the emergent vegetation of freshwater marshes, such as the extensive marsh that once covered the floor of Boquerón Valley (Danforth 1926).

The occupation of such a variety of habitats and nest sites by the Yellow-shoulder is probably possible only under the conditions of lowered competition for nest sites. On islands species often exhibit ecological release, one manifestation of which is an increase in the average number of habitats occupied per species (Cox and Ricklefs 1977). I found *A. xanthomus* using all available cavities in salinas habitat. In continental regions, icterids rarely nest in cavities (cf. Nero 1956b, Maxwell et al. 1976, Orians, Erckmann, and Schultz 1977), perhaps because of the presence of other species competing for these limited sites. The only other birds that I found using cavities in the Puerto Rico salinas were Stolid Flycatchers *(Myiarchus stolidus)* and their smaller size probably enabled *A. xanthomus* to outcompete them for holes.

The cues that tropical birds use to time their breeding vary with species and region: photoperiod, rainfall, and changes in vegetation and insect populations may be stimuli (Keast and Marshall 1954, Marchant 1959, Crook 1964). Breeding may be timed so that the most food is available for dependent young (Lack 1954). Alternately, breeding may only commence when females have attained proper body condition (Jones and Ward 1976, Greenlaw 1978). For *A. xanthomus* the spring growth of vegetation and insect populations most likely act as the ultimate cues for the initiation of breeding, by allowing females to accumulate sufficient energy reserves.

The long delay between pairing and egg-laying in the Yellow-shoulder may reflect the delay in the availability of suitable food. At La Parguera pairing began in late March in 1975 but egg-laying did not start until late May. Similarly for Yellow-shoulders on Mona Island, Barnés (1946) noted a long delay between the start of gonadal growth and actual deposition of eggs. Five males and two females he collected in late March and early April had enlarged gonads, but he found no eggs that year until early July.

While egg-laying coincides with a peak in new vegetation, most dependent young are in the nest during the summer dry period, when there are few new leaves (Figs. 4-5). This may have several advantages. First, the nestling period of some tropical species may be timed to occur outside the rainy season because of the difficulty parents have in obtaining food in wet weather. Insects are less active during rain because of impeded flight and lowered temperatures (Foster 1974), but as *A. xanthomus* seldom catches insects from the air, and most of the arthropods it takes are inactive during the day regardless of weather conditions, this may not be an important factor. Second, as Morton (1971) proposed for the Clay-colored Robin (*Turdus grayi*), it may be advantageous for nesting to occur during periods when predators are less active, such as a dry season. Third, it may be advantageous for breeding activity to be timed so that young leave the nest when food is abundant. Most Yellow-shoulder young fledge just before or during the September rainy period. The peak of new vegetation growth and fruit, and probably of associated arthropod populations, occurs at this time. Postnuptial molt also begins then, and abundant food would be available to partially dependent young and to molting adults. Similarly the monkey breeding season at La Parguera appears to be timed so that females are lactating during this autumn period of new vegetation and fruit growth (Vandenbergh and Vessey 1968). Other insectivorous birds, such as Yellow Warblers and Gray Kingbirds (*Tyrannus dominicensis*), also have young in the nest during the dry summer period, while granivores and nectivores, such as Ground Doves (*Columbina passerina*) and Bananaquits, begin most of their nesting activity during the September rainy period.

In species such as the Yellow-shouldered Blackbird, which do not defend a territory, mate choice may be based primarily on the characteristics of the individual. But as males also display at prospective nest sites, a female may base her choice, at least in part, on the suitability of the site. Characteristics of the male that might be reliable predictors of its fitness or future commitment to offspring are frequency and intensity of displaying, any behavior that might indicate readiness to defend the female or nest site from competitors or predators, and persistence in following or guarding the female when she is away from the nest site. Predictors not relating to male characteristics per se relate to the suitability of the nest site at which the male displays. Even if these sites were not used ultimately for egg deposition, the male would presumably select or defend a similar site. Criteria for a good nest site would be safety from predators, stability and shelter afforded to nest structure, proximity to other nesting pairs (as group mobbing may be an important anti-predator behavior in the Yellow-shoulder; see below), and distance to feeding grounds.

In species such as the Red-winged Blackbird and Yellow-headed Blackbird where males establish territories several weeks before females arrive, territory features may be the main influence on female choice (Orians and Christman 1968). Red-winged Blackbird females may assess male suitability by estimating the vulnerability of the nest site (male's territory) to predation and by estimating food availability on the territory, but they probably do not choose a male on the basis of its future nest defense or its future investment in reproduction (Searcy 1979).

In species that pair away from their nesting grounds, such as the Brewer's Blackbird and Common Grackle, the choice of mates must be based more on the characteristics of the individual. In the Brewer's Blackbird pairing occurs in foraging flocks (Williams 1952), and pairs arrive on the prospective colony already mated. The paired birds stay together, and the female chooses and defends a nest site and then builds a nest (Horn 1970). This species shows a high degree of heterosexual coordination through contagion of precopulatory displays and mate guarding (Horn 1970). Such coordination is characteristic of species that pair away from their nest sites and also have large, overlapping home ranges (Wiley 1976b). The Common Grackle is similar to the Brewer's Blackbird in that the pair bond also emerges from interactions of the sexes in group activities away from the nesting grounds. Mate guarding by the male and antiphonal singing between paired individuals are common means of coordinating activities between the sexes (Wiley 1976a, b, c).

In the Tricolored Blackbird the sexes arrive on the nesting grounds in mixed flocks, and territory establishment and nest building are completed in several days (Orians and Christman 1968; Payne 1969). The very small territory of the male and the rapidity of pairing may mean that mate choice is based more on male characteristics than in the Red-winged Blackbird (Orians and Christman 1968).

The mate acquisition pattern of the Yellow-shouldered Blackbird is similar to that of other nonterritorial icterids, whose pairing is not contingent upon the male's establishing and defending a fixed site over a period of time. Initial maintenance of the pair bond depends on two processes. First, the sexes meet in the nesting area of previous years, and repeated contact at these sites may facilitate individual recognition. Wing-raise displays (see below, under action patterns) are exchanged between individuals, providing opportunities for individual identities to be learned. Second, the association of individuals with specific sites may provide additional information on the identity of the partner. After repeated encounters on the nesting grounds, birds begin to associate as pairs persistently and independently of site.

Yellow-shouldered Blackbirds pair long before (6-10 weeks) they begin to breed. An extended period of affiliation may be advantageous to a female if it reduces the changes of male desertion once insemination has occurred. The female's ability to force loyalty by a long period of courtship is possible if the male considers prior investment when deciding whether to desert (Trivers 1972; Weatherhead 1979). Long periods of association before breeding should be found in species like the Yellow-shouldered Blackbird and Common Grackle (Wiley 1976b) in which the male contributes significantly to parental care.

In the Yellow-shoulder it is also possible that a long period of affiliation before mating is a means of assuring rapid initiation of breeding in response to irregular events. In *A. xanthomus* breeding may be delayed until the spring rains, when sufficient protein for egg formation becomes available (see above, under breeding season).

In being monogamous, the Yellow-shoulder fits the general pattern of Icteridae, where 45 of 57 species have been determined to have this mating arrangement (modified from Orians 1972). Monogamy may be maintained for a variety of reasons, and the specific ecological condition for each species must be analyzed separately, although in general monogamy is favored if the individual's fitness is increased by aiding its mate in caring for the young. The individual male's choice whether to invest additional time and energy in the progeny of one mate is weighed against the chance of success of this brood, with and without the individual's aid, as opposed to switching aid, in whole or part, to the progeny of another mate (Dawkins and Carlisle 1976; Maynard Smith 1977). If it is in the interests of a female *A. xanthomus* to assure her mate's fidelity, the possible means to this end are: (1) a long courtship before mating, (2) aggressiveness toward intruders near the male or nest, (3) rejection of cuckoldery when she is away from the male (Gladstone 1979), (4) spatial coordination of intrapair activities (Horn 1970; Wiley 1976c), and (5) mutual displaying and vocalizing with the male (Wiley 1976a).

In Icteridae the evolution of polygamy is associated with two ecological conditions: (1) extreme disparity in resources of defensible activity spaces (Verner 1964, Orians 1969), and (2) limited nest sites. Both of these routes for the evolution of polygamy assume that the conditions for male emancipation exist, i.e. the male's fitness will not be reduced if he reduces aid to his first brood. But the requirements of male aid are not alone sufficient to explain the maintenance of monogamy in situations where food is plentiful and the breeding season is extended over a long period. Under these conditions, for example, if male aid was still required, serial polygamy might evolve (Martin 1974). In addition, the conditions necessary for polygamy to evolve may not occur under some environmental regimes, such as when breeding takes place during a short period (Weatherhead 1979). Factors that reduce the chances of finding more than one mate are: (1) most potential mates in the population are already paired, (2) many other competitors for mates are still unmated, (3) availability of resources necessary to raise young may decrease with time, (4) most resources needed to attract a mate are already claimed, and (5) receptivity of potential mates drops with time (Boucher 1977). A number of species that group their nests, among them the Yellow-shouldered Blackbird, the Greater Antillean Grackle (Post, unpublished data) and the Common Grackle (Howe 1979), are not usually found to have more than one mate simultaneously. In the Yellow-shouldered Blackbird and Great Antillean Grackle, scarcity of predator-free nest sites may force pairs to build their nests in places that are not near feeding grounds. From a consideration of the distribution of the Yellow-shouldered Blackbird's food and the fact that it does not engage in cooperative foraging, one would predict that nests should be regularly distributed (Horn 1968; Waser and Wiley 1979), as in another icterid that feeds on arboreal arthropods, the Jamaican Blackbird (*Nesopsar nigerrimus*) (Wiley and Cruz 1981). For *A. xanthomus* I suggest that the best nest distribution in relation to food is not possible because of a scarcity of suitable nest sites. Having to nest in inaccessible places (mangrove islands and salinas) forces feeding parents to commute long distances, and in such situations male emancipation may not be possible.

Some of the primarily monogamous species are polygamous under conditions of limited nest sites. Williams (1952) found a population of Brewer's Blackbirds in which some pairings were polygamous, but the more general situation was described by Horn (1968), who found that Brewer's Blackbirds nesting in sagebrush, where nest sites were plentiful, were all monogamous. The Yellow-shouldered Blackbirds that I studied were monogamous in all the habitats where I examined them: 25 marked pairs nesting on mangrove islands, pastures with scattered trees, mangrove salinas, and palms in suburban areas.

Birds nested in groups on isolated islands from which they flew as far as 2 km to reach feeding grounds. Birds also aggregated to nest on the fronds of tall palms, the outer canopies of large trees in pastures, and in clusters of isolated mangroves growing in wet salinas. As in open colonies of Brewer's Blackbirds (Horn 1968), group defense may be an important antipredator strategy for the Yellow-shoulder, and the large number of displays used by mobbing Yellow-shoulders is correlated with the importance of joint defensive behavior.

Delayed breeding has been reported for other icterids, but the mechanism whereby breeding is delayed is not fully understood, as experimental removal of older male Red-winged Blackbirds demonstrates that first year males are capable of holding territories and breeding (Orians 1961). Possibly older Red-wings have the advantage over younger individuals of prior tenancy as well as earlier seasonal development of aggressiveness (Wiley and Hartnett 1976). In the Yellow-shoulder competition for limited nest sites, in combination with lowered breeding success for young birds of both sexes, may select against their breeding activity. Thus the factors that contribute to delayed breeding in Red-wing males may operate for both sexes in the Yellow-shoulder. As the species is monogamous and the adult sex ratio is equal, females have the same chance of breeding as males. Further, in a sedentary species such as the Yellow-shoulder, dominance related to prior occupancy could be crucial, especially as both sexes prospect for mates on their old nesting grounds and use their old nests as display sites. Flocks that visit the nesting areas in early spring are composed of breeders of previous years. Already established social units may play a role in allowing access to mates. Possibly delayed maturation in both sexes is more widespread in Icteridae than has been assumed; recent studies of the nesting of first-year female Red-winged Blackbirds show that they breed later within the same season that do older females (Crawford 1977).

POPULATION DYNAMICS

REPRODUCTIVE SUCCESS.—Pairs nesting on offshore mangrove cays had higher reproductive success than those nesting in mainland habitats (Table 9), even though they often flew longer distances to gather food for their young. Cay-nesting blackbirds had lower fledgling/nestling success than the mainland nesters at La Parguera, and their higher overall success is due to the greater proportion of eggs that they hatched (Table 9).

Yellow-shouldered Blackbirds that nested in cavities fledged over three times as many young per nest as did pairs using open nests in the same habitat (Table 10). Higher nesting success for cavity- or niche-nesting species is usual (Nice 1957, Ricklefs 1969). Most of the increased success of Yellow-shouldered Blackbirds using cavities was due to their significantly greater hatching success: 74% vs. 28% for open nests. The proportions of nestlings that fledged were not significantly different between the two nest types.

TABLE 9.—Reproductive success of Yellow-shouldered Blackbirds in Coastal Puerto Rico.

	Offshore nests,	Mainland nests	
Variable	La Parguera	La Parguera	Ceiba
Nest success	0.58 (11/19)	0.40 (14/35)	0.17 (3/18)
Eggs/nest	2.58 (49/19)	2.60 (91/35)	1.61 (29/18)
Fledglings/nest	0.89 (17/19)	0.77 (27/35)	0.17 (3/18)
Egg hatched/egg laid	0.49 (24/49)	0.37 (34/91)	0.21 (6/29)
Fledgling/nestling	0.67 (16/24)	0.79 (27/34)	0.50 (3/6)
Fledgling/egg	0.33 (16/49)	0.30 (27/91)	0.10 (3/29)

Mortality was much greater during the egg stage than during the nestling stage. About half the egg losses were within broods: 58% of 81 blackbird egg losses and 56% of 52 cowbird egg losses fell in this category (Table 11). Predation accounted for about 35% of the combined egg losses of blackbirds and cowbirds (Table 11). The remaining egg mortality was for the most part caused directly or indirectly by cowbird brood parasitism.

All 35 mainland nests, but only 3 of 14 island nests were parasitized by Shiny Cowbirds. The reproductive interactions of the Shiny Cowbird and Yellow-shouldered Blackbird have been treated in detail elsewhere (Post and Wiley 1977) and are outlined here for clarity. The nesting success of cowbird-parasitized and unparasitized nests may be compared to assess the impact of the cowbirds, and this comparison is tenable because nest losses due to causes other than cowbird parasitism, such as predation, were the same in mainland and cay habitats. Of 35 mainland nests, 31% were destroyed by predators, in comparison to 26% of 19 cay nests. A contrast between the nesting success of open nests that were parasitized

TABLE 10.—Reproductive success of Yellow-shouldered Blackbirds placing their nests in the open or in cavities.[1]

Variable	Nests in the open		Nests in cavities
Nest success	0.27 (6/22)	*[2]	0.86 (6/7)
Eggs/nest	2.59 (57/22)		2.71 (19/7)
Fledglings/nest	0.50 (11/22)		1.71 (12/7)
Egg hatched/egg laid	0.28 (16/57)		0.74 (14/19)
Fledgling/nestling	0.69 (11/16)		0.86 (12/14)
Fledgling/egg	0.19 (11/57)		0.63 (12/19)

[1] All nests were in mainland mangrove habitat near La Parguera, 1975.

[2] * = $P < .05$ that difference between two values is due to chance alone.

TABLE 11.—Causes of mortality in Yellow-shouldered Blackbird nests at La Parguera 1973-1975.

	Eggs						Nestlings					
	Yellow-shouldered Blackbird			Shiny Cowbird			Yellow-shouldered Blackbird			Shiny Cowbird		
Cause	Total	%	% composed of partial losses[1]	Total	%	% composed of partial losses	Total	%	% of composed of partial losses	Total	%	% composed of partial losses
Failed to hatch or live	13	16.0	100.0	12	23.1	100.0	11	68.7	100.00	11	84.6	100.0
Disappearance	19	23.4	73.7	1	1.9	100.0	0	-	-	0	-	-
Predation by Shiny Cowbirds	2	2.5	100.0	3	5.8	100.0	0	-	-	0	-	-
Faulty nest construction	2	2.5	100.0	1	1.9	100.0	3	18.8	0	0	-	-
Desertion	20	24.7	50.0	14	26.9	42.9	0	-	-	0	-	-
Predation	25	30.9	4.0	21	40.4	28.6	2	12.5	100.0	2	15.4	100.0
Total	81	100.0	51.9	52	100.0	55.8	16	100.0	81.3	13	100.0	100.0

[1] Losses due to various causes are partitioned as to whether they were composed of partial (within brood) mortality or whole brood mortality.

and not parasitized, making adjustment for the slightly larger number of eggs in unparasitized nests, indicates that brood parasitism reduced Yellow-shouldered Blackbird production by about 0.39 fledglings per nest (Post and Wiley 1977). The success of unparasitized nests was significantly higher than that of parasitized nests. Again, this comparison shows that brood parasitism had its main effect during the egg stage, with a reduction in nestlings from unparasitized to parasitized nests (Post and Wiley 1977).

Hatching failure, which accounted for 18.8% of the combined egg losses of blackbirds and cowbirds (Table 11), may have been because of the large number of eggs found in parasitized nests. Female blackbirds may have been unable to turn, incubate, or shade an excessive number of eggs properly, and some nests had as many as nine eggs. Hatching failure was high: 33% of 70 blackbird and 33% of 57 cowbird eggs did not hatch. In contrast, Caccamise (1976) found a hatching failure of only 7.4% for 497 Red-winged Blackbird eggs in New Jersey.

Desertion, which accounted for a combined loss of 25.6% of the eggs of both species, was also often related to cowbird visitations. Blackbirds may have deserted nests that contained large numbers of eggs, that had cowbird-damaged eggs, or that had eggs removed.

Egg disappearance was also an important source of egg mortality, accounting for 23.4% of the blackbird's egg losses, but only 1.9% of the cowbird's. This difference suggests that cowbirds were doing most of the egg removing, at least that proportion (73.7%) that were only partial losses, as predators usually remove all the nest contents.

Mortality in the nestling stage was relatively low and was due mainly to death in the nest. In most cases the nestling disappeared from an intact brood and lost weight before its disappearance. I infer that most of these young died of starvation and were removed by their parents. Young usually disappeared or starved when they were less than five days old. The average age of disappearance of 12 young was 4.3 ± 3.0 days. Caccamise (1976) also found that most deaths in Red-winged Blackbird nests occurred at about this age, but in comparison to the Red-winged Blackbird, a much lower proportion of nestling Yellow-shouldered Blackbirds died in the nest. The more variable food supply of temperate-zone, marsh-dwelling icterids probably is the main cause of their higher nestling mortality (Ricklefs 1969).

The lower fledgling/nestling success of cay-nesting Yellow-shouldered Blackbirds was at least in part due to starvation. Pairs nesting offshore delivered food at a lower rate than those on the mainland (Table 5). The number of young of both blackbirds and cowbirds fledged per successful island nest was 1.55 (17/11, Post and Wiley 1977), and the corresponding figure for open nests on the opposite mainland was 2.56 (28/11). The number of young fledged per successful cavity nest was higher: 3.29 (23/7), and the maximum number fledged from any nest, five (three cowbirds and two blackbirds), was from a mainland cavity nest. In contrast, the maximum number from any cay nest was only two Yellow-shoulders.

SEX RATIO.—In the populations sampled at La Parguera and among museum specimens that I examined (Table 12), males outnumbered females. The unbalanced sex ratio prevailed during the non-breeding season, but during the summer breeding period the sex ratio was close to unity. For reasons enumerated below, I believe that the samples taken during the non-breeding period may be biased toward males. I recognize five possible sources of error in determining the sex ratio:

1) Sampling error due to finite size of population: the large number of birds captured at several sites throughout the year reduces the chance of error from this source.

2) Most birds were captured during the winter and possibly a seasonal bias exists. Unlike the Red-winged Blackbird, the Yellow-shoulder is not migratory, nor do the sexes use different wintering ranges. Neither does the Yellow-shoulder show the extreme sexual segregation exhibited by Red-winged Blackbirds in winter. My data indicate a tendency for different proportions of the sexes to use different winter feeding grounds locally. This is demonstrated by comparing the sex ratio of groups of birds captured in La Parguera with those taken on La Cueva and El Guayacán (Table 12). In subsequent samples of marked birds, the proportions of males and females feeding on La Cueva and in La Parguera differed significantly from the ratios in the marked populations at the time of the samples (Table 13). Because of male dominance in intersexual competition during the winter, females may avoid some feeding areas. Similarly, the sex ratio of Evening Grosbeaks (*Hesperiphona vespertina*) competing at small feeding trays has been shown to favor the more aggressive male (Balph and Balph 1976). In contrast to the winter, the numbers of male and female Yellow-shoulders captured and seen at feeding sites in the summer were about the same (Table 12).

3) Female Yellow-shoulders show greater feeding site specialization than do males (Table 14), and if males use different feeding stations more frequently, they might be more susceptible to capture than females. This supposition is supported by the fact that marked males were more conspicuous than females: the average number of times that 202 marked males were seen was 12.6 ± 0.9 each, whereas 118 females were seen an average of 9.2 ± 1.0 times each, a significant difference ($P < .05$, Student's t test).

4) Male and female Yellow-shoulders have different parental roles which might make males more conspicuous during the nesting period.

TABLE 12. —Sex of newly-captured adult Yellow-shouldered Blackbirds in SW Puerto Rico and of museum specimens.

	La Cueva and El Guayacán Islands			La Parguera			Museum		
	Male		Female	Male		Female	Male		Female
Winter (Nov-Apr)	152	* ($\chi^{2*} = 33.9$)	66	50		28	-		-
Summer	48		43	10		9	-		-
Total	200	* ($\chi^{2*} = 28.8$)	109	60	* ($\chi^{2*} = 5.5$)	37	58	* ($\chi^{2*} = 6.3$)	34

An asterisk between 2 values indicates a significant difference ($P < .05$).

TABLE 13. — Sex composition of groups of color-marked Yellow-shouldered Blackbirds at La Parguera.

Location	Date	Duration of sampling period (hr)	No. of Marked birds	Ratio M:F	No. of birds marked locally at time of sample	Ratio, M:F	Test of Significance[1]		Total No. of birds marked at time of sample	Ratio, M:F	Test of Significance[2]	
							χ^2	P			χ^2	P
Feeder no. 1, La Cueva	24Oct74	1	22	10.00	317	1.59	6.4	<.05	422	1.54	6.9	<.01
Feeders no. 5-8, La Cueva	15Feb75	2	71	3.73	324	1.63	6.5	<.05	432	1.57	7.6	<.01
	19Apr75	2	34	5.80	328	1.62	6.4	<.05	436	1.56	7.0	<.01
Feeders no. 19-22, El Guayacán	16Feb76	3	53	3.42	328	1.62	4.1	<.05	444	1.57	4.1	<.05
	13Feb76	2	62	1.95	328	1.62	0.4	NS	444	1.57	0.2	NS
E La Parguera	26Jan75	8	19	8.50	106	1.30	7.4	<.01	429	1.57	6.3	<.05

[1] The numbers of each sex in the sample are compared to numbers of each sex that had been color-marked in the local area where the sample was made.

[2] The numbers of each sex in the sample are compared to number of each sex that had been color-marked in the entire study area.

TABLE 14.—Number of individuals seen at only one feeding site and at more than one site.

	Seen at:		
Sex and Age Category	One site only	More than one site	Test for differences between sex and age categories
Adult males	31 (16%)	167 (84%)	$\chi^2 = 4.2$; $P < .05$
Adult females	24 (27%)	66 (73%)	
Total adults	55 (19%)	233 (81%)	$\chi^2 = 1.2$; N.S.
Total juveniles	5 (11%)	40 (89%)	

Females incubate and brood, while males engage in defense of the nest area to a greater degree than do females. At San Germán males were often trapped while females were on the nest, and the sex ratio of captured birds there was 7 males:3 females.

5) The 36 mm nets used to catch the blackbirds probably did not favor one sex; if anything, the smaller females were captured more readily because of the greater tendency for smaller birds to become entangled. However, males mobbed more frequently than females. Mobbing birds sometimes landed on net shelves in response to the screams of netted birds, perhaps increasing the chances of males' being captured.

Male Yellow-shouldered Blackbirds usually dominated females in competition for food. I have data for 20 aggressive two-way interactions between marked males and marked females at winter feeding stations: in 17 cases males dominated females, while in three the reverse occurred. As males are larger, their dominance is to be expected, at least during the nonbreeding season. Male dominance may affect the social structure of Yellow-shoulder populations during the nonbreeding season. Some winter flocks had significantly more males than females (Table 13).

SURVIVAL.—The annual survival of 250 adults was 82.4% (Table 15). This calculation is based on a composite population (Hickey 1952) of color-marked individuals, captured from December 1972 to May 1974. Recaptures were made either by trapping or by sighting during censuses at feeding and nesting sites. I continued censuses through February 1976. Birds that were not seen or captured again were considered dead, and surviving up to the time of their last appearance (von Haartman 1971). These 250 individuals (Table 15) were classified as residents of the La Parguera-El Guayacán area; birds that were not seen or captured at least once after their first capture were excluded from this analysis. This exclusion is warranted by the fact that a few of the birds captured in winter may have been transients, stopping to feed on El Guayacán while they were on their way to the roost at Collao (Fig. 1). Most of these individuals were prob-

Table 15.—Annual survival of Yellow-shouldered Blackbirds.

	Numbers marked			Numbers surviving at least one year			Numbers surviving at least two years	
Marking Period	All Males	All Females	Juveniles	Males	Females	Juveniles	Males	Females
Dec. 72-Jan. 73	53	21	-	48	21	-	41	15
Feb.-Mar. 73	12	7	-	11	7	-	8	4
Apr.-May 73	8	2	-	7	2	-	4	1
Subtotal, Dec. 72-May 73	73	30	-	66(90%)	30(100%)	-	53(73%)	20(66%)
Jul.-Aug. 73	7	6	-	7	4	-	-	-
Feb.-Mar. 74	45	19	17	35	10	11	-	-
Apr.-May 74	48	22	12	36	18	8	-	-
Subtotal, Jul. 73-May 74	100	47	29	78(78%)	32(68%)	19(65.5%)	-	-
Total, excluding individuals not seen at least once after original capture	173	77	29	144(83%)	62(81%)	19(65.5%)	-	-
Total, including all birds captured	196	95	32	144(74%)	62(65%)	19(59.4%)	-	-

ably residents in the Pitahaya-Bahía Sucia area, west of the study tract. In fact most of the birds that were residents in the La Parguera—El Guayacán area were seen much more often than once: 320 marked birds were seen an average of 11.4 times each. I believe 82.4% to be an accurate estimate of survival, as the proportion of birds that died shortly after being marked probably was small, and undoubtedly balanced by the proportion that emigrated from the study area.

Including all the birds captured between December 1972 and May 1974 in the analysis would increase the size of the sample to 291. The corresponding numbers surviving to one year would remain the same, but the annual survival rate estimate would decrease to 70.8% (Table 15).

For the population captured between December 1972 and May 1973, I was able to compute the survival rate to two years: 70.9% of 103 individuals survived at least two years after capture. The weighted annual survival rate (Farner 1945) of this group is 69.8%.

My data do not allow the computation of time-specific survival, but as the adult birds were captured throughout the year and were presumably a cross section of the total population, their annual survival represents the average for the adult population. Such data must be used with caution in computing parameters such as longevity (Botkin and Miller 1974).

The data do not show a sex difference in annual survival for the first or second year after capture. Comparing the numbers of each sex surviving after one year (group captured December 1972—May 1973; Table 15) shows that 53 of 66 males (80.3%) and 20 of 30 females (66.7%) survived for two years, and this difference is not significant ($\chi^2 = 1.4$; $0.25 < p > 0.1$, 1d.f.)

The survival to adulthood of 29 individuals that were marked as juveniles was 65.5% (Table 15). Again birds that were not seen at least once after capture were excluded from the analysis, but if all the juveniles captured during this period are included, the survival rate is 59.4%. The juveniles considered here were caught in their first winter or spring, and the survival value is for one year from capture, i.e. through their second year.

During the same period that I caught these 32 juveniles (February-May 1974; Table 15), I also took 158 adults. This gives a juvenile:adult ratio of 0.203/1.000, which agrees fairly closely with the estimated annual adult mortality of 17.6%. This ratio is also close to the 0.210/1.000 ratio among the 92 birds collected throughout Puerto Rico that I examined in museums.

In the nesting seasons of 1974 and 1975 I color-marked 29 fledglings. Eight of these were later seen flying about, independent of their parents. Although the sample is small, it gives an estimated fledgling to juvenile survival rate of 27.6%. The product of the survival rates of fledglings to juvenilehood and of juveniles to adulthood is 18.1%, which again is close to the average annual adult mortality rate of 17.6%.

Determining survival by sighting color-marked individuals is more accurate than any system dependent on recaptures, which are often biased by the vagaries of trapping (Grosskopf 1964; Coulson and Wooller 1976). This system is particularly effective with Yellow-shoulders because they are sedentary and conspicuous, and the census stations, widely spaced in nesting and feeding areas, were manned throughout the year.

Discussion. — The success of open, unparasitized nests at La Parguera is similar to that Marchant (1960) reported for nine open-nesting passerines in an arid tropical region of Ecuador, where nest success was 51% and overall egg success was 44% (versus 63% and 35% for Yellow-shoulders).

Open, cowbird-parasitized nests at La Parguera had a lower success than the above, and their success was similar to that of some species that occupy cleared edges of humid tropical forests, where partial losses related to such factors as brood parasitism are high. For example, the Clay-colored Robin had nest success of 25% and egg success of 16%, while, as with parasitized Yellow-shoulder nests, its fledgling/nestling success was relatively high: 53% (Skutch 1966).

No information is available on the reproductive success of cavity-nesting birds in the arid tropics, but the success of cavity-nesting Yellow-shoulders at La Parguera exceeds the average success of 16 species of hole nesters in the humid tropics (Ricklefs 1969). These species had a nest success of 54%, and 44% of their eggs produced fledglings, in comparison to 86% and 63% for the Yellow-shoulder cavity nests.

In comparison to icterid nests in the temperate zone of North America, Yellow-shouldered Blackbird nests not parasitized by cowbirds have lower success in the percent hatched of eggs laid, but higher fledgling/nestling success. In addition, overall nest success was higher in the Yellow-shoulder. Robertson (1972) found that Red-winged Blackbirds nesting in marshes (where there was no cowbird parasitism) had nest success of 53%, fledgling/nestling success of 65% and fledgling/egg success of 44%. In continental icterid populations, nestlings appear to be subjected to more predation, and because of larger clutch size may experience greater starvation, both of these effects increasing with age of nestlings (Smith 1943, Young 1963, Robertson 1972). Egg loss in the Yellow-shoulder greatly outweighs loss of nestlings, while in temperate zone Red-winged Blackbird populations mortality is fairly constant throughout the nest period.

Red-winged Blackbirds nesting in fresh water marshes in Costa Rica had a nest success of 21.5% (Orians 1973), in comparison to 27% for Yellow-shouldered Blackbird open nests (Table 10). As with Costa Rican

Red-wings, most of the Yellow-shoulder losses during the nestling stage were due to starvation. Whole nest losses, occurring during both egg and nestling stages, and usually by predation, were more important in Costa Rica than in Puerto Rico, but partial losses in Puerto Rico, directly or indirectly attributable to brood parasitism, nearly equaled whole-nest loss in Costa Rican Red-wings. As expected, cavity-nesting Yellow-shouldered Blackbirds at La Parguera had much higher nest success than open-nesting Red-winged Blackbirds in Costa Rica.

In comparison to estimates of survival rates based on similarly gathered data for Red-winged Blackbirds, Yellow-shoulders have a higher rate of survival. Data for 325 Red-wings marked and retrapped in coastal Massachusetts gave an annual (weighted) adult survival rate of 53.4% (Fankhauser 1967). Significantly lower than my weighted estimate of 69.8% ($\chi^2 = 9.6$; $p < .005$, 1 d.f.) for the Yellow-shoulder. Another estimate of Red-wing survival generated from shootings of banded birds throughout North America gave a figure of 51.1% (Fankhauser 1967).

High survival rates appear to be characteristic of some tropical bird species, although further research, particularly in disturbed neotropical areas, needs to be done. On Sarawak, Fogden (1972) found a minimum annual survival rate of 86% for a composite sample of species occupying forest habitats. Snow and Lill (1974) estimated minimum annual survival for the White-bearded Manakin (*Manacus manacus*), a species occupying tropical forests in Trinidad, to be 89%. Although my estimate is for a tropical species occupying open, disturbed habitat, for which category there appear to be no other survival estimates, some of the factors contributing to the increased longevity of tropical forest birds must apply to species in disturbed habitats, i.e. stable climate, buffered food supply, and lack of migration.

BEHAVIOR

HOME RANGE. — The marked birds that I studied seem to be permanent residents around La Parguera, and I detected no seasonal movements by any significant proportion of the population. Some individuals that I had marked on the coast were seen inland during the non-breeding season; 11 birds (6 males and 5 females) appeared occasionally in flocks of 50-70 Yellow-shoulders that fed around the cattle barns at the Lajas Experimental Station, 7.3 m N of La Parguera. During this time several of these birds were also seen on the coast, where they apparently returned nightly to roosts.

Individual birds ranged widely (Table 16; Fig. 7), but I detected no seasonal differences in size or usage pattern of their home ranges. This is probably due to (1) the year-round use of communal roosts, which were usually distant from nesting and feeding areas (Fig. 1); (2) year-round use

TABLE 16. — Home ranges and distances between captures.

	Males			Females		
	N	x	Range	N	x	Range
Home ranges (km^2)	26	2.56 ± 0.50[2]	0.27-13.34	12	1.73 ± 0.36	0.39-3.70
Distances between recaptures (m)[1]	200	1325 ± 95.2[2]	25-5440	200	1630 ± 131.5	25-7260

[1] Only distances between sightings or recaptures at successively different localities counted.

[2] Standard error of the mean.

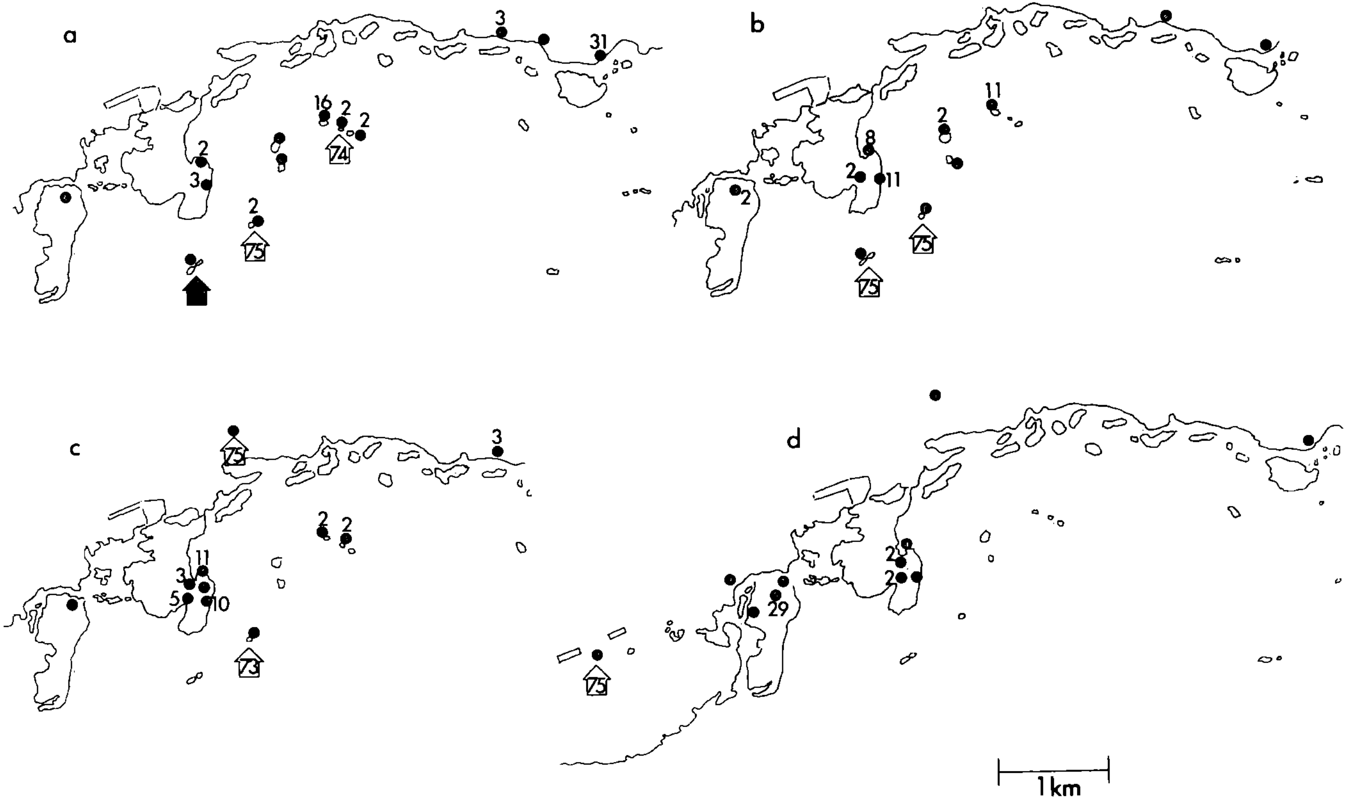

FIGURE 7.—Home ranges of Yellow-shouldered Blackbirds. For localities, refer to Fig. 1. Black dots indicate sighting or capture points. Single dots mean one instance; multiple instances are indicated by numbers. Open arrows indicate nesting sites, with year; solid arrow is roost site. (a) male GYG-A; (b) male BA-RG; (c) female YA-XY; (d) female RYR-A.

of communal feeding grounds such as those on La Cueva and El Guayacán; and (3) distant feeding behavior.

The large sizes of the home ranges are reflected in the distance between successive recaptures. Distances between recaptures (Table 16) are reasonable estimates of daily movements: birds using the La Cueva and El Guayacán feeding grounds often flew to one of the La Parguera roosts (Fig. 1), making daily round-trip flights of 10-12 km. Other individuals used feeding station in La Parguera and flew nightly 5.5 km to a roost in Bahía Montalva E of the study area.

Most of the marked birds whose nests I located used winter feeding grounds near their nest sites (Fig. 7). The main nesting places, Salinas Arcelay and Salinas Carlos, were 1600 m and 800 m from the nearest monkey feeders on El Guayacán and La Cueva. At least seven birds marked as nestlings used one of these feeding grounds the winter after they hatched. The average distance between their hatching places and winter feeding grounds was 1549 m, range 980-2680 m.

FOOD AND FORAGING. — During the nesting season Yellow-shouldered Blackbirds brought two types of food to dependent young; the bulk of the food was arthropods, the remainder vegetable matter (Table 17). Arthropods were mainly gathered in the canopy and subcanopy layers of trees, while vegetable matter was obtained by birds visiting feeding sites of domestic animals. The main bulk of the 25 food samples that I took from young birds consisted of large items such as wood-boring beetles (Buprestidae), with an average length of 11 mm, tree crickets (Gryllidae), averaging 20.6 mm, larvae and pupae of moths (Olethreutidae and Noctuidae), the larvae averaging 11.9 mm and pupae averaging 14.1 mm, and arboreal spiders (Anyphaenidae) with a mean length of 9.1 mm. Observations of foraging sites and tactics of the blackbirds (Table 18) and the behavior of the arthropods showed that the blackbirds get most of their food by probing into crevices in trunks and branches, epiphytes, and leaf clusters. Most of the forms brought to the young are either always hidden (Buprestidae and immature Olethreutidae) or are nocturnal and hide during the day in crevices, leaf clusters, or epiphytes (Noctuidae, Gryllidae, and Anyphaenidae). Among the noctuids collected from nestling *A. xanthomus*, *Melipotis* sp. were common. Larvae of these moths feed in the tree canopy at night and during the day move down the trunk to hide in crevices in the bark, which is also screened by surrounding shrubs. They also pupate in these sites (D. H. Habeck, pers. comm.). Immature Olethreutidae, the most common food delivered to young blackbirds, infested leaf buds of red mangroves, where I often saw Yellow-shoulders probing.

Small arthropods such as leafhoppers (Fulgoridae), about 2 mm, were occasionally taken (Table 17). These insects infested patches of scrub such as *Bumelia* spp. One leafhopper, *Petrusa epilepsis*, was utilized by groups of warblers and was so abundant that foraging birds flushed 5-10 insects with each move (Post 1978). I saw Yellow-shoulders take these only four times. The long distances that nesting blackbirds often flew to gather food for their young may have precluded their bringing such small items to the nests (Emlen 1966), and they may have been used mainly by the adults that encountered them while searching for larger items. Yellow-shouldered Blackbirds may have delivered small items more frequently than my samples indicate because small pieces of food may slip past neck collars (Orians 1966).

When delivering to the young, adults usually carried more than one arthropod at a time. They also regurgitated food from their gullets, mainly plant material and occasional small fragments of arthropods. I determined this by collecting food from the throats of some collared young immediately after I saw a parent regurgitate material to them. Vegetable matter appeared in 15 of the 25 food samples I collected (Table 17): rice or grain (7 out of 25 samples), bread or flour products (5 of 25), and monkey chow (4 of 25). The average representation by volume of vegetable material in the 15 samples was 29%, range 5-100%.

Birds nesting offshore usually foraged in trees in pastures along the mangroves, flying up to 2 km between these sites and their nests. I also saw Cay-nesting birds foraging in red mangroves near their nests. Birds nesting in red mangroves occasionally fed on the roots and trunks, but a cursory examination of these sites revealed few arthropods, possibly because of the high tannin content of red mangrove bark.

In salinas the birds did not forage on the open mud around their nests. Birds nesting in salinas occasionally foraged on the trunks and branches of dead mangroves, although they most often flew relatively long distances (0.5-1 km) to forage in trees in pastures. These birds, as well as those nesting in the pastures themselves, did not forage for arthropods on the ground there either.

The foraging behavior of Yellow-shoulders varied. On trunks and branches they used their bills to probe crevices, flake off pieces of bark, and enlarge holes. Yellow-shoulders gaped inside crevices, fruit, buds, and cocoons. Individuals clung to the sides of vertical trunks or to the undersides of branches to probe or to glean surfaces. Birds gleaned leaves and twigs as they walked along branches, but more often they flew between leaf clusters. They commonly probed epiphytes (*Tillandsia recurvata),* usually standing on top of the tangled balls of vegetation and inserting their beaks up to the base of their skulls in the clumps, but sometimes they hung under the clumps to probe the undersurfaces. Other species I saw probing the *Tillandsia recurvata* clumps were Adelaide's Warblers (*Dendroica adelaide)* and Black-cowled Orioles (*Icterus*

TABLE 17. – Food brought to young in nests at La Parguera, 1974-1975.

Order or Group Family and stage	Number of samples[1] in which found	Total No. found	[3]Length (mm)	
			Average	Range
Lepidoptera				
Olethreutidae, larvae	14 (56)[2]	46 (28.2)	10.4±3.6	5-22
pupae	4 (16)	4 (2.5)	7.0	7
Noctuidae, larvae	4 (16)	10 (6.1)	18.7±1.6	15-20
pupae	3 (12)	31 (19.0)	15.0±0	15
Unidentified pupa	1 (4)	1 (0.6)	7.0	-
Araneae				
Anyphaenidae	10 (40)	16 (9.8)	9.1±1.5	6-12
Salticidae	5 (20)	6 (3.7)	7.4	5-12
Araneidae	2 (8)	2 (1.2)	7.5	5-10
Unidentified	5 (20)	5 (3.1)	7.6	6-10
Orthoptera				
Gryllidae	7 (28)	16 (9.8)	20.6±7.0	5-30
Blattidae	1 (4)	1 (0.6)	6.0	-
Homoptera				
Fulgoridae	2 (8)	17 (10.4)	2.0	2
Tropiduchidae	1 (4)	1 (0.6)	piece	-
Coleoptera				
Buprestidae	2 (8)	3 (1.8)	11.0	10-13
Elateridae	1 (4)	1 (0.6)	10.0	-
Unidentified	1 (4)	1 (0.6)	piece	-

Hymenoptera				
Unidentified	1 (4)	1 (0.6)	piece	-
Arachnida				
Unidentified	1 (4)	1 (0.6)	5.0	-
Vegetable Matter[3]				
-	15 (60)	-	-	-
Total	25	163	-	-

[1] One sample is the food from all young of nest during 1 h period.
[2] Values in parentheses are percentages of total.
[3] Bread, rice and monkey chow.

TABLE 18. – Foraging behavior of the Yellow-shouldered Blackbird during breeding season (May-September).[1]

	Foraging Zone								
	Canopy			Subcanopy			Herb	Ground	Total and
Foraging Tactic	Outer	Middle	Inner	Outer	Middle	Inner	Layer	Layer	(Percent)
Gleaning Leaf	28[2]	3	2	25	28	9	5	0	100 (15.4)[3]
Gleaning Twig	3	1	0	17	17	5	0	0	43 (6.6)
Gleaning or Probing Branch	15	1	1	22	29	44	0	0	112 (17.3)
Flycatching and Hovering	18	0	0	3	2	32	0	0	55 (8.5)
Chasing	5	0	0	0	0	0	0	12	17 (2.6)
Probing Flower	1	0	0	0	0	0	38	0	39 (6.0)
Probing Fruit	1	0	0	2	5	5	0	14	27 (4.2)
Probing Terminal Bud	1	2	1	21	6	16	0	0	47 (7.3)
Probing Epiphyte	46	0	0	96	27	8	0	0	177 (27.3)
Pecking Ground	-	-	-	-	-	-	-	31	31 (4.8)
Total and	118 (18.2)	7 (1.1)	4 (0.6)	186 (28.7)	114 (17.6)	119 (18.4)			
(Percent)		129 (19.9)			419 (64.7)		43 (6.6)	57 (8.8)	648(100.0)

[1] Does not include foraging at human food sources. See methods section for procedures.

[2] Number of times behavior was performed in each foraging zone.

[3] Number in parentheses are percent of total observations.

dominicensis), both of which were rare in the pastures where these epiphytes were common. I saw Yellow-shoulders flycatch, most often after they had flushed insects as they moved, but occasionally they sat on exposed perches and sallied.

When foraging on the ground, Yellow-shoulders walked, occasionally scratching with one foot. They gaped under monkey biscuits to turn them over, thereby pushing the food away from the body. Orians (1961) saw Red-winged Blackbirds turn rocks by this method. Yellow-shoulders also turned the food over with their closed mandibles. Individuals also inserted the lower mandible under monkey biscuits and lifted them toward the body. Yellow-shoulders used the sides as well as the tip of the beak to break off material from large pieces of food, the sides of the beak being moved back and forth in a shearing motion.

The birds probed for nectar commonly in January and February when *Aloe vulgaris* was blooming, and during this period small groups were in constant attendance at patches of aloe. They probed flowers by inserting their beaks up to the bases of their skulls, gaping to enlarge the entrances. On one occasion I noted three Yellow-shoulders probing Yucca flowers. Wetmore (1916) saw Yellow-shoulders probe bucare (*Erythrina* sp.) blossoms, and Danforth (1926) reported Yellow-shoulders taking nectar from guama *(Inga laurina),* as well as fruits of several species of cacti, e.g. *Selenicerus* sp. and *Cephalocereus royenii.*

During the nesting period, adult *A. xanthomus* foraged mainly in the subcanopy (64.7% of 648 observations; Table 18) and canopy (9.9%) layers of trees. Within these layers most foraging maneuvers were performed in the outer zones. Probing epiphytes, the most common foraging tactic, composed 27.3% (177 of 648) of the maneuvers observed. Of the total, 21.9% were preformed in the outer canopies and subcanopies. Similarly leaf gleaning, the third most common foraging tactic, occurred mainly in the outer zones of the canopy and subcanopy (8.2% out of a total of 15.4%). Gleaning and probing of branches occurred mainly in the subcanopy (14.7% out of 17.3%), the zone of vegetation which has the greatest mass of branches. Flycatching was a relatively important activity, and it occurred mainly (4.9% out of 8.5%) in the inner subcanopy, which was relatively open in vegetation such as red mangroves, and where lower turbulence may have allowed easier capture of flying insects. Flycatching and hovering also took place in the outer canopy and subcanopy (2.3% of total). Probing of terminal buds was accomplished mainly in the subcanopy (6.6% of total), and most of this activity was seen in red mangroves. Most flower probing, a relatively uncommon behavior in the breeding season (6%), involved aloe, and therefore occurred in the herb zone.

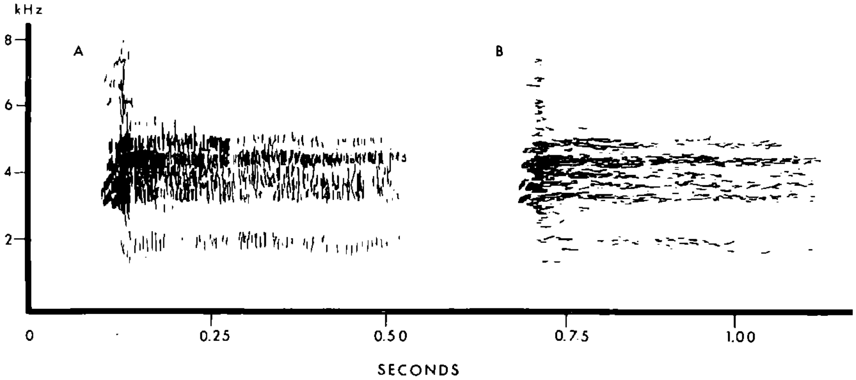

FIGURE 8.—Sound spectrograms of Yellow-shouldered Blackbird vocalizations. (a) growl, wide band filter; (b) same as preceding, but with narrow band filter.

VOCALIZATIONS

GROWL.—Lasting about 1 sec, this sound is composed of a short introductory note and a buzzy trill. The click-like introduction extends beyond 16 kHz, and resembles a *chwip* or *check* call (below). The introductory figure is probably imperceptible to humans, as it is overlapped temporally by the more audible buzz component, which has a frequency range of 1.5-5.0 kHz, with energy concentrated at 4-5 kHz (Fig. 8). I noted some individual variation in the structure of the growl, such as interruption in the trill, abbreviated and lengthened trills, as well as incorporation of other vocalizations such as *gueea* in the beginning of the vocalization.

The growl is probably homologous with those vocalizations given during "song-spread" (Nero 1956a) by other icterids. The structure of the growl resembles the trill part of the buzzing song of the Yellow-headed Blackbird *Xanthocephalus xanthocephalus* (Orians and Christman 1968; Figure 14b).

Both sexes utter growls during the song-spread and during wing-raise. With song-spread the growl is given as the wings reach their full height, the sound continuing as the wings are lowered. No head movements are associated with the utterance of growl, but the beak is opened (see Action Patterns). The rate of singing varied from 1.2 to 2.3/min by some birds perched near their nests, while others in communal roosts wing-raised (with growls) 12 to 17 times/min. Juveniles sometimes rapidly uttered a short, muted growl accompanied by a wing-raise. These may have been examples of subsong (Thorpe 1961).

On nesting areas growls as well as *pee-puus* (see below) were exchanged by neighboring birds that were out of each other's sight. In April

Table 19.—Contagion of growls on nesting grounds.

No. of growls initiated per 10 consecutive sec interval[1]:	0	1	2	3 or more
Observed	267	83	51	17
Expected[2]	238	134	38	7

[1] Observation periods, totalling 70 min, were each 300 sec long.
[2] Calculated from the Poisson series. The observed number of calls in each category is significantly different from the random distribution ($\chi^2 = 41.7$; $P < .001$; d.f. = 3).

1975 I recorded the incidence of growling by individuals in groups of 6-8 that were visiting nesting sites in the red mangroves on W. Matita. I found a significant contagion between growls: a growl from one bird was usually followed within an unexpectedly short interval by one or more growls from other individuals (Table 19). Birds sitting next to each other and engaging in song spread occasionally initiated growls and *pee-puus* before neighbors had terminated their growl, and in several instances 3 or 4 individuals overlapped their growls to form a continuous sound lasting about 4 sec.

As discussed under wing-raise, growls as well as *gueeas* were sometimes repeated erradically in mass by flocks of birds that were mobbing humans, or at least reacting to their presence. These may have been instances of group performance of antipredator strategy (Smith 1977), as the "indefinably confusing, all-pervading sound" (Grinnell 1903) made localizing any one individual difficult.

Rasp.—This call, rendered *vvvt*, is structurally similar to growl, although its fundamental is lower, at about 1.5 kHz, with discernible overtones at 3 and 4.5 kHz. To humans the call sounds thinner and less resonant than a growl. The rasp was heard only during agonistic encounters, and it was uttered by flying birds or by ones about to fly, as when preparing to dive at predators. Yellow-shoulders also gave the call when supplanting and being supplanted from feeding positions.

Greeah.—This call, which sounds to me like the scold of the Red-eyed Vireo (*Vireo olivacus)*, has a complaining, nasal quality. I heard it on numerous occasions, but only in the vicinity of nests, and most often from parents around the time young were fledging. It was associated with a tendency to fly or move. With disturbances near the nest, both sexes gave the call as they moved around, often accompanying each other. In addition, I once heard *greeahs* given by a fledgling that was being fed near its nest. The female that was feeding it also gave *greeahs.* On another occasion a female that was mobbing me wing-trailed while giving *greeahs.* The nearby young gave *pink* calls (below) and moved toward the *greeah*-calling female. Individuals often uttered *greeah* when they engaged in

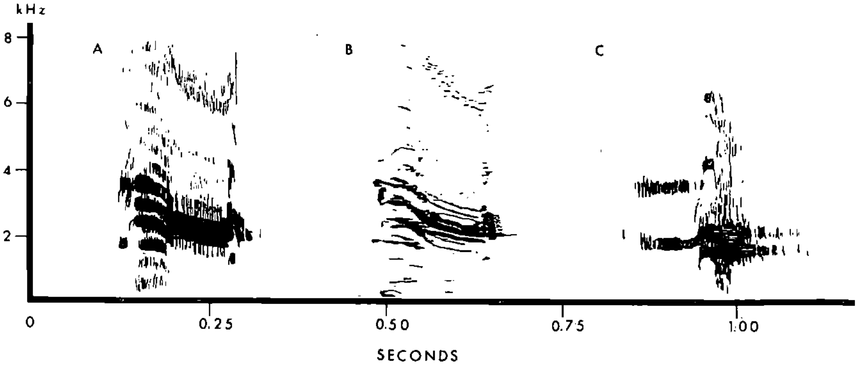

FIGURE 9.—Sound spectrograms of *cut-zee* type vocalizations. (a) *cut-zee,* made with wide band filter; (b) same as preceding, but with narrow band filter; (c) a *tslink* variants, wide band filter.

moth flight. On one occasion I noted that a male's *greeahs* merged into growls, given with song-spread.

SCREAM.—This harsh noise is similar in structure to screams given by other icterids (Orians and Christman 1968, Figure 21d). The scream was most often uttered by birds that were being handled, but also by those confined in nets or traps.

CUT-ZEE.—A common alarm call with much individual variation, *cut-zee* is composed of two parts: a short introduction followed by a slightly longer, falling element. There is temporal overlap in the two figures, indicating the use of two or more syringeal membranes (Fig. 9).

Both sexes utter *cut-zee* when mobbing of predators around nest sites, and I also heard it throughout the year in feeding and roosting areas. *Cut-zee* is given with or without wing-raise and tail flip. Wing-trailing birds also give *cut-zee.* It is occasionally combined with other vocalizations: on 25 May 1974 female XAGR, 4 m from her nest, in 3 min gave eight *cut-zees* that intergraded into growls. Some of these combinations were repeated rapidly with only a 5-sec lapse.

During mobbing *cut-zee* is often associated with *checks* and *queeas.* The information provided by *cut-zee* is probably similar to that made available by *queea,* but *cut-zee* appears to be used in more intense mobbing, as indicated by the closer approach of *cut-zee* calling birds to predators. Nestling Yellow-shoulders may recognize *cut-zee* as an alarm. On 25 June 1974 a female perched under her nest repeatedly gave *chwips,* while the young continued to beg loudly. The female then began uttering *cut-zees,* and the young immediately became quiet. Occasionally only part of *cut-zee* is given; the second note, *zee,* or a close variant sounding like *tslink,* was recorded (Fig. 9). On other occasions this sound was repeated rapidly in flight, sounding like *zeenk zeenk zeenk.*

QUEEA.—*Queea* is composed of two figures, the fundamental of the first being about 3.5 kHz, with two discernible harmonics. The second note, which temporally overlaps the first, falls slightly in pitch, and has its fundamental at about 5 kHz (Fig. 10). This variable call is occasionally repeated in series with wing-raises, and is often combined with other vocalizations such as growl and *chwip*. *Queea* is usually given with tail flip.

Queea is frequently given by birds mobbing predators, such as humans, monkeys, or cats, or by birds that are disturbed in any way. The call is also given by females that are being pursued persistently during sexual chases.

Average rate of calling was 18/min, range 7-28/min (602 calls from 13 birds timed for 30 min). *Queea* is given in association with other sounds such as *check*. For example, on 18 February 1975 male RARG, sitting with two other Yellow-shoulders, gave 13 *queeas*, 20 *checks*, and 1 growl as I approached, switching from *check* to *queea* each time I moved.

Although *queea*-type calls appeared to be used most often as alarms, I also noted that they were occasionally used when birds seemed to be undisturbed. At these times the call was often given rapidly with wing-raises, 2-6 times in succession, to form what sounded like a chatter. When repeated rapidly as a chatter, *queea* may function as a social or contact signal between members of feeding flocks or nesting groups. This chatter may be homologous with the female song of the Red-winged Blackbird (Nero 1956a).

CHWIP.—Relatively simple in structure (Fig. 10), *chwip* resembles *check* of the Yellow-headed Blackbird (Orians and Christman 1968; Fig. 20p-r). Young in the nest begin to give *chwip* when they are 6-7 days old,

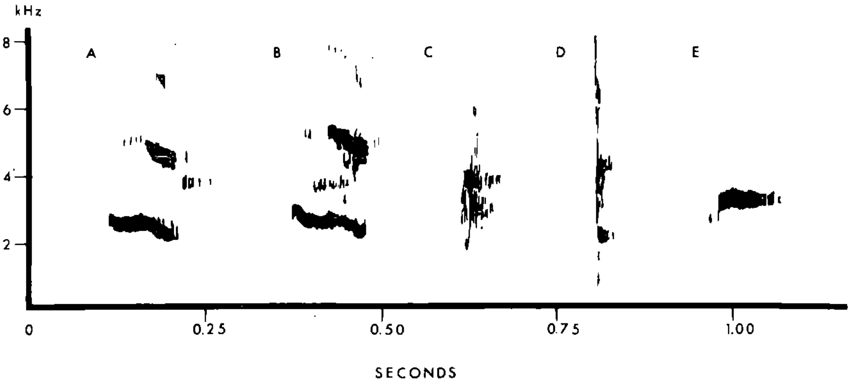

FIGURE 10.—Sound spectrograms of Yellow-shouldered Blackbird vocalizations, all made with wide band filter; (a) *queea*, variant 1; (b) *queea*, variant 2; (c) *check*; (d) *chwip*; (e) *pee* (first part of *pee-puu*).

so after begging calls and *pink* (below), it is one of the first vocalizations young Yellow-shoulders give. *Chwip* is used in practically all situations, by birds in flocks or alone, flying or sitting, and may indicate that a bird is seeking association, may fly, escape, or is indecisive. *Chwip* is usually accompanied by tail-flip. Average rate of calling was 14/min, range 1-41/min (36 birds timed for 75 min).

CHECK.—Somewhat more structured than *chwip*, *check* shows a distinct harmonic, and the call lasts about twice as long. The energy of *check* is centered around 4 kHz, but the call extends over a wide frequency (Fig. 10). *Check* is given by birds that are scolding predators, are engaged in agonistic encounters, or possibly are disturbed in some way. *Check* probably provides information about the individual's readiness to attack, escape, or fly, or indicates that it is acting indecisively. It is often uttered in association with other vocalizations that function as alarms, such as *queea*, *cut-zee*, and *chwip*. The associated action pattern is the tail-flip. Average rate of calling was 13/min, range 1-47/min (16 birds timed for 30 min).

PEE-PUU.—The *pee-puu* is composed of two components: the introductory *pee* is a clear, slightly rising note, while *puu*, also unslurred, falls in pitch. This vocalization, for which I have a spectrograph for only the *pee* component (Fig. 10), probably functions mainly in communication between paired individuals. I frequently heard it on nesting grounds, and *pee-puus* from females were usually answered by growls from their males. On 5 August 1974 male GABR inspected his nest. His female, XAGR, perched 4 m away, gave a *pee-puu*, which was immediately followed by the male's song spread. The female repeated her *pee-puu* 30 sec later. On 11 April 1975 male GYGA, perched next to a 1974 nest, in 3 min gave nine song-spreads, each immediately followed by a *pee-puu* from the female with whom he was associated. These *pee-puus* were also returned by neighboring birds.

PINK.—To my ear, *pink* sounds remarkably like the flight note of the Bobolink. It was given as a contact call between young and their parents. I first heard the call given by nestlings when they were six days old. Free-flying young gave *pinks* as they followed their parents about, either singly or as a double call. Adults leading their young in flight also gave the call. Rate of utterance by one young just fledged on 1 July 1974 was 122 in 3 min.

FLIGHT SERIES.—A flight series, usually uttered when birds were first air-borne, appeared to have no unique components, but rather was a composite of different calls, such as *cut-zee*, *queea*, *pee-puu*, and *chwip*. I noted a large amount of individual variation in the composition of the call. The call was given all year, in the winter from birds leaving feeding flocks or secondary roosts, but most commonly during the nesting period from birds that were leaving their nests on distant feeding flights. The flight vocalization may be important as a means of contact between mated birds traveling between nesting and feeding areas.

ACTION PATTERNS

SONG-SPREAD.—Initially the head may be pointed upward (Fig. 11). After about 2 sec the bird lowers its beak and begins to raise its wings, the tail becoming increasingly fanned and the body plumage fluffed. The wing elevation phase takes about 1 sec, at the end of which the beak touches the breast and the ventral plumage is ruffled (Fig. 11). The wings are held up for about 2-3 secs, and lowered in about 1 sec, then the head is again pointed up. During wing elevation the carpus is rotated forward, providing maximum frontal exposure of the epaulets. I noted much individual variation in song-spread, mainly in asymmetry of wing and leg positions and in angle of body tilt. The bill-up at the start of the song-spread was sometimes omitted, but the terminal bill-up was nearly always present.

Both sexes sing in many situations, but most commonly in (1) close quarter agonistic encounters with conspecifics, usually near the nest, but also in feeding flocks and roosts; (2) the presence of predators in the nest vicinity; (3) instances when mated birds meet near their nest; (4) agonistic encounters with other bird species; and (5) nest-site advertisement by the male (see below).

Representative rates of singing are (1) 9 times in 3 min by a male near his nest and mate; (2) 18 times in 15 min by a male near his nest; and (3) 17 times in 7.5 min by a female near her nest. The only vocal signal that I heard given with song-spread, and one that accompanied it invariably, was the growl, which lasted about 1 sec, and was initiated as the wings reached their full elevation.

WING-RAISE.—Less complex than song spread, wing-raise may correspond to a less ritualized stage of the former display, in which some components are lacking (bill-up and bill-down) and others are less exaggerated (wings and body plumage not as elevated). In the less extreme form, the carpus may be rotated upward only slightly, with the tips of the remiges remaining in contact with the body. In the more extreme form, the wings may be spread and raised more fully, but the tips are seldom raised more than 30° above the horizontal.

Wing-raise is usually repeated rapidly, every 3-5 sec; in April 1975 a juvenile Yellow-shoulder sitting alone in the mangroves wing-raised 55 times in 4 min, giving an abbreviated growl with each wing-raise. This may have been an instance of practice singing (see p. 182).

Wing-raise occurred in the following situations: (1) during close-quarter intraspecific and interspecific agonistic encounters on and off

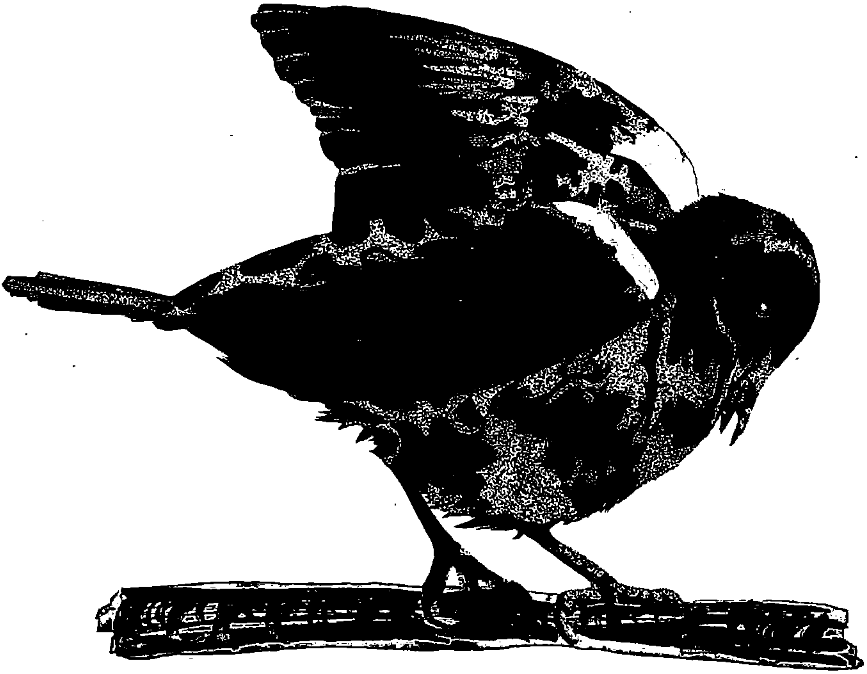

FIGURE 11.—Song-spread of the Yellow-shouldered Blackbird, showing lateral (a) and frontal (b) aspects.

nesting grounds; (2) during mobbing of predators; and (3) when a bird was alone, either on or off nesting areas. Rapidly repeated wing-raises, given with growls and *queeas,* were occasionally uttered in mass by birds sitting close together in roosts. These massed displays seemed to be elicited by disturbances and may have been instances of group mobbing or confusion chorus (Grinnell 1903).

Vocal signals given with the wing-raise were growl, *pee-puu, queea,* chatter (*queea* in series), and *cut-zee.* When repeated rapidly, the wings may be lowered and raised with each utterance, as usually occurred with growls, or they may be held up continuously and fluctuated only slightly with the repetition of each vocalization, as usually occurred with chatter.

BILL-UP.—In this posture the head is rotated upward, near the vertical. The neck may be extended, normal, or contracted. The body plumage is normal or fluffed, while the wings are folded normally or drooped slightly. The displaying bird may gape. I saw bill-up throughout the year, but only in close-quarter interactions, in feeding, roosting, and nesting areas. Yellow-shoulders gave bill-ups to other Yellow-shoulders as

well as to grackles, cowbirds, and Troupials. Mated birds also gave bill-ups when near each other. Bill-up appears to have become incorporated into the beginning and ending of the song-spread. Bill-up displays are widespread among icterids and other passerines (Nero 1956a, Andrew 1961).

BILL-DOWN. — The head is lowered and the bill is pointed toward the abdomen. The head plumage may be ruffled. Yellow-shoulders give the bill-down when near conspecifics in situations similar to those in which they gave bill-ups, but the posture may indicate a greater tendency to escape or a greater conflict between escape and attack than does bill-up. Bill-down is also often given by birds that are moving or about to move while in the presence of conspecifics. Unlike bill-up, the display is given by birds that are alone. Andrew (1961) suggested that bill-down ("bill lowering") is an example of a "reverse movement" to bill-up ("bill raising") in species in which the latter has a threat function, e.g. it may act as an appeasement gesture. In this regard it is interesting that bill-down has been incorporated in song-spread and wing-raise.

HEAD-FORWARD. — In this posture, similar to that described for other passerines (Andrew 1961), the head is extended toward an opponent, while the legs may be flexed and plumage normal, fluffed, or sleeked (see illustrations in Post and Wiley 1976). The wings may be raised slightly at the shoulders and the bird may gape. Head-forward was seen most often in agonistic encounters at feeding sites, and it was frequently preceded by bill-up.

HEAD-IN. — The bird usually crouches, bringing its head in to the body. The body plumage may be fluffed or ruffled. The beak is often directed at the nearby individual, and perhaps gaped. This posture is seen most often during agonistic encounters in the feeding areas, but occasionally near nests by birds that are challenged upon entering the activity spaces of others. Males also occasionally give the head-in when they approach females that are giving wing flutter.

WING-FLUTTER. — The body feathers are fluffed, and belly feathers ruffled, while the wings are held out from the body and vibrated. The legs are flexed. The tail is spread, and may be elevated or held normal. Wings are occasionally raised asymmetrically when they are fluttered.

I saw this display from females that were begging food from their mates or soliciting, usually near their nests. Once a male gave wing-flutter repeatedly to a female that had just been released from a trap. The female was trying to remove her bands and exhibited no special behavior. Another time a male wing-fluttered in the presence of a female that was nest-building. In many species wing vibration in male courtship is probably homologous with female precopulatory display (Andrew 1961). Wing-flutter of both male and female Yellow-shoulders resembles the precopulatory displays of Red-winged Blackbirds and other icterids (Nero 1956a).

On those few occasions when I saw copulation, prior to it the female's tail was above the horizontal, while on other occasions males were repulsed by wing-fluttering females whose tails were held normally. The head-up tail-up variant is homologous with the female precopulatory display of other female passerines (Andrew 1961), but other than the position of the tail, there is little difference between this form of the display and that given when a female begs for food. The wing-flutter probably functions as a distance decreasing mechanism when mated birds are attempting to approach one another. Some males brought food to brooding or incubating females, and the females wing-fluttered and gaped for food only when they both were at the nest. In the case of males that did not regularly deliver food to females, their mates often food-begged and wing-fluttered when the males arrived at the nest with food for the young and the females were present. The females took the food, sometimes mandibulated it, and then gave it to the nestlings.

WING-TRAIL.—As the bird walks slowly, the wings are lowered at the carpals and the remiges are spread so that the feathers may touch the ground. Body feathers are raised to varying degrees, but the rump feathers are usually ruffled. The rectrices are spread and may also drag the ground. The beak is horizontal or pointed slightly down. Wing-trail was given by both sexes when I approached nests containing young. On several occasions I handled young without their parents' wing-trailing, but when the young screamed, the adults began to wing-trail and also utter screams. Other vocalizations given with wing-trail were *queea*, *chwip*, *greeah*, *cut-zee*, and *check*. When used by parents whose young are threatened, the wing-trail may be a relatively unritualized form of distraction display, as described for many other passerines, including Red-winged Blackbirds (Orians 1973) and Bobolinks (*Dolichonyx oryzivorous*) (Nero 1955).

MOTH FLIGHT.—This display takes the form of short flights in which the wings are moved slowly and with small amplitude. I saw this peculiar flight pattern given only by females around their nests. Females gave moth flights when either approaching or leaving the nest and the male was near it. Once moth flight preceded the female's wing-trailing, and several times it preceded wing-fluttering. Females gave the display frequently around the time the young fledged, especially when a human was near. At these times many short moth flights were accompanied by vocalizations such as *greeah* and *cut-zee*. As pointed out by Andrew (1956), moth ("impeded") flight may occasionally form part of distraction display, and in general appears in situations of strong conflict between escape and approach tendencies. On the other hand, it may also be used during courtship, as by male Red-winged Blackbirds during symbolic nest-site selection (Nero 1956a).

MALE NEST ADVERTISEMENT.—Although females actually construct nests, during the period of early pairing males stand in the cups of old nests and pull or jab at nest material. They also try to form the nest cup by crouching and pushing against its edge with their breasts. Sometimes males carried nest material away from the nest, but usually dropped it nearby. All of these activities are associated with the presence of a female with which the male is attempting to pair. Symbolic nest-building by males of species in which only the female constructs the nest has been recorded for several other icterids (Nero 1956a). According to Nero's descriptions, in the Red-winged Blackbird this behavior seems to be more fully developed than in the Yellow-shoulder, and seems to be associated with the period of egg-laying rather than that of pair establishment.

TAIL-FLIP.—The tail is moved rapidly up and down (duration about 1.3 sec). During tail-flip other body parts are usually positioned normally. Tail-flip is given in all situations, with nearly all vocalizations. Typically, a call such as *chwip* or *check* was uttered as the tail reached its highest point or was just beginning to be lowered. Rate of tail-flipping varied; for example, a bird that was mobbing humans gave 54/min, while a preening bird gave 4/min.

SLEEK.—The body plumage is compressed, while the bird may flex its legs, indicating a tendency to fly. Occasionally the bird assumes an erect posture and sleeks the neck and breast feathers, in which case sleek may indicate readiness to fly at an opponent. Sleek is probably homologous with similar postures of other icterids (Orians and Christman 1968).

FOOD-BEGGING.—Begging postures of young Yellow-shoulders are similar to those described for other icterids. The head is held in, the beak is pointed up and gaped. Wing tips are held into the body, while the wing is vibrated at the carpus. I saw food-begging by young that had been out of the nest 24 days.

BREAST-TO-BREAST FIGHTING.—Fighting occurs frequently in territorial disputes, and also at feeding locations. Opponents rise in the air, clawing at each others' breasts and beating their wings against one another. Occasionally protagonists fall in the water while fighting. Breast-to-breast fighting is sometimes preceded by a form of pouncing, in which an attacking individual hops with outstretched feet on the opponent's back.

SEXUAL CHASING.—Infrequently I saw group sexual chasing, such as described for Red-winged Blackbirds (Nero 1956a). On the nesting cays 2-4 birds occasionally chased a female, ending in one bird's pursuing her down into the mangrove roots, and even into the water. These chases were accompanied by loud calls of *queea, check*, and *cut-zee*.

BILL-WIPING.—Under relevant conditions, bill-wiping serves to clean the bill, usually after feeding or preening. The bird simply wipes one side of the beak from base to tip on a branch, then perhaps repeats on the other side. These movements also occurred often in seemingly irrelevant circumstances, and more frequently than body maintenance alone seemed to warrant. On 15 February 1973 a bird waiting to feed inside a monkey cage bill-wiped 24 times in 105 secs. It was probably showing strong conflict between approach and escape tendencies, as during the same period it gave 33 *queeas*, each with a tail-flip. Bill-wiping was also common during mobbing.

DISCUSSION

The distances that nesting Yellow-shoulders commute to gather food suggest that food distribution is not the determining factor in nest placement. Considering: (1) the energy costs of flying to foraging sites, (2) that birds do not seem to exchange information about the location of food, and (3) that food is not highly concentrated within the large areas (e.g. groves of trees in pastures, scattered trees in savannahs, mangroves) foraging blackbirds visited, one would expect nests to be spaced uniformly within the feeding areas (Horn 1968; Waser and Wiley 1979). Wiley and Wiley (1980) found a similar discrepancy between food distribution and ideal nest locations in their study of the Yellow-hooded Blackbird in Venezuela. These birds nested in small patches of suitable marsh vegetation and flew, independently of each other, long distances outside the nesting marshes. Similar examples of limited nest sites and widespread feeding grounds occur in populations of Clay-colored Sparrows (*Spizella pallida*) (Knapton 1979) and Seaside Sparrows (*Ammospiza maritima*) (Post 1974). In these cases the critical factor may be finding secure nest sites, and the energy budget model (Horn 1968), which considers nest distribution a function of food supply, is not appropriate, or food may not be limiting in any of these situations. Adult Yellow-shouldered Blackbirds usually delivered 3-6 items per trip to the nest, indicating that food was readily available. In contrast, female Red-winged Blackbirds in Costa Rica (Orians 1973) and Yellow-hooded Blackbirds in Venezuela (Wiley and Wiley 1980) usually delivered one item per nest visit.

The varied foraging behavior of the Yellow-shoulder may be attributable to ecological release (Crowell 1961, 1962). Reduced competition on islands may allow a species to use niches occupied by other forms on continents. The Yellow-shoulder uses some foraging maneuvers and foraging sites that in adjacent continents are preempted by woodcreepers (Dendrocolaptidae), woodpeckers (Picidae), and wrens (Troglodytidae): probing and gleaning the branches and trunks in the inner zones of trees. Only one member of these families, the Puerto Rican Woodpecker

(*Melanerpes portoricensis*) is sympatric with *A. xanthomus*. In the SW coastal zone where the Yellow-shoulder was most common, the Puerto Rican Woodpecker was rare. Another niche *A. xanthomus* occupied is that of orioles: gleaning leaves and probing leaf clusters and terminal buds in the outer zones of trees, and probing fruit and flowers in all strata. Only one species of oriole, *Icterus dominicensis*, is native to Puerto Rico, and it is uncommon in the habitats *A. xanthomus* occupies. An introduced oriole, *Icterus icterus*, was fairly common in the SW coastal zone, but it foraged in the herb layer and was mainly frugivorous (Post, unpubl. data).

The phenomenon of expanded niche use in the absence of competition is well illustrated by the behavior of the Jamaican Blackbird (*Nesopsar nigerrimus*), closely related to *Agelaius* (Bond 1950, Cruz 1978, Wiley and Cruz 1980). Like *A. xanthomus*, *N. nigerrimus* is arboreal, and a prober of epiphytes (58% of its observed foraging activity, Cruz 1978) and branches and trunks (10%). The Jamaican Blackbird forages more on the trunks and inner branches and less in the outer zone of trees than does the Yellow-shouldered Blackbird. In the Jamaican habitats Cruz (1978) studied, the Jamaican Oriole (*Icterus leucopteryx*) foraged mainly in the outer parts of trees.

The foraging behavior of the Yellow-shoulder has diverged from that of marsh-dwelling *Agelaius*, most species of which are ground feeders in the breeding season. This difference may be a result of reduced competition combined with scarcity of marsh habitat on Puerto Rico. In North America Red-winged Blackbirds occasionally feed in trees (pers. obs.). Another West Indian *Agelaius*, the Tawny-shouldered Blackbird, is probably arboreal in the breeding season (Lack 1976) and also nests in palms (Barbour 1923).

That the two insular species, which presumably evolved from a marsh-dwelling form similar to *A. phoeniceus*, are partly arboreal may be attributable to the elimination of Cuban marshes during the post-Pleistocene rise in sea levels, though Bond (1950) considers it more likely that the ancestor of *A. humeralis* and *A. xanthomus* evolved arboreal foraging behavior during a period of competition with the Red-winged Blackbird (*A. p. assimilis*), which occupies marshes on Cuba. Whether the ancestor of *xanthomus* was arboreal when it arrived on Puerto Rico is conjectural, but there may have been some large marshes such as those that existed until recently in the Yauco-Boquerón Valley, covering an area of about 150 km^2 (Danforth 1926).

The Yellow-shoulder uses at least 26 distinct displays and vocalizations. This repertoire appears to be larger than that of other monogamous icterids that have been studied (Orians and Christman 1968), and its size is closer to that of polygynous species such as the Tricolored and Red-winged Blackbirds. Male Red-wings, for instance, have 18 vocalizations and 12 action patterns, females 6 and 9 (Orians and Christman 1968). Estimates of the number of displays of various species vary according to authors' procedures and preferences (Smith 1977). As I lack adequate spectrographic material in some cases, I reserve judgement on variants of some vocal signals. More detailed study of the vocal repertoire of the Yellow-shoulder may reveal it to be larger.

Unlike Red-winged and Tricolored Blackbirds, the Yellow-shoulder has few intersexual differences in its display repertoire. Each sex appears to have only one unique visual display, and all the remaining displays, visual and vocal, are shared by both. Orians and Christman (1968) note a tendency for males of polygynous species to have a larger number of displays than females, this disparity being correlated with their advertising for and holding more mates than monogamous species. The sexual dimorphism reflected in display repertoire is also found in body size and plumage of polygamous species. Hamilton (1961) suggested that as those species breeding farthest from the equator are generally migratory, and on returning to their breeding grounds have little time for pairing, dimorphism is also advantageous in reducing intersexual strife and allowing rapid pair formation. Intersexual differences in display repertoire facilitate rapid mating in these northern species, but species such as the Yellow-shoulder, that pair well in advance of mating, may be under little selective pressure to segregate displays sexually. The ancestral condition was presumably one of intersexual equality in display repertoire size, but with the evolution of non-monogamous mating systems, sexual segregation of displays was accentuated, and eventually each sex appropriated certain displays.

Some differential use of certain displays may occur in the Yellow-shoulder, such as has been shown for the Black-capped Chickadee, *Parus atricapillus* (Ficken et al., 1978). Examples of different degree of usage by each sex probably occur in *pee-puu* and *queea* in series (chatter), both used more often by females, and (single) *queeas* used more often by males in mobbing.

Among species of North Temperate icterids that are not cryptic, those having large territories usually have more displays than others that defend only a small area around the nest (Orians and Christman 1968). Yellow-headed and Red-winged Blackbirds have more displays than Brewer's Blackbirds or Common Grackles. This difference is related to the larger number of displays transmitting messages over long distances that the first two species have, such as flight displays and song.

More needs to be learned about the influence of winter social organization on size of display repertoire, but Orians and Christman (1968) suggested that the large number of displays of the Tricolored

Blackbird may be due in part to year-round association of both sexes. A similar effect may occur in the Yellow-shoulder, whose display repertoire is about the same size as that of the Tricolor.

As Wiley (1976a) found for the Common Grackle, few of the vocal signals of the Yellow-shoulder transmit unequivocal information about the internal state of the transmitter, but most vocalizations are given in close-quarter interactions, whether in nesting or feeding places, and more precise information is available to the receiver by reference to context or to accompanying visual display. Most of the Yellow-shoulder sounds are abrupt, broad spectrum signals that are easily located in noisy environments such as exist in nesting colonies, feeding flocks, or roosts.

The growl vocalization given with song-spread has a simpler structure than similar sounds of other icterids. There has probably been little selective pressure for further elaboration of song, because of the small territory size of the Yellow-shoulder, and of relaxation of selection for specific distinctiveness in the absence of closely related species (Grant 1972).

In species occupying large territories, song must be transmitted without distortion over relatively long distance. The song (growl) of the Yellow-shoulder is highly modulated, and it covers a wide frequency range, so it is probably of little use in long-range communication. Rather, the growl is used repetitively in close-quarter interactions, and coupled with action patterns such as song-spread and wing-raise. Song-answering, a form of antiphonal singing that Wiley (1976c) considers to be important in the vocal coordination of Common Grackle pairs, was also characteristic of Yellow-shoulders during their period of pairing and nest site selection. The timing of song-answering is thus similar to that of grackles.

In the Yellow-shoulder, song-spread is always accompanied by song (growl), and growl is invariably accompanied by some form of wing elevation.

In the Red-winged Blackbird, song-spread and song are not always coupled (Peek 1972). Red-wing song is given most often with incipient song-spreads, and also without any wing elevation. The Red-wing's song-spread is used mainly in close-quarter interactions, while its song is used for both long and short range communication. In the Red-wing, the vocal component of song-spread is perhaps diverging in function from the visual component, because of its importance in long-range communication.

Most of the vocal signals of the Yellow-shoulder are emphasized at high frequencies, have wide frequency ranges and are highly modulated. These characteristics make them easily localized and identified, but mainly by nearby individuals in the open, as these characteristics also lead to rapid attenuation and distortion over distance or through dense vegetation such as mangroves (Morton 1975). One vocalization, *pee-puu,* appears to be composed of pure tones, and was used frequently for long-range communication by birds nesting in red mangroves.

Correlated with the historic rarity of predators on Puerto Rico, the Yellow-shoulder has no specialized predator ("hawk") alarm calls as do several continental icterids. Instead, the Yellow-shoulder uses general alarm calls such as *queea*, that appear to have functions besides predator warning. *Cut-zee* seems to be the one vocalization most closely associated with predator mobbing response, and its use is largely restricted to the nest vicinity. Even this degree of specialization is interesting, and possibly *cut-zee* has evolved primarily in response to aerial predators such as gulls and frigatebirds that have probably been present in Puerto Rico since the blackbird's ancestors arrived.

Unlike some open-country icterids, such as the Red-winged and Yellow-headed Blackbirds (Orians and Christman 1968), the Yellow-shoulder does not have stereotyped flight displays, and its flight vocalization is composed of a recombinable series of other signals. Displays related to bonding are also few: wing-flutter, probably homologous with precopulatory displays of other passerines; male nest-building display; and *pink* call, given between parents and young. Displays relating to establishment of pair bonds may be more important for polygynous, usually highly dimorphic species, in which male dominance is well developed, but mollified by the use of these displays to facilitate pairing.

In the presence of predators Yellow-shoulders use a variety of visual displays, but as with vocal displays, no single one has become specialized as a predator warning. As with *cut-zee*, one visual display, wing-trail, occurs mainly in the presence of predators, and it may be homologous with distraction displays given by other passerines in the vicinity of their nests.

CONCLUSIONS

The Yellow-shouldered Blackbird, probably derived from marsh-dwelling and ground-feeding blackbirds of North America, has diverged from the behavior of its closest mainland relatives. Its foraging behavior is similar to that of orioles and woodpeckers. This may be a result of reduced competition, and also lack of suitable feeding sites on the ground, particularly marshes, in Puerto Rico.

The species does not engage in coactive feeding as do some relatives, nor exhibit cooperative breeding, though it aggregates when nesting. As colony sites are isolated from feeding grounds, and the types of food delivered to the young are widely distributed within relatively large patches, it would be predicted, on the basis of maximum foraging efficiency, that nests should be uniformly distributed in the food field. As this is not the case, nest dispersion is probably a result of selective pressure exerted by predation. This conclusion is supported by the frequency with which colony members engage in communal mobbing, the large number of displays and vocalizations used in the presence of predators, the inaccessible sites used for nesting, and the relatively high prevalence of nest predation.

Yellow-shouldered Blackbirds were monogamous in all the habitats in which they were studied. Among other icterid species that nest in colonies and visit remote feeding grounds, polygamy is seen at least occasionally. In the Yellow-shouldered Blackbird, I conclude that the conditions for male emancipation are not realized because of the crucial role of the male in parental care. The mate acquisition and pair maintenance behavior of the species, in which birds affiliate long before breeding, and in which pairing takes place around nest sites of previous years, assures high levels of intra- and interseasonal mate loyalty. A long period of affiliation before breeding may also be advantageous if it allows pairs to respond rapidly to unpredictable events (spring rains). The size and complexity of the display repertoire has probably evolved as a response to pressure for a closely coordinated monogamous pair bond of relatively long duration. The species' social behavior, in the context of its high reproductive success, lack of dispersal, high annual survival, and especially delayed breeding of both sexes implies that a conservative reproductive strategy has been evolved.

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