

## SPACING AND TIMING IN THE NESTING ECOLOGY OF A TROPICAL BLACKBIRD: COMPARISON OF POPULATIONS IN DIFFERENT ENVIRONMENTS<sup>1</sup>

R. HAVEN WILEY AND MINNA S. WILEY

Department of Zoology and Curriculum in Ecology, University of North Carolina,  
Chapel Hill, North Carolina 27514 USA

**Abstract.** Populations of the Yellow-hooded Blackbird *Agelaius icterocephalus* (Icteridae) in northern South America fall into two patterns, according to the seasonal duration of nesting and the spacing of males' territories and nests. These differences among populations of the same species result from interacting adaptations for exploiting food resources and reducing nestling mortality from predators and brood parasites.

All populations breed in marshes, where males defend territories within which they build nests. In moderately seasonal areas, like Trinidad and Surinam, males' territories were 15-50 m in diameter, active nests were 2-10 m apart, and egg laying continued for most of the rainy season. A male often had a succession of females nesting in his territory, but rarely had more than one or two active at any one time. In an extremely seasonal area, the llanos bajos of central Venezuela, conditions were suitable for nesting blackbirds for no more than 2 mo at the end of the rainy season. Blackbirds migrated to this area several months before breeding, males established territories 4-8 m in diameter in discrete colonies, and females laid eggs within a 3-wk period. A male's territory had as many as five nests active at one time. Many small colonies were soon abandoned after massive brood parasitism by Shiny Cowbirds *Molothrus bonariensis*; a large colony nested successfully.

Cowbirds parasitized 33% of nests in this large colony in Venezuela, the same as in populations in Trinidad and Surinam. Male blackbirds chased cowbirds out of their territories and thus restricted opportunities for uninterrupted searching by female cowbirds for blackbird nests. Blackbirds began incubation with the first egg, so a cowbird had to lay her egg within 1 or 2 d to have any chance of success. In Venezuela, cowbirds failed to respond immediately to the sudden availability of blackbird nests in the large, successful colony. Predation accounted for many nest failures, particularly in Trinidad and Surinam, but starvation of some nestlings, especially those hatched last, occurred in the majority of nests that escaped predation.

Females feeding young brought only one item to the nest each trip, an indication that food was difficult to find. They increased their rate of feeding and selected larger items as the nestlings grew. Food for nestlings consisted almost entirely of herbivorous insects, primarily Orthoptera, collected in marshes often several hundred metres from the nest and always outside the male's territory. In Venezuela, suitable insects were sparse and widely distributed in marshes. This situation and the lack of cooperation by females in locating food suggest that aggregated nests probably had disadvantages for foraging. Males helped to feed nestlings at one, or rarely two, nests in their territories. Although males contributed less than the females, nests that received male help on >1 d before day 8 of the nestling period had heavier young on day 8 than did nests that received less male help.

Tropical marsh-dwelling *Agelaius* experience greater nest failure from both predation and starvation of nestlings than do temperate marsh-nesting blackbirds. The staggered hatching of nestling Yellow-hooded Blackbirds, as a result of incubation starting with the first egg, leads to brood reduction, which could have advantages for parents when they confront an unpredictable, sparse food supply, but could also result from parent-offspring conflict over the optimal brood size. Nest building by males permits females to spend all of their time on the best feeding areas until immediately preceding egg laying, presumably an adaptation to sparse food resources at a distance from safe nest locations.

The seasonal restrictions on breeding in the Venezuelan llanos make Yellow-hooded Blackbirds more vulnerable to brood parasitism by cowbirds, except in large, dense, synchronized colonies. Coloniality reduces brood parasitism as a result of the increase in male vigilance permitted by smaller territories. Blackbirds also obtain a "head start" on cowbirds as a result of synchronized laying. Coloniality possibly also reduces predation by solitary predators that detect nests at close range, such as mammals and snakes.

**Key words:** *Agelaius icterocephalus*; brood parasitism; brood reduction; coloniality; polygyny; predation; synchronized reproduction.

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## INTRODUCTION

The Yellow-hooded Blackbird *Agelaius icterocephalus* of tropical South America provides a clear case of variation in social behavior and ecology among populations of the same species. Like its northern congeners, the Red-winged and Tricolored Blackbirds *A. phoeniceus* and *A. tricolor*, Yellow-hooded Blackbirds inhabit marshes where males defend territories within which females nest. In northern South America, populations of Yellow-hooded Blackbirds fall into two patterns. In the extremely seasonal climate of central Venezuela, this species nests in dense colonies during a brief period at the end of the rainy season. In the moderately seasonal climate of coastal areas in Trinidad and Surinam the species nests throughout the rainy season and males defend territories  $\approx 10$  times larger than those in Venezuelan colonies. Our studies of Yellow-hooded Blackbirds indicate that these differences among populations in the spacing and timing of nests, which correlate with differences in seasonal patterns of rainfall, result from interacting adaptations for exploiting food resources and reducing nestling mortality.

The evolution of aggregation and synchrony by nesting birds depends on characteristics of the available food and sources of mortality (Alexander 1974, Bertram 1978). Food with an even, stable distribution within a habitat is not efficiently exploited by birds nesting in aggregations (Brown 1964, Horn 1968, Brown and Orians 1970, Waser and Wiley 1979). Aggregation increases competition among nesting individuals for the nearby food. On the other hand, food in patches that shift unpredictably in location places no constraints on aggregation. Either dispersed or aggregated nests have equal access to the fluctuating patches (Waser and Wiley 1979). Aggregations, however, would have advantages in exploiting spatio-temporally unstable patches of food, if individuals cooperated in locating the patches (Horn 1968, Ward and Zahavi 1973, Krebs 1974). Thus the net effect of aggregated nests on each individual's success in finding food depends on the intensity of competition and possibilities for cooperation.

Aggregation would reduce risks of predation if individuals could cooperate effectively to detect predators at a distance (Pulliam 1973) or to repel them once detected (Kruuk 1964, Hoogland and Sherman 1976). Cooperative defense only works against certain predators on colonial birds. Thus Black-headed Gulls *Larus ridibundus* can effectively repel aerial attacks on their colonies by crows but not attacks by foxes (Kruuk 1964). Aggregation can also reduce each individual's chances of encounter with a predator, provided predators take prey one at a time, search independently, and do not adopt special search strategies after the first contact (Brock and Riffenburgh 1960, Olson 1964, Williams 1964, Patterson 1965, Cushing

and Harden Jones 1968, Hamilton 1971, Vine 1971, Treisman 1975, Taylor 1976). Aggregation is disadvantageous when a predator can decimate a large proportion of an aggregation after discovering it, either by wholesale attack or area-restricted search (Kruuk 1964, Tinbergen et al. 1967, Croze 1970). Predators might also find aggregations more easily than solitary prey, although the zone of detection for a predator might not increase in proportion to the number of prey in a group (Triesman 1975). The consequences of aggregation for the risks of predation, like the consequences for feeding, thus depend in part on possibilities for cooperation among individuals in the colony.

Synchrony in nesting augments the advantages of aggregation. Cooperation of individuals, either in obtaining food or avoiding predation, ordinarily requires temporal as well as spatial coordination of activities. Thus cooperation in finding food would enlist the greatest number of individuals if all had nestlings, and thus faced the maximum demand for food, at the same time (Emlen and Demong 1975). Cooperation in repelling predators would similarly succeed best if all individuals had nests at one time (Hoogland and Sherman 1976). On the other hand, like aggregation, synchrony can increase competition among individuals for evenly distributed, stable food supplies.

Synchrony can also yield an advantage, in conjunction with aggregation, by saturating the functional response of predators, the capacity of available predators to prey on nests (Solomon 1949, Holling 1959, Lloyd and Dybas 1966, Royama 1970, Janzen 1971). In addition to this "saturation" or "satiating" of predators, synchrony might also give nesting birds a "head start" on predators, if predators encountered some delay in detecting or exploiting the availability of nests. This effect would reduce the total time that each nest was exposed to risks of predation. A "head start" could reduce the numerical response of predators, in other words, attraction of predators to the vicinity of a colony or reproduction by predators in time with the availability of prey nests (Solomon 1949, Holling 1959), as well as the functional response. To obtain a "head start" on predation, the timing of nesting by the prey species would have to have some degree of unpredictability as well as synchrony. Although several studies have documented probable effects of breeding synchrony and aggregation in "saturating" predators (Kruuk 1964, Patterson 1965, Lloyd and Dybas 1966, Gosling 1969, Janzen 1971, Roberston 1973a, Estes 1976), no information is available about the effects of synchrony in obtaining a "head start" on predators.

The manifold consequences of aggregation and synchrony for finding food and reducing mortality are not in general mutually exclusive. Adaptations in the spacing and timing of reproduction thus usually result from the joint effects of multiple selection pressures. In order to evaluate the interacting influences on the spac-

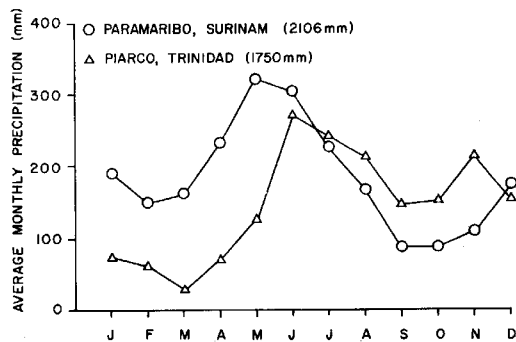


FIG. 1. Average monthly rainfall at two moderately seasonal sites in Trinidad and Surinam near our study areas.

ing and timing of nesting Yellow-hooded Blackbirds, we first describe the habitat of this species in relation to the seasonality of the climate at three study sites in Trinidad, Surinam, and Venezuela and document the spacing and timing of nesting blackbirds in each location. We then turn to the interactions between the blackbirds and their common brood parasite, the Shiny Cowbird *Molothrus bonariensis*, the nesting success of the blackbirds, and their feeding behavior. In locations that differ in seasonality, the blackbirds confront different problems in adapting to brood parasites, predators, and food supplies.

#### DISTRIBUTION AND NESTING HABITAT

Yellow-hooded Blackbirds are widespread in northern South America. They occur throughout most of the Amazon basin as well as northern Colombia, Venezuela north of the Orinoco River, Trinidad, and the coastal regions of the Guianas. Throughout this range, Yellow-hooded Blackbirds nest in emergent vegetation in herbaceous marshes and occasionally in shrubs and small trees adjacent to marshes. The species is particularly abundant in the vicinity of rice agriculture. Often abandoned or fallow rice fields, overgrown with sedges, grasses, and other herbaceous vegetation in standing water, provide nesting areas. In Surinam and French Guiana, the species also nests in grass and sedge marshes with numerous isolated shrubs and fringing forest in the vicinity of rice cultivation.

Nesting at a moderate distance from rice cultivation occurs in some areas with large expanses of emergent vegetation. In the eastern half of the Caroni Swamp, Trinidad, males held territories in a large freshwater marsh. In Surinam, these blackbirds nested in several square kilometres of sedges north of the Commewijne River. Both of these areas lay within 1–4 km of rice fields. Without nearby rice cultivation, these blackbirds nest in the vicinity of large, permanent lakes, including Lago Sonso, an oxbow lake north of Cali, Colombia, and Lago Valencia, Venezuela.

In the western basin of the Orinoco, the llanos ba-

jos, in which vast areas of flat topography flood during the rainy season, Yellow-hooded Blackbirds nest in emergent herbaceous vegetation in close association with expanses of the wild rice *Oryza perennis*. The blackbirds that nest in the llanos must withdraw to permanent water during the dry season, probably 200 km to Lago Valencia. Thus in the Venezuelan llanos bajos, a region that lacks permanent marshes, Yellow-hooded Blackbirds move seasonally from roosts near permanent lakes in the dry season to breeding localities in the rainy season. In contrast, throughout most of its range marshes remain available throughout the year, and Yellow-hooded Blackbirds are permanently resident.

#### COMPARISON OF STUDY SITES: CLIMATE AND HABITAT

We conducted intensive studies of Yellow-hooded Blackbirds in three localities: (1) in Trinidad, on the eastern edge of the Caroni Swamp, 8.5 km southeast of Port-of-Spain (10°34.5'N, 61°25'W), 20 June–8 August 1971; (2) in Surinam, in fallow rice fields on the south side of the Commewijne River, 11 km northeast of Paramaribo (5°52'N, 55°05'W), 21 June–23 July 1973 and 15–17 July 1974; (3) in Venezuela, at Fundo Pecuario Masaguaral, a ranch in the llanos bajos, 42 km south of Calabozo, Guarico (8°46'N, 67°47'W), 14 June–17 November 1974 and 18 December 1975 to 7 January 1976. The three localities divide into two distinct categories with respect to climate, characterized by moderate (Trinidad, Surinam) or extreme (Venezuela) seasonality in rainfall.

#### *Localities with moderate seasonality*

*Climate.*—Most of Trinidad and the coastal regions of the Guianas average over 1500 mm of rain annually. In Trinidad a major dry season lasts for 4 mo, January through April, and a lesser one occurs in September and October (Fig. 1). Eastward along the coast of the Guianas, the relative importance of these two dry seasons reverses. In Surinam, the major dry season comes in September to November and the lesser one in February and March. The dry seasons throughout this area, however, are not without rain; no month averages <25 mm of rain. Large marshes, like the Caroni and Nariva Swamps in Trinidad and the coastal marshes of the Guianas, have water throughout the year although levels drop during dry seasons. The studies in Trinidad began ≈1 mo after the end of the major dry period; those in Surinam, although at the same time of year, ended ≈1 mo before the onset of the major dry period.

*Habitat.*—The site for intensive studies in Trinidad lay within at least 25 ha of abandoned rice fields overgrown with emergent vegetation. Water depth in this area ranged from 10 to 50 cm. Two sedges dominated the emergent vegetation, *Eleocharis interstincta* and *Cyperus ferax*. Both formed dense single-species



FIG. 2. View of abandoned rice fields in Trinidad at our intensive study area. Blackbirds used the clumps of the large sedge *Cyperus ferax* (foreground) for nesting.

patches that reached as much as 1.5 m above water (Fig. 2). The blackbirds seemed to prefer areas where patches of tall sedges intermingled with patches of open water and short emergent vegetation. Nests were usually located in clumps of tall *Eleocharis* or *Cyperus*, but usually not in the middle of large, dense patches. Nine nests ranged from 50 to 90 cm above water.

In Surinam the study site consisted of  $\approx 5$  ha of fallow rice field and adjoining dikes. The field had 30–40 cm of standing water in which grew single-species stands of the sedge *Eleocharis mutata* that reached  $\approx 1$  m above water. These patches ranged from a few metres to 40 m across. The lower vegetation between these patches consisted primarily of a grass in the genus *Echinochloa* with leaves that reached some 30 cm above water and small lily pads. The dikes and ditches supported dense stands of cattails *Typha angustifolia* and grasses 2–3 m tall, as well as dead bushes, stands of the large fern *Blechnum indicum*, a few small trees, and scattered *Cyperus* sedges. Male blackbirds built their nests primarily in patches of taller vegetation, cattails, grass, or *Eleocharis* sedges. This area resembled the one in Trinidad in having a diversity of emergent vegetation arranged in patches of different heights above water and in its location adjacent to rice agriculture.

#### Localities with extreme seasonality

**Climate.**—In contrast to the preceding sites, the Orinoco basin experiences severe drought for 4 mo of the year, mid-December through mid-April. January, February, and March average  $<10$  mm of rain (Fig. 3). An erratic, but usually heavy rainy season begins between May and July and lasts through November. The average annual precipitation approximates 1500 mm. Our work at Fundo Pecuario Masaguaral (FPM) included periods at the end and the beginning of dry seasons and extended throughout the rainy season of

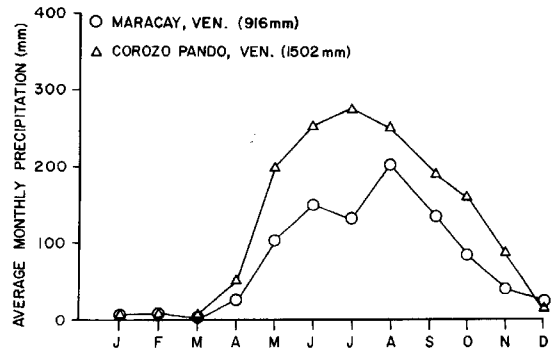


FIG. 3. Average monthly rainfall at two extremely seasonal sites in Venezuela; Coroza Pando is in the llanos bajos 8 km south of our study area at Fundo Pecuario Masaguaral.

1974. In a given year the rainiest month can fall as early as June or as late as October. In 1974 a rain gauge at FPM recorded the heaviest rainfall in August (376 mm), with July and September the next rainiest months (186 and 180 mm). The total rainfall recorded at FPM in 1974 was  $\approx 25\%$  less than a 10-yr average.

**Habitat.**—FPM lies at an elevation of  $\approx 70$  m within the vast, nearly flat Quarternary basin below 100 m, which forms the western llanos bajos. The ecology of FPM corresponds closely to the hyperseasonal savannas described by Sarmiento and Monasterio (1975). Away from major river courses, the terrain supports a savanna of groves of trees interspersed with grassy openings. The fine soils in these areas bake hard by the end of the dry season. At this time most of the herbaceous vegetation between the groves of trees dies back and is grazed by cattle to form a sparse covering for the soil.

During the rainy season the savanna is progressively transformed into a vast marsh. The wet soil becomes virtually impervious to water and the extremely low relief prevents rapid runoff. By the second half of the rainy season, water begins to accumulate on the surface and eventually reaches depths of a few centimetres to  $>1$  m. Flooded areas often extend for many kilometres between low sandy ridges. In 1974, water levels rose rapidly to a maximum depth during the 1st 20 d of August. Thereafter, with fluctuations that corresponded to variations from week to week in rainfall, water levels declined progressively. By early December most of the ground is dry once again.

Nesting blackbirds used the areas of flooded herbaceous vegetation for nesting and feeding. Areas with the deepest and most prolonged flooding support two major types of herbaceous vegetation: grass-sedge communities dominated by the wild rice *Oryza perennis* (Fig. 4); and tall stands of the broad-leaved ginger *Thalia geniculata* (Marantaceae) (Fig. 5). The wild rice begins to grow in June and July when the ground becomes wet. It becomes the dominant species in areas that have 20–80 cm of water during the second



FIG. 4. View of wild rice *Oryza perennis* in standing water at the end of the rainy season at Fundo Pecuario Masaguaral.



FIG. 5. View across the top of a bed of *Thalia geniculata* near colony GC at Fundo Pecuario Masaguaral. The plants reach 1.5–3 m above the water level.

half of the rainy season. In early October the seeds of the female plants begin to ripen. The mature seeds approximate in size those of cultivated rice, some 5 mm in length, and lie clasped within two hard bracts. Several birds feed on these seeds, particularly the blackbirds and species of *Sporophila*. By mid-November the rice begins to dry out; almost all of the seeds have either dropped or been eaten. By mid-December the plants have dried brown, except around the remaining pools of water, and no seeds remain.

Within the fields of wild rice grow patches of tall *Thalia*. The phenology of this plant closely matches that of the wild rice. In late September and early October 1974 it began to grow rapidly, although the plants had first sprouted in July when the ground became wet. By mid- or late October the *Thalia* had reached 2 m or more above water and formed thick, irregular patches growing in 20–80 cm of water. Within these patches grew the grass *Leersia hexandra* with stems that reached some 50 cm above water. The *Thalia* flowers in November and December. By mid-December the plants turn brown, eventually die back to the ground, and disintegrate. Areas that support thick stands of *Thalia* 3 m tall in November will have nothing by the middle of the dry season but scant vegetation scattered on the baked soil.

At FPM male blackbirds settled in the stands of *Thalia* in October and built their nests around the vertical stems of *Thalia* and *Leersia*. As described below, both the males and females used the expanses of wild rice for feeding. Thus the habitat is suitable for breeding for 2 mo each year, approximately early October to late November.

#### ANNUAL CYCLE AND SPACING

In all populations, males construct nests within their territorial boundaries by weaving wet decaying grass around the stems of emergent vegetation  $\approx 50$  cm above water. A territorial male usually concentrates on building one nest at a time but if he is unsuccessful

in attracting a female to that nest he may abandon it to start a new one or work on two nests alternately. A male leads receptive females to his nests with a special fluttering flight. Territorial males engage in boundary encounters with their neighbors, which usually consist of singing, song-spread displays (Fig. 6) and agonistic displays more or less similar to Red-winged Blackbirds (Nero 1956, Orians and Christman 1968). Territorial males also evict intruding males by approaching them, singing, or chasing. Females visit the males' territories alone or in small groups and remain for varying lengths of time. Often females simply preen or rest and show little interest in the males. They avoid a male if he approaches too closely. A receptive female will follow the male to his new nest and enter the nest briefly.

As we were unsuccessful in marking females near nesting areas without causing their desertion, we could not follow the stages of an individual female's choice of a nest in detail. However, once a female has selected a nest, she becomes, often in the course of 1 d, a regular visitor to the vicinity of the nest and spends long periods preening and resting near the nest. The

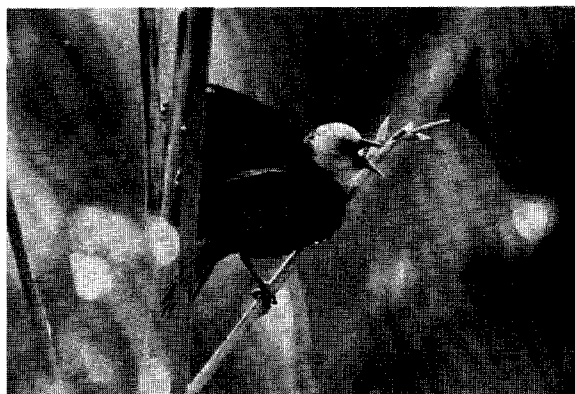


FIG. 6. Territorial male Yellow-hooded Blackbird performs a song-spread display.

presence of female visitors near a nest or a regular visitor that has chosen a nest, stimulates the male to redouble his efforts at building the nest. A female is a regular visitor to a nest for only 2–5 d prior to laying her first egg. This time between settling on a territory and laying her first egg is much shorter than the corresponding period in the Red-winged Blackbird, which can reach 20 d (Nero 1956).

Females usually only select completed or nearly completed nests. After a female has begun visiting a nest regularly and remaining in its vicinity, the male usually ceases or greatly reduces his nest-building trips. The female then adds fine grass for the lining of the nest; rarely she adds a little material to the cup as well. Males never participate in lining the nests.

Females laid one egg/d and usually completed a clutch of three. In Trinidad and Surinam all definitely determined clutches had three eggs ( $N = 10$ ); however, owing to the extremely high rates of predation on nests in these areas, we avoided frequent visits to nests and thus have a small sample of nests with known clutch sizes. At FPM we could check a large sample of nests daily in a large colony without causing desertions or affecting predation (see below). There we verified the termination of laying in 38 nests, of which 32 had three eggs and 6 had two (mean = 2.8). In our complete sample of 69 nests at FPM, the average clutch is the same as in the preceding sample; no clutches of four were found and only one clutch of one. Clutches of three averaged 8.2 g ( $N = 11$  clutches) on days 2–5 of incubation. As adult females weigh  $\approx 27$  g (Snow and Snow 1963), a clutch of three amounts to  $\approx 30\%$  of a female's mass.

In all known instances eggs were laid in the morning before 0900. Incubation began with the first egg. The female sat for long periods during the 1st d, but the efficiency of incubation was probably lower in some nests on the 1st d, since the first two eggs often hatched  $< 24$  h apart. Nevertheless, differences in size and development were always apparent, even when the first two young both hatched between our daily visits.

Incubation lasted between 10 and 11 full days for the second and third (if present) eggs in the clutch. Among 19 nests with clutches of three observed throughout incubation, the second egg hatched in  $< 10$  full days only once and never in more than 11 full days. Fifteen of the 19 first eggs in the sample also hatched between 10 and 11 full days after laying; four hatched between 11 and 12 days. The territorial male remains attentive to an incubating female for a day or two, but then returns to courting other visiting females and constructing a new nest.

Although the general cycle of male-female interactions remains similar in strongly seasonal and less seasonal environments, the following sections show that the females are far more synchronized in their breeding behavior in the strongly seasonal llanos than in the

less seasonal coastal regions, and the males' territories and distribution of nests are much denser.

### *Trinidad and Surinam*

We were unable to determine the onset or termination of the breeding season in either of these two areas. In an intensive study area in Trinidad  $\approx 15 \times 60$  m, eight nests had laying dates in June, five in July, and two in the first third of August. Laying dates extended from 10 June through 8 August, almost the entire duration of our stay. Although some males were more successful in one month than another, we could discern no overall peak or trend in laying during our visit. Others have reported eggs from June to November, with the greatest numbers in July (Belcher and Smooker 1937) or October (Snow and Snow 1964). In Surinam, territorial males were more noticeable near Paramaribo in late July than in late June. In contrast, at our intensive study area territorial activity seemed slower at the end of July than earlier. During our study, females began laying at irregular intervals between 1 and 22 July. Haverschmidt (1968) reports eggs from March through September, though local residents near Paramaribo told us that nesting was most concentrated in July and August. Thus both in Trinidad and Surinam, eggs are laid throughout a period of 5–6 mo, although perhaps most often in 1 or 2 mo.

At any one time, substantial numbers of both males and females were not breeding. Territorial males and females with nests are distinguished by a purposiveness in their activities. When territorial males left their territories they flew directly to feeding grounds and returned directly, usually within 10–15 min. Territorial males were absent before 0900 in the morning only  $\approx 10\%$  of the time (Wiley and Wiley, *in press*). Nesting females likewise flew directly to and from feeding grounds during their trips away from their nests. A regular feature of all study areas, however, was the frequent visits to territories by males and females that loafed aimlessly until approached by the resident male, whereupon they left either to fly out of sight or to move to the next territory. Although many of the males showing this behavior had incompletely developed plumage and thus were probably in their 1st yr, some of them appeared to have full plumage. Apparently these males had no territories of their own. In Surinam, large numbers of nonbreeding adults of both sexes used a roost in a rice field near Paramaribo at a time when many birds in the area were breeding.

Both in Trinidad and Surinam, active nests were 2–10 m apart, depending on the locations of favored nesting substrates, usually patches of tall, dense sedges (Fig. 7). The closest simultaneously active nests were two in Surinam 2 m apart and two in Trinidad 3 m apart. Territorial males defended areas 15–50 m in diameter (Fig. 8).

In Trinidad and Surinam, nesting territories were aggregated in the sense that, within large tracts of

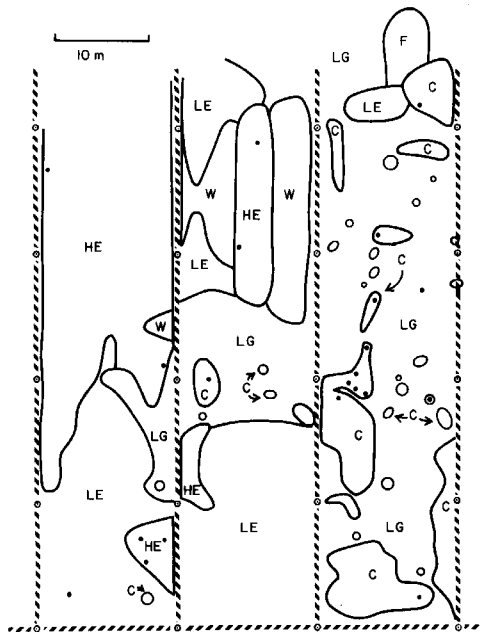


FIG. 7. Vegetation and nest locations at our study area in Trinidad. Solid lines enclose patches of similar vegetation: C, *Cyperus ferax*; HE, high *Eleocharis interstincta*; LE, low *E. interstincta*; LG, low grasses; F, forbs; W, open water. Dashed lines indicate the positions of low dikes; dots within circles, the locations of small flags in a grid; small dots, nests that received eggs.

marsh, blackbirds would sometimes use an area of 20–100 ha and not other similar areas within the marsh. Belcher and Smooker (1937) mentioned such a colony in Trinidad. In our studies, we found certain tracts of the Caroni Marsh in Trinidad unoccupied, although blackbirds on territories were widespread in this area. In Surinam, blackbirds left much of a vast expanse of emergent sedges unoccupied. In general, the blackbirds occupied areas closest to good feeding areas, such as cultivated rice. In small marshes, territorial blackbirds often occupied all suitable habitat. The formation of colonies in large marshes in Trinidad and Surinam still differed markedly from the dense aggregation of territories within the patches of vegetation suitable for nests in the llanos of Venezuela.

In Trinidad and Surinam, we could obtain only rough estimates of the breeding sex ratio (the numbers of breeding males per breeding female) and the variation in mating success among males. In Trinidad one of four intensively observed males had three simultaneously active nests and another had two. In Surinam one of four intensively observed males had two simultaneously active nests. However, the rate of nest loss was so high and the females so unsynchronized in breeding, that males more often had a succession of unsuccessful nests in their territory than several simultaneously active. Thus in Trinidad, four males had, respectively, at least 4, 2, 2, and 1 active nests

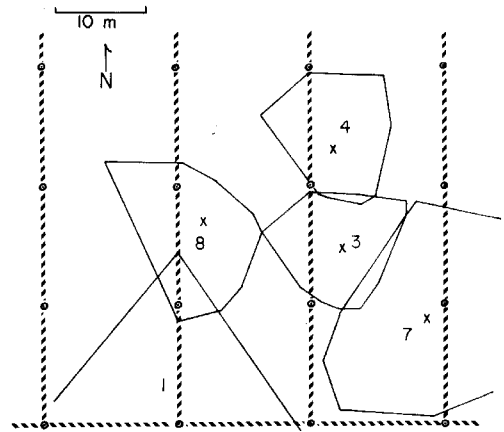


FIG. 8. Territories of five males at our study area in Trinidad. For each territory, a polygon encloses 68% of the male's positions while singing. An X marks the vector mean of each male's positions while singing. Other males, not studied in detail, occupied territories adjoining those shown here. Southern portion of the grid shown in Fig. 7.

in their territories during our observations; in Surinam, four males had 3, 2, 0, and 0 active nests during our observations. During our observations, some males were more successful than others in attracting females; in addition, in Trinidad, some males were more successful one month than the other.

In general, in Trinidad and Surinam females seemed ready to desert their nests, perhaps particularly before hatching, with little provocation. For this reason, we were unable to capture females near their nests. In Surinam we managed to dab a little paint on a female by means of a small wad of cotton wired at the lip of her nest. Perhaps because we were careful to approach this nest during her absences, she did not desert. Nearly 1 wk later a predator destroyed her nest, although we had not visited it in the intervening time. With this one marked female, we confirmed that three successive females in the male's territory were different individuals, although the first (the marked female) and the last did not overlap.

Because we were unable to mark females permanently, we could not determine whether they renested after a failure; presumably they could renest, provided their failure did not come too close to the end of the rainy season.

Individual territorial males were recognizable by their distinctive songs. In our study areas in Trinidad and Surinam, all males retained their territories throughout our observations, except two males that disappeared suddenly and apparently died. Both in Trinidad and in Surinam, established males changed their boundaries with neighbors on several occasions, and once in Surinam a new male managed to insert himself between two established males. In general,

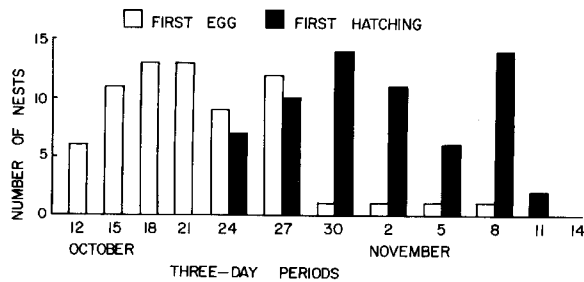


FIG. 9. Dates on which laying and hatching began in nests at colony GC at Fundo Pecuario Masaguaral.

however, males retained their territories for at least 1–2 mo and perhaps throughout the breeding season.

In summary, in the less seasonal environments in Trinidad and Surinam, females begin laying throughout a period of >2 mo, and male blackbirds defend territories throughout most of the rainy season. An individual male thus has a succession of females nesting in his territory, some of them overlapping. We presume that a female renests if she has enough time after an attempt fails.

#### Venezuelan llanos

Although the activities of breeding blackbirds are similar in the llanos and coastal areas, their timing and spacing differ strikingly in these two areas. At FPM in 1974, 94% of 69 nests, for which we could calculate or observe the date of the first egg, received their first eggs within a period of 18 d (Fig. 9). Nesting was restricted to dense, discrete colonies within tall stands of *Thalia*.

Most colonies were deserted after only a few nests had received eggs. We observed one colony (MF) develop daily between 12 and 21 October, by which time females had stopped visiting and territorial activity had almost ceased. We then shifted to a successful colony (GC) which we observed from 21 October through 17 November, from approximately the middle of the laying period until 4 d after the last nest hatched.

These blackbirds first appeared at FPM in the middle of August, when we regularly saw small flocks of both sexes flying roughly southwest in the evenings. Small groups gathered in the emergent vegetation in flooded areas, where the males often sang but showed no aggression toward each other. Males sing regularly in nonbreeding flocks that we have observed elsewhere. By the middle of September males had become more active during the 1st 2 or 3 h after sunrise; single males sang from clumps of growing *Thalia*, where they performed occasional song flights, agonistic displays toward nearby males, and fluttering approaches toward females, but these males showed little tendency to localize their activities. The males' activity increased gradually until, between 5 and 10 October, their behavior rapidly changed to full territoriality. Males now held their positions throughout the day,

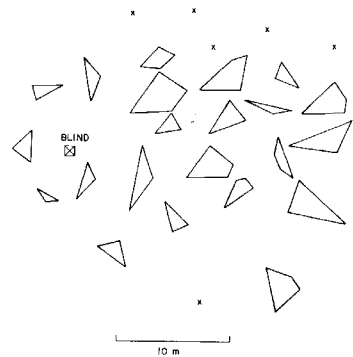


FIG. 10. Territories of males in the central portion of colony GC. Polygons enclose the locations of the most frequently used singing perches of each male; crosses indicate the approximate centers of territories of additional males.

repeatedly performed song flights and aggressive behavior toward intruding males. Approaching females were received with fluttering approaches, and on 11 October we saw the first collection of nest material by males. Throughout this period groups of both sexes foraged in the marshes of ripening wild rice. The onset of territorial activity by males was largely synchronized throughout FPM. We periodically checked activity at different locations and found no evidence of nest building or territorial localization by males before 5–10 October.

At site MF, five males held territories in an intensively studied area 60 × 60 m on 12 October; by 16 October nine males held territories in this area. On 18 and 19 October two nests in different males' territories received their first eggs. Female cowbirds frequently and persistently patrolled the colony, and both nests received cowbird eggs within 1 d. By 21 October, the males in this area had started a total of 14 nests, and the two nests that had first received blackbird eggs now had a total of five cowbird eggs. Few female blackbirds visited the area, although female cowbirds remained frequent. Territorial activity of the males had slackened noticeably. On 21 October the area was abandoned. This intensive study area was one of several in patches of *Thalia* within a diameter of ≈500 m. The recruitment of males, activities of females, and eventual desertion by both sexes was similar in each of these patches. About this time, males ceased territorial activity in a number of other patches of *Thalia* in the marshes in other locations at FPM.

Activity at site GC began on approximately the same schedule as that at the unsuccessful sites. By 21 October, males' territories had stabilized in an area ≈30 × 40 m located eccentrically in a large bed of *Thalia* some 80–100 m in diameter. The nesting area stretched from ≈10 m in from one edge to near the center of this patch of *Thalia*. The tallest *Thalia*, 3–4 m above ground, was generally avoided by the nesting



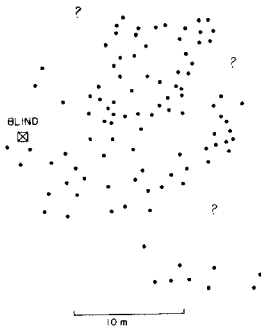


FIG. 11. Locations of nests that received eggs in colony GC. Question marks indicate areas in which our surveys were incomplete. Map has same orientation and scale as Fig. 10. (Error for superposition on Fig. 10 is  $\approx \pm 1$  m.)

blackbirds, which preferred plants 2–2.5 m tall. Nests were densest in an area  $15 \times 25$  m where  $\approx 15$  males held territories 4–8 m in diameter (Figs. 10 and 11). The colony included a total of  $\approx 35$  territorial males.

We observed this colony daily from a blind on a platform within the colony and near one edge of the area with active nests. The nests were so dense in the center of the colony and the males' boundaries so difficult to establish in the tall stand of waving *Thalia* that it was often not possible to determine precisely which nests were included within each territory. Some males at the edge of the colony definitely had no nesting females. At least a third of the males fell into this category. The area of dense nesting activity within 10 m east of our blind included  $\approx 16$  males' territories and a total of 106 nests constructed by males, of which 62 received eggs, an average of 6.6 nests per territory and 3.9 nests with eggs per territory. Probably all of the males in this sample of territories from the center of the colony had 2–5 nesting females. The entire colony averaged  $\approx 2.2$  nests with eggs per territorial male. The temporal restriction of laying and the high success of hatching (see below) largely excludes the possibility of any substantial number of renestings in this colony.

During the period of nesting activity at site GC, we encountered occasional large flocks of nonbreeding males, with few females, feeding in wild rice. On 14 November, we observed large flocks with both sexes for the first time since August and September. About this time we began to see small flocks flying north over the ranch in the evening. Some birds, however, remain until the last water dries out. In late December and January flocks of both sexes stay close to the last pools of water in the formerly vast marshes of wild rice.

In summary, the extreme seasonality in the llanos bajos barely permits one full nesting cycle by the blackbirds each year. The *Thalia* stands used for nesting and the wild rice eaten by the blackbirds only become available in early October; by late November both are withering. The blackbirds begin to arrive in

the area some 2 mo before nesting begins, then concentrate their nesting in a 6-wk period between mid-October and late November, and barely finish before the marshes dry out. The seasonal cycle of blackbird activity at FPM is largely the same in other years (B. Thomas, *personal communication*). In East African savannas, the ploceid finch *Quelea quelea* has a similar annual cycle; it begins breeding after 2–3 mo of good rain, when grasses are beginning to form seeds (Jones and Ward 1976).

#### PARASITISM BY COWBIRDS

At all of our study sites, in Trinidad, Surinam, Colombia, and Venezuela, Shiny Cowbirds *Molothrus bonariensis* posed a continual threat for nesting blackbirds. Belcher and Smooker (1937) reported that a "large proportion" of blackbird nests in Trinidad had cowbird eggs. We found cowbird eggs in 33% of 15 nests in Trinidad. In the Venezuelan llanos, cowbirds parasitized 33% of 72 nests in a successful colony and every nest in the colony that was eventually abandoned by the blackbirds. Cowbirds are thus likely to have major effects on the breeding adaptations of Yellow-hooded Blackbirds. Our information suggests that the seasonal restriction of breeding by blackbirds in the llanos tended to increase the risks of brood parasitism but that smaller territories and possibly the sharp onset of breeding served to hold parasitism to moderate levels, at least in large colonies.

At each study site, male cowbirds sang from trees or bushes overlooking the marshes in which blackbirds nested. When female cowbirds landed near a singing post, the males circled them in whirring flight with song; on one occasion in Surinam a copulation followed one of these interactions. Female cowbirds spent the daylight hours from shortly after dawn until late afternoon perching at lookouts beside or in the marsh and flying back and forth across the marsh, often slowing almost to a hover in order to inspect the emergent vegetation for blackbird nests. On several occasions a female cowbird flew directly to a blackbird nest as soon as the male blackbird left the nest after a period of building. In general, searching female cowbirds made little attempt at stealth. Because the male blackbirds chased them vigorously, female cowbirds generally avoided the immediate vicinity of a perched male blackbird and always retreated immediately when chased. When ready to lay an egg, female cowbirds changed their behavior. Once when we observed a female lay an egg, she darted straight to the nest at 0600, during a period when the territorial male was absent, laid her egg and left after only 30 s.

Male cowbirds on their display perches performed bill-up displays (bill jerked alternately upward and downward) when another male passed close by. We could not, however, determine whether individual males had exclusive use of particular perches. Females also behaved aggressively toward each other on



FIG. 12. Nest of a Yellow-hooded Blackbird in Trinidad with three blackbird eggs and three cowbird eggs (densely speckled).

their perches in the marshes. When two females landed near each other, they performed bill-up displays and occasionally one would supplant the other. Individual females did not maintain exclusive areas within the blackbird nesting marshes, but the agonistic behavior between females suggests that they might have had spheres of dominance.

Female cowbirds thus spend considerable time searching for blackbird nests and possibly monitoring them in order to determine the optimal day for oviposition. As discussed below, cowbird eggs have little chance unless they are laid in a blackbird nest within a day or two after the blackbird's first egg. The rapidity of approaching a nest, laying, and leaving suggests that female cowbirds have selected nests in advance.

The Shiny Cowbird parasitizes a wide variety of species (Friedmann 1963, Friedmann et al. 1977). At FPM our incidental observations confirm that cowbirds parasitized a number of other species in the same general area and at the same season as the nesting blackbirds. Nevertheless, it is clear that the Yellow-hooded Blackbird serves as a major host for at least a portion of the cowbirds at each of our study areas.

Aside from their searching behavior, the cowbirds had no specializations for parasitizing blackbirds (see Payne 1977). Unlike Shiny Cowbirds parasitizing other species (Post and Wiley 1976, 1977a, b, Fraga 1978), cowbirds at our study sites rarely, if ever, removed or damaged blackbird eggs when laying their own. At two nests, both at colony MF in Venezuela, a single blackbird egg was removed from the nest within the same 24-h period in which a cowbird egg appeared. No removal or damage of blackbird eggs occurred at any

other nest. The numbers of blackbird eggs in nests with and without cowbird eggs were essentially the same. Cowbird eggs did not resemble blackbird eggs (Fig. 12); they were more rounded than blackbird eggs and whitish with fine reddish-brown speckling, rather than faint blue with larger dark spots. The difference in shape between blackbird and cowbird eggs would have allowed us to detect any cowbird eggs with coloration similar to blackbirds' eggs. Unlike cowbirds parasitizing marsh-nesting icterids in Argentina (Friedmann et al. 1977), all cowbirds at our study sites laid similar eggs.

Even though nesting blackbirds were beset continuously with female cowbirds, they had several important means of minimizing the effects of cowbird parasitism. Selective removal of cowbird eggs occurred infrequently. At least four cowbird eggs were removed from nests at site GC, of a total of 28 cowbird eggs laid in 24 nests. In each case the cowbird egg was laid at least 2 d after the blackbird had finished laying and was removed within 24 h. At nine other nests which received cowbird eggs after the blackbird's clutch was completed, the cowbird egg was not removed. In one instance, at site MF, a cowbird egg was covered with nest lining in the floor of the nest before the female blackbird laid her first egg the following day.

Female blackbirds apparently desert nests that receive three or more cowbird eggs, as no such clutch ever hatched. The two nests at GC that received two cowbird eggs both hatched. There is no evidence that one or two cowbird eggs increased the chances that a nest would be deserted.

More effective defense against cowbirds undoubtedly resulted from the male blackbirds' vigilance. Male blackbirds vigorously chased female cowbirds as soon as they were detected within their territories. Each territory was thus guarded against cowbirds except during the male's brief absences. Female blackbirds seldom chase cowbirds; the only two occasions we observed occurred during absences of the territorial male. Male blackbirds even cooperate mutually to some extent in guarding each other's territories from cowbirds. Particularly when a territorial male was absent, his neighbors would occasionally fly even to the center of his territory to evict a female cowbird. Some intrusions into a neighboring territory in order to evict a cowbird occurred even during the territorial male's presence. Although these intrusions were a regular feature of the male's behavior, nevertheless the absence of a territorial male permitted female cowbirds much more time to flutter slowly above the vegetation searching for nests. Evicting female cowbirds from a neighbor's territory could have selfish effects, since an undisturbed female cowbird could presumably locate the approximate positions of nests in neighboring territories by watching the activities of the male and female blackbirds.

Even though the harassment of female cowbirds

TABLE 1. Frequencies of nests that fledged blackbirds in relation to the presence or absence of cowbird parasitism ( $N = 47$  nests in which blackbird eggs hatched and for which outcome is known;  $G = 1.98$ , NS).

	At least one blackbird survived to day 9	No blackbird survived to day 9
No cowbird hatched	22	8
Cowbird hatched	9*	8*

\* Each total includes two nests that fledged cowbirds.

does not prevent them from returning later, it does limit the opportunities for undisturbed searching by the cowbirds. A successful cowbird needs to know more than the simple location of a blackbird nest. Because the precise timing of the cowbird's egg in relation to the blackbird's clutch is critical for the success of the cowbird egg, cowbirds need to monitor blackbird nests carefully (see below). Harassment by blackbirds thus presumably interferes with a cowbird's ability to monitor blackbird nests with the necessary accuracy.

Perhaps the blackbirds' most important defense against nest parasitism is the early start of incubation. Incubation of three cowbird eggs at site GC lasted 10–11 d, exactly the same duration as for blackbird eggs. Because the female blackbird began to incubate with her first egg and because the chances of survival for nestlings hatched after the first 2 d were low, a cowbird had to lay her egg on the day of the first or second blackbird egg in order to have a chance for success. Only 4 of 28 cowbird eggs resulted in fledged young, and all of these eggs hatched between the day before and the second day of the hatching of blackbird eggs. Of 15 nests that received cowbird eggs on known days, only two received cowbird eggs before the blackbird's clutch was completed. One of these two nests was the only one of the 15 to fledge a cowbird.

Cowbirds had little success in fledging young from blackbird nests. In Trinidad, none of five nests that hatched had cowbirds. At FPM in Venezuela, 13 of 52 nests that hatched had one or (in one case) two cowbirds. Of the total of 24 nests that received cowbird eggs (28 eggs), in 4 the cowbird eggs were removed, 1 was destroyed by rice rats *Oryzomys* before hatching, 13 hatched cowbirds (14 eggs), 2 were destroyed by predators after hatching, and 4 fledged one cowbird each. Thus 54% of parasitized nests hatched at least one cowbird (50% of cowbird eggs) and 17% fledged one cowbird (14% of eggs). Of the four that fledged, two had hatched on the day after the blackbird eggs had begun to hatch. Both nests fledged blackbirds (one and two, respectively) as well as the cowbird; both of these cowbirds had grown much more slowly than the two which hatched earlier in relation to the blackbird eggs.

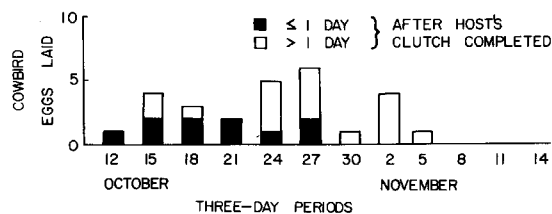


FIG. 13. Dates on which cowbirds laid eggs at colony GC. Dark bars, eggs laid within 1 d of the completion of the blackbird's clutch in the same nest; open bars, eggs laid >1 d after the completion of the blackbird's clutch. Compare with Fig. 9.

The effects of cowbird parasitism on the nesting success of blackbirds took several forms. First, some nests in Trinidad, Surinam, and at the unsuccessful site MF in Venezuela received so many cowbird eggs that the female blackbirds deserted. This situation was not observed at the successful colony GC in Venezuela. The multiple parasitism of the first nests at the unsuccessful site MF seemed to explain the prompt desertion of this colony. Heavy cowbird parasitism has also been associated with abandoned colonies of *Agelaius ruficapillus* in Argentina (Hoy and Ottow 1964).

Second, in the successful colony GC, nests with cowbird eggs were less likely to fledge blackbirds (Table 1). This result, however, is difficult to explain since cowbirds seldom laid their eggs to hatch at the appropriate time in blackbird nests. Probably part of the reason that nests with cowbird eggs were less likely to succeed stems from the lag in laying by cowbirds in comparison to blackbirds (see below); as later nests were less likely to succeed regardless of parasitism (see below), nests with cowbird eggs were incidentally less successful.

Temporal synchrony in laying by female blackbirds could have both advantages and disadvantages for risks of nest parasitism. Temporal concentration of hosts' nests up to a point would make it easier for cowbirds to detect the availability of nests. Greater synchrony, however, could make it difficult for cowbirds to respond immediately to the sudden appearance of host nests. In fact, at the successful colony GC in Venezuela laying by cowbirds reached its peak between 24 and 29 October (Fig. 13) at the end of the blackbirds' laying period (see Fig. 9). Those cowbirds that managed to lay early were more successful in placing their eggs in host nests at the optimum time, before the host completed her clutch. Evidently most female cowbirds could not respond immediately to the sudden availability of host nests presented by a large synchronized colony. Synchrony thus permitted the blackbirds to get a "head start" on the cowbirds.

Some evidence indicates that synchrony of nesting also reduced nest parasitism by "saturating" the cowbirds. The proportion of nests that received cowbird

TABLE 2. Number of nests that received cowbird eggs in relation to the total number of nests with clutches completed on the same day ( $G = 6.93$ ,  $P < .005$ , 1-tailed).

Number of nests with clutches completed on same day	Number of nests	
	Received cowbird egg	Did not receive cowbird egg
1-3	8	3
4-6	10	32

eggs was greater among nests with clutches completed on days with only a few other nests, in comparison to nests with clutches completed on days with many others (Table 2). When nests are synchronized with a number of other nests, they are less likely to be parasitized.

The frequency with which territorial males chased female cowbirds per hour of observation indicates a colony's exposure to cowbirds. Unsuccessful colonies in the Venezuelan llanos had greater harassment from cowbirds than did study areas in Trinidad and Surinam (Table 3). Thus the seasonal restriction of nesting in the llanos exposes the blackbirds to greater risks of nest parasitism. In these circumstances, it should pay the blackbirds to start their nests as synchronously as possible in order to avoid inundation by cowbird parasitism. Evidently some smaller colonies are unsuccessful in recruiting blackbirds fast enough to avoid crippling nest parasitism.

#### NESTING SUCCESS

Nesting losses were high at all study areas, but the timing of losses and the importance of starvation and predation as causes of losses differed in the two seasonal patterns.

In Trinidad, of 12 nests with eggs for which we knew the outcome during incubation, two hatched (16%). Because we quickly discovered that nest mortality during incubation was high, we curtailed our visits to nests in order to minimize any effect we might have on risks of predation. Consequently, the preceding sample of nests presumably does not include some nests with eggs that were lost before we found them, nor does it include five nests with eggs for which the outcome was not established. If we assume that mortality per day is constant throughout incubation, we can use observations on the known survival of six nests with eggs to estimate a minimum survival rate of nests with eggs. Fitting a negative exponential function to the survival curve for these nests yields a daily survival of 0.83. Survival through the 11-d incubation period would then have a minimum value of 13%. Both of these approaches suggest that the survival of nests through incubation approximated 15%. Six nests with young included three for which we knew the outcome; one of these fledged a single bird, a nest success of 33% during the nestling period. This small sample sug-

TABLE 3. Rates at which male blackbirds chased female cowbirds out of their territories at two study sites ( $U = 2$ ,  $P = .057$ , Mann-Whitney U Test).

Site	Male	Hours observed	Evictions/h	Mean
Trinidad	1	12	0.4	2.38
	3	18	1.2	
	7	9	5.6	
Venezuela (MF)	B	3	6.7	8.52
	C	3	3.7	
	D	3	5.3	
	E	4	18.4	

gests that only 5% of nests with eggs fledged at least one young. In Surinam we made no attempt to search for nests. Three nests with eggs in one intensively observed territory all failed to hatch.

Our visits to nests to check their contents might have increased their risks of predation. One nest, at which we netted the female, was deserted; this nest is not included in our analysis of nest mortality. Otherwise, we tried to minimize disturbance near nests. Because we could observe nesting females from a distance, we could tell when a nest was lost or deserted shortly after one of our visits. Nests seemed no more likely to fail shortly after our visits than at other times, although the sample is too small to detect a weak effect. Overall, we believe our activities had no major effect on nest success.

Nesting success might well differ from one area to another or from 1 mo or yr to another. The rarity of dependent juveniles following females in the vicinity of our study sites in Trinidad or Surinam precludes the possibility that our study sites had abnormally low success, at least by any wide margin. In Venezuela, where nesting success did vary dramatically from site to site, dependent juveniles were readily detected as far as a kilometre from successful nesting areas. Wide annual variation in nesting success also seems unlikely. A brief visit to our study site in Surinam in 1974 revealed no indication of marked changes in nesting success. We also noted no seasonal trends in nesting success in our studies in Trinidad and Surinam, which coincided with the main breeding season, but our data again do not exclude small changes. Although our figure of 5% seems too low for overall nest success, the average figure could hardly exceed 15-25%, allowing for all possible sources of error.

Nest losses during incubation in Trinidad and Surinam all resulted from predation, with one exception. A nest that received three cowbird eggs as well as three blackbird eggs was deserted. Usually all of the eggs were removed from the nest overnight without significant disturbance to the nest, clues that suggest predation by snakes. In Trinidad one nest was pulled down on one side, evidence of a larger predator. On one occasion we watched a Purple Gallinule *Porphyrio*

*martinica* perch atop a blackbird nest and eat the eggs. In Surinam two nests were destroyed by rice rats *Oryzomys*. In both cases one side of the nest had been pulled over the top in order to create a completely enclosed chamber. In one instance the rodent was discovered in the nest when we inspected it the following day. The rodents ate the eggs and left the shells either below the nest or inside.

Of the six nests with young in Trinidad, in two cases only one young hatched, although all had three eggs. Two nests were presumably lost to predators, for the entire contents were removed. The one successful nest, a case of partial brood loss, fledged only two young although three had been present halfway through the nestling period. The female at this nest, who had a white feather in her wing, remained in the vicinity for at least 1 mo. One of the two fledglings disappeared quickly, but the other remained with her in juvenile plumage and begged for food throughout this month until the end of our observations. Thus in Trinidad, brood mortality after hatching included both predation and probably starvation, to judge from the case of partial brood loss, but our observations are too few to establish the relative importance of these two factors.

In the Venezuelan llanos, at site GC, we mapped the locations of 122 nests, 72 of which received eggs. Judging from our observations from the blind, these nests comprised at least 80% of those in the colony, and virtually every nest within the central 15 × 25 m of the colony east of our blind. Seventy nests were located on 21 and 22 October, the remainder at intervals until the end of our observations. We checked each nest daily between 0900 and 1200 until 17 November. To minimize disturbing the nests we used a small mirror at arm's length to check the contents of each nest. There were no indications that our visits increased the chances of predation or desertion. There was only one instance of desertion in this colony.

Nest losses in the successful colony GC were low prior to hatching. Only 13% of 38 completed clutches sustained total loss before hatching. Altogether 83% of the eggs in completed clutches hatched. Rates of loss during laying seemed somewhat higher; of 29 nests observed during laying, 3 sustained total loss in the 2 d before the clutch was complete (10%).

After hatching, mortality rate of young increased progressively during the nestling period (Fig. 14). In this colony, 52 nests that hatched were followed for at least 9 d during the nestling period. Of these, 10 nests sustained total loss, 31 partial loss, and 11 no loss. The total losses (19% of nests, 20% of young) resulted from predation (see Ricklefs 1969). One of these nests was appropriated by *Oryzomys*, and three were destroyed by larger predators. The remaining fit the pattern for predation by snakes: all nestlings or eggs were removed without disturbance to the nest other than some derangement of the nest lining, pre-

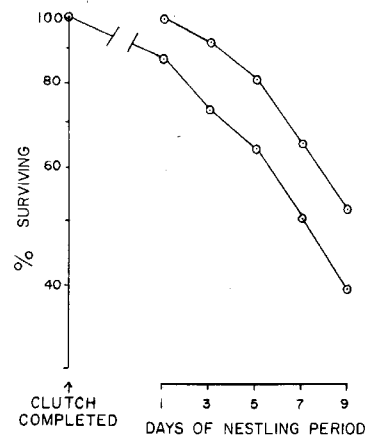


FIG. 14. Survivorship of eggs and nestlings of blackbirds in colony GC. Upper line, survivorship of nestlings only; lower line, combined survivorship of eggs and nestlings. Day 1, day first nestling hatched.

sumably by the grip of the nestlings as they were pulled from the nest. One or two cases of partial loss also resulted from predation by snakes. These partial losses differed from starvation because the older nestlings, rather than the younger ones on the bottom of the nest, were removed and the nest lining was partially pulled away. We were familiar with this derangement of the nest lining, because nestlings lifted from their nests for weighing gripped the lining and partially pulled it after them.

One cluster of nests on the north side of the colony sustained eight total losses, including three nests with eggs, and two partial losses on or before day 9 of the nestling period, all of which fit the preceding pattern. Presumably a snake discovered the colony about 7 November and preyed on these nests during the following week. In the remainder of the colony, only one other nest sustained total loss that fit the pattern for predation.

Most of the partial losses had all the manifestations of starvation. Altogether only 44% of the young that hatched reached day 9 with approximately normal size (37% of the eggs in complete clutches). The remaining young by day 9 of the nestling period usually differed in mass. After day 9, the oldest young often left the nest if we approached closely to examine its contents, so we had to terminate our close inspections. By day 11 of the nestling period, many of the young had left spontaneously. Since many of the surviving young at the end of the nestling period were still far below normal mass for their age, it seemed certain that mortality of the smaller and younger fledglings continued after they left the nest.

In as many nests as possible, we weighed all of the nestlings on the day the second egg hatched, on day 4 after the first egg hatched, and on day 8 after the first hatching. For the first two weighings, we mea-

TABLE 4. Masses of blackbird nestlings (grams) on the day the second egg hatched.

	Mean mass (SD)		<i>t</i>	<i>P</i>
	Older nestling	Younger nestling		
First and second eggs hatch in same 24-h period ( <i>N</i> = 11)	2.91 (0.36)	2.30 (0.26)	4.5	<.01
First and second eggs hatch in successive 24-h periods ( <i>N</i> = 21)	3.58 (0.36)	2.43 (0.22)	12.4	<.01

sured to a precision of 0.1 g, for the third 0.5 g. Our activities only temporarily disturbed the birds. In many cases, the female was absent during the handling of the nestlings. From our platform blind, we could see that females resumed normal feeding of nestlings within 10 min after our visits to the nest. Recall that one egg usually hatched each day but that in a minority of the nests two eggs hatched between daily visits. Even when two had hatched in the same day, we could recognize one as older by its more developed feather tracts. Young of a given parity had unimodal distributions of mass, so we could not sex the nestlings and thus have no information on sex differences in mass, such as those reported in Red-winged and Yellow-headed Blackbirds (Willson 1966, Holcomb and Tweist 1970). The differences among nestlings according to their parity of hatching outweighed any differences between sexes.

Asynchronous hatching gave the first nestling an immediate advantage. When the first two young hatched on successive days, the first was significantly heavier by the time the second hatched (Table 4). Even when two eggs hatched between visits, the older nestling (as judged by development of feather tracts) averaged significantly heavier. By day 4, the nestlings were well separated in mass (Figs. 15 and 16). By day 8, the mass differences between nestlings continued with approximately the same proportionalities. Thus the absolute differences in mass increased. If we separate

the masses of nestlings that died before or on day 10 from those that survived, we see that surviving nestlings grew faster (Fig. 17). The proportionate differences between masses of dying and masses of surviving young were least for the oldest nestlings, greatest for the youngest, and intermediate for the second. Thus the chance of starvation increased with increasing parity.

In spite of starvation which affected the youngest the most, the proportion of young reaching day 9 had no significant relationship to the number of young hatching in a nest: 59% of nestlings reached day 9 in nests that hatched two, 43% in those that hatched three (*N* = 20 and 81, respectively, *G* = 0.7). Masses of the oldest and second-oldest nestlings on day 4 did not differ between nests that hatched two or three young. No differences in mass appeared by day 8.

In early nests (hatching on or before 1 November), the mean masses of the first and second young on day 8 were slightly higher than in late nests (Table 5), but this trend was not statistically significant. The effects of late nesting become much more apparent if we consider the fate of the young. Although early nests were only slightly more likely to fledge at least one young than were late nests, they were substantially more likely to fledge two or three young (Fig. 18). The evidence thus suggests that starvation was the major source of mortality among nestlings and that starvation of the youngest nestling became more likely later

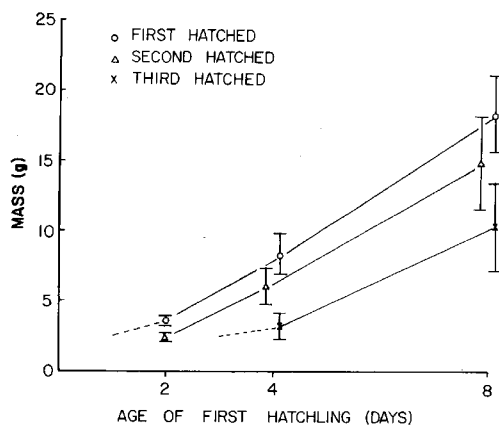


FIG. 15. Masses of nestling blackbirds in colony GC. Circles, masses of the first young hatched in each nest; triangles, masses of the second hatched; crosses, masses of the third hatched. Vertical bars indicate one SD around the mean.

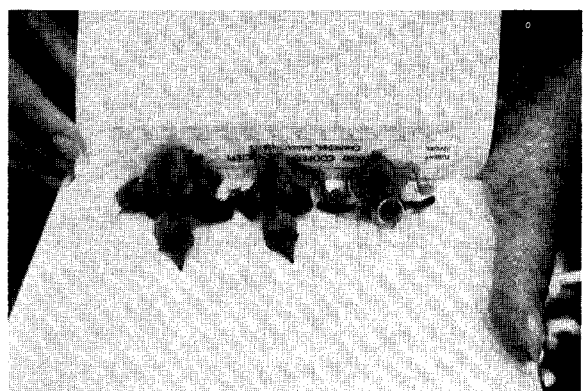


FIG. 16. Three nestlings from one blackbird nest on day 4 of the nestling period, when they were  $\approx$ 4, 3, and 2 d old, respectively. Note that the smallest is the only one hungry enough to beg for food while being handled. The upper scale shows millimetre and centimetre marks.

TABLE 5. Masses of the oldest and second-oldest nestlings (grams) on day 8 of the nestling period in relation to the date of hatching (differences between early and late hatching not significant).

	Mean mass (SD)	
	Oldest	Second-oldest
Hatch on or before 1 November (N = 18)	18.38 (2.74)	15.74 (2.59)
Hatch after 1 November (N = 18)	17.51 (2.72)	14.84 (3.18)

in the season. Our observations of the food brought by females to their nests, reported in the next section, suggest that the availability of food decreased in the course of the season.

FORAGING BY ADULTS AND FEEDING THE YOUNG

Tropical populations of Red-winged Blackbirds have greater difficulties finding food for their young than do red-wings in temperate marshes (Orians 1973). Not only is starvation an important form of mortality among nestlings, even in spite of the smaller clutches in tropical populations, but females usually bring only a single item of food to the nest on each trip, while temperate red-wings usually bring several items at once. Tropical red-wings feed primarily on herbivorous Orthoptera, which are sparse and evenly distributed in tropical marshes.

Yellow-hooded Blackbirds at our study sites, like tropical red-wings, had substantial difficulties finding enough food for their young. At least in the Venezuelan llanos, these blackbirds fed primarily on Orthoptera, often brought one at a time to the nests from long distances. In all populations, females obtained their food away from their mates' territories. Unlike red-

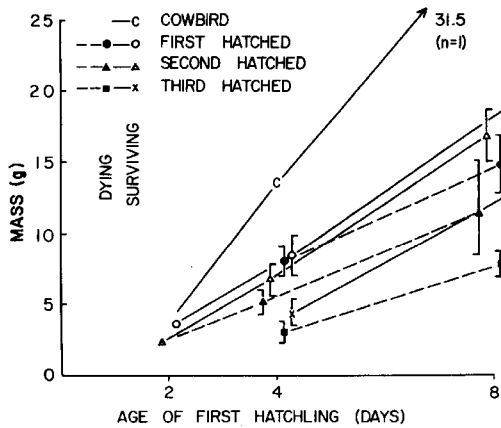


FIG. 17. Masses of nestling blackbirds separated by parity and eventual survival. Solid lines, surviving young; dashed lines, young that die before fledging; line marked C, one cowbird nestling that survived; other symbols as in Fig. 15.

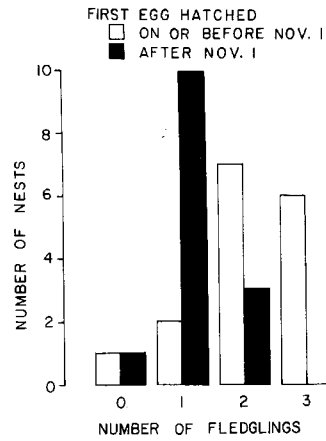


FIG. 18. Comparison of the numbers of fledglings from nests that began to hatch early and late in the season.

wings, male Yellow-hooded Blackbirds regularly helped to feed nestlings.

Yellow-hooded Blackbirds searched for food in the emergent vegetation of marshes and, when possible, in recently plowed rice fields. In Trinidad and Surinam, birds flew to plowed fields and searched the mud for food. In emergent vegetation, they normally hopped from stem to stem just above the water and peered intently at the bases of emerging stems. On occasion, birds probed with their beaks, using the spreading action typical of icterids (Beecher 1951), into the bases of the sheaths of grass leaves. Usually periods of regular hopping from stem to stem, probing here and there, alternated with periods lasting 15-30 s of intent investigations at one spot.

In Trinidad and Surinam, we never observed blackbirds eating the grains of cultivated rice. All foraging occurred in plowed and fallow fields and in emergent vegetation in ditches and marshes. In Venezuela, blackbirds, especially males, fed regularly on the seeds of wild rice. Males perched across the rice stalks, weighing them down horizontally, and concentrated mostly on the basal seeds in the stalks. During the breeding period, females rarely participated in the large flocks of males that fed on wild rice seeds. Instead they fed among emergent vegetation, as described above, as did males also. Although birds often foraged in places where emergent vegetation mingled with patches of open water, rather than in continuous vegetation, nevertheless nesting females on foraging trips often landed in the midst of continuous wild rice-sedge marshes.

On one occasion, when a flock of nonbreeding males and females foraged for >1 h in the canopy of a large broad-leaved tree near Lago Valencia, we could clearly see that the females were more agile in their foraging actions than the males. Females often hung sideways or upside down to collect items from the surfaces of the leaves, whereas males usually remained upright.

It is impossible to follow blackbirds feeding in emergent vegetation long enough to compare males and females, but it seems probable that the smaller, more agile females could feed in denser vegetation than could males.

Females did almost all of their foraging away from the males' territories. On occasion, a female leaving her nest would alight in the periphery of her mate's territory, some 5–10 m from her nest, and forage briefly there. Even in these instances, the female usually left quickly to fly at least 100 m to feeding grounds. In Venezuela, females left their nests to fly 100–500 m to search in the marshes of wild rice. Territorial males regularly left the nesting areas and flew toward the same feeding grounds used by females, but males also searched regularly in the emergent vegetation of their territories. The males collected nest material, dead grass stems plucked from the water, by searching in the same manner in which they foraged, hopping from stem to stem just above the surface of the water. Consequently, we could not determine how much of a male's searching within his territory contributed to feeding rather than obtaining nest material. In contrast to *Agelaius xanthomus* in Puerto Rico (Post, *in press*), our birds never regurgitated food to nestlings.

#### *Feeding at nests: Trinidad*

At two nests with young, females brought food 2–10 times/h (mean = 5.11,  $SD = 2.67$ ,  $N = 9$  hour-long watches evenly distributed during the first 4 h and the last 1 h of activity during the day). The data are too few to reveal any association of feeding rates with the age of the nestlings; three samples came from a nest in the first half of the nestling period, six from a nest in the second half. Females brought one item or several small items each visit.

Males helped to feed the young at two nests. Both of these males collected food for the nestlings within their own territories or nearby, 25–100 m from the nest. This behavior contrasted with the females feeding at these two nests, who never collected food within 100 m. At four other nests with young, males did not feed. Two of these were observed only during the early days of the nestling period; the other two were the second and third nests that hatched within 1 wk in the same territory. In the last case, the male fed the nestlings in the first nest to hatch but not in the other two.

Observations of the nest in male 8's territory suggested that the male's contribution increased during the nestling period. In six hour-long watches distributed over four consecutive days, male 8 fed the nestling 0–12 times/h; on the first 2 d, he fed 0–3 times/h in four observation periods, while on the second 2 d, he fed 8 and 12 times/h in two periods.

On the second 2 d, this male devoted himself almost exclusively to feeding the nestlings and virtually abandoned territorial activity. He sang infrequently and

often failed to challenge intruders within his territory. At the same time he repeatedly ignored territorial boundaries in his excursions for food and was chased peremptorily by his neighbors when he intruded into their territories. He once approached with agonistic displays, but failed to evict, two intruding males. Four days later, the nest was empty, probably lost to predators, and the male had abandoned his territory although no other had replaced him. A similar, but less extreme, decrease of territorial behavior occurred during and following the time that male 1 spent feeding the nestlings in the first three nests that hatched in his territory. Following the destruction of two of these nests and the successful fledging of one, male 1 entered a 3-wk period of desultory activity, during which he spent little time building nests and had no regular female visitors. Subsequently, he shifted the focus of his territory into an adjacent vacancy and resumed more normal territorial activity including regular nest building. Although the data are scant, males seem to feed nestlings mostly during the second half of the nestling period and to reduce their territorial activity while feeding.

#### *Feeding at nests: Venezuela*

We tried several techniques to obtain more complete information about the feeding of nestlings in the successful colony GC. Attempts to collect samples of food from nestlings' beaks by wrapping a pipe cleaner around their necks failed (Orians 1966). Although we colored our collars gray to reduce their conspicuousness, we observed females pecking at the collared nestlings, behavior never directed toward normal young. In addition, either the collars were too loose and permitted the nestlings to swallow the items, which often were rather small, or the females simply refused to leave unswallowed food in the nestlings' mouths. We often observed females place an item in a nestling's mouth and then grab it out again, sometimes several times in succession. Young birds had to swallow items immediately or the female removed them. Food seemed too valuable to leave unswallowed.

We could often identify food items brought by females to their nests and estimate their sizes simply by observing the returning females from our platform blind. Females sometimes perched in clear view before proceeding to their nests, so that we could study the items they brought. Some nests lay no more than a few metres from our blind and thus permitted detailed views of the returning females. Between 30 October and 15 November, we conducted daily hour-long watches from our platform blind, during which we recorded all males and females that brought food to nests within the 15 × 25 m area east of the blind. Whenever possible we identified the item and estimated its size. These observations began between 0915 and 1020 each day. On three days, 13–15 November, we observed



TABLE 6. Rates at which females brought food to nestlings at different stages of the nestling period.

Days after hatching	Trips per hour (mean and SD)
≤4 (N = 24‡)	2.46 (2.04)*
5-8 (N = 39)	4.95 (2.84)*†
≥9 (N = 61)	6.56 (3.77)†

\*  $t = 3.74$ ,  $P < .001$  (1-tailed).†  $t = 2.28$ ,  $P < .025$  (1-tailed).

‡ Hour-long samples of activity at nests.

feeding trips during a second hour-long period, which began earlier, between 0655 and 0720, in order to determine whether or not feeding behavior differed markedly early in the morning and later. Our most complete information comes from females that visited nests near our blind.

Feeding visits by females increased with the age of the nestlings, from 2.46 trips/h during the first 4 d of the nestling period to 6.56 trips/h on day 9 and thereafter (Table 6). Rates of feeding during the three samples early in the morning did not differ significantly from those later.

The majority of items brought to nestlings was a species of pale green Conocephalinae (Tettigoniidae, Orthoptera), usually delivered intact with wings and antennae. They included both wingless nymphs as small as 10 mm in length (head to abdomen) and adults that reached 25 mm in length. Other items were extremely diverse: egg cases; small spiders; beetle larvae; small moths ≈15 mm in length; odonate larvae 2-3 cm in length; limp abdomens of adult Odonata, probably teneral, up to 3 cm in length. Aside from the common tettigoniid, females rarely brought the same item in successive trips. Usually a female brought only one item per trip; in <10% of trips, she brought two small items and only twice, in over 600 identified loads, more than one large item. Females brought large tettigoniids (at least 20 mm long) more frequently late in the nestling period, on and after day 9, in comparison to earlier (8.8% and 2.2% of identified deliveries, respectively, Table 7). Large tettigoniids were equally common early and late in the morning ( $G = 2.41$ , NS,  $N = 529$  trips).

As Orians (1973) has argued for tropical Red-winged Blackbirds, the tendency of females to return from foraging trips with a single, often rather small item suggests that suitable food was not abundant. Temperate marsh-nesting blackbirds typically return to their nests with a number of large items each trip. Five standardized samples of 25 sweeps with an insect net at scattered locations (10-30 m apart) in the wild-rice marshes, where the females did most of their feeding, yielded a total of ≈30 of the tettigoniids fed to nestlings. Most were nymphs <5 mm long. The samples also included numbers of adult beetles and flies, items never delivered to nestlings, and a few other insects

TABLE 7. Frequencies of feeding trips on which females brought large tettigoniids to nestlings in relation to stages of the nestling period ( $G = 5.86$ ,  $P < .02$ ).

Days after hatching	Trips with large tettigoniids	Trips without large tettigoniids	Trips per large tettigoniid
≤4	1	58	59
5-8	2	89	45
≥9	34	354	11

and lepidopteran larvae. These samples all had similar yields of the tettigoniids. Items suitable for delivery to nestlings, tettigoniids at least 10 mm long and lepidopteran larvae, were thus sparse in these marshes.

Changes in the food delivered to nestlings during the course of the breeding season suggested that the tettigoniids became progressively scarcer. During the 1st 10 d after the nests began to hatch, the single most abundant item delivered to nestlings were small (15 mm or less) tettigoniids (Fig. 19). As the season progressed, the proportion of small tettigoniids dropped steadily and the proportion of other small items increased. The proportions of large tettigoniids remained roughly similar throughout the season; other large items were so scarce that they would have little effect on these percentages. Apparently the tettigoniids ceased hatching before the middle of November, so the blackbirds switched to other small items when they could not find large tettigoniids. The proportion of large tettigoniids did not increase as the season progressed. Since the blackbirds tend to bring more large tettigoniids to older young, the lack of an increase in the proportion of large tettigoniids late in the season suggests that blackbirds were having more difficulty finding them.

We detected no indications that females followed each other to good locations for foraging. Females on foraging trips flew 50 to >500 m from the colony (mean = 175 m before landing or disappearing from view still in flight,  $N = 24$ ). All of those observed to

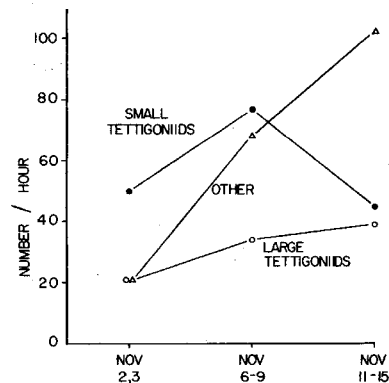


FIG. 19. Kinds of food brought by females to nests in colony GC during three periods in November.

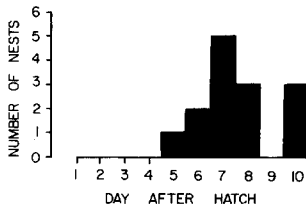


FIG. 20. Day of the nestling period on which males began to feed young at nests in colony GC.

land did so within the expanses of wild-rice marsh that extended in all directions from the colony. A female often arrived and departed from the same direction for a series of trips; apparently they tended to return to the same general area on successive trips. On occasion, most females in the colony preferred one general direction during a given hour-long watch, but they usually left the colony in all directions. Although females often perched in the open near their nests for 10–60 s before leaving, there were no indications that they used this period to observe the directions taken by other females. The tendencies of a female to fly in the same direction on successive trips outweighed any indication that they followed other females.

Other evidence that females might learn the locations of food patches by observing others includes greater nesting success in the center rather than the edges of a colony. For these blackbirds, it is difficult to imagine that females near the center of the colony could see the directions of departing birds more easily than those 20 m away at the edge of the colony. Although nests near the edge of the colony probably succeeded less well than those in the center, the difference is entirely a result of the episode of predation along one edge of the colony.

In conclusion, no evidence indicates that these blackbirds followed each other to good feeding grounds. In general, females departed singly, without reference to others, and searched singly in the marshes. Of course, a chance to observe the directions taken by others might prove critical only once or twice during the course of the day.

While feeding their young, females spent  $\approx 7\%$  of their time flying. By timing flying females, we esti-

mated that they required  $\approx 20$  s to fly 250 m. At 6 trips/h, flying time amounted to  $\approx 4$  min/h. Given that a round trip averaged 10 min and included 1–1.5 min in the colony and flying, a female had 8.5–9 min on the average to find food for her nestlings and herself.

Many males fed the nestlings and recent fledglings in this colony. Approximately three-quarters of the males were observed to feed young at some time during the breeding season. A male always fed at one nest on a given day. Two males each fed at one nest until the young had fledged and then, after an interval of several days, began to feed at a second nest. Males never fed fledglings once they had left their territories. Males flew short distances, rarely  $> 100$  m, to search for food for the nestlings. During their first few days of feeding, the males seemed not to know the locations of the nests well; they often perched near the nest, sang several times, and even descended into the *Thalia* at incorrect places before eventually going to the nest. Males tended to feed nestlings less often than the females and to bring smaller items. Sometimes a male fed regularly one day, but not the next. In addition, their activity could shift markedly from hour to hour.

As in Trinidad, males tended to feed more frequently at nests during the second half of the nestling period. None was observed to begin feeding until day 5 after the first egg hatched; most began on day 7 (Fig. 20). By comparing nests at which males helped with those at which no male helped or male help began late, we attempted to determine the significance of the male's contribution to nesting success. For this comparison we had four nests at which no male helped or at which a male began to feed after day 8 and three nests at which males helped on  $> 1$  d prior to day 8. Both of these samples excluded nests in which cowbirds hatched.

The masses of both the oldest and second-oldest young on day 8 of the nestling period were higher in those nests that had received previous male help (Table 8). The difference is greater for the second young than for the oldest young, as we might expect if the oldest gets first choice of the food delivered, so that extra food would primarily affect the younger nestlings. In addition, on day 9 our small sample of nests that had received male help included two nests with

TABLE 8. Masses of nestlings (grams) on day 8 of the nestling period in relation to differences in the male's contribution to feeding on preceding days (data from nests in which no cowbird hatched).

	Mean mass (SD, N)	
	Oldest nestling	Second-oldest nestling
Male fed nestlings on $> 1$ d before day 8	22.7 (0.58, 3)	19.2 (0.76, 3)
Male fed nestlings on 1 d or 0 d before day 8	20.1 (1.89, 4)	16.2 (1.04, 3)
<i>t</i>	5.68	8.05
<i>P</i> (1-tailed)	$< .005$	$< .005$

three surviving young; our sample of nests that received no male help until after day 8 included none with three nestlings but one that had only a single nestling. Even though we could only detect effects of male help that were expressed within 1 or 2 d after the onset of male help, the evidence establishes that feeding by males did increase the mass of nestlings and hence probably increased their survival.

Once a male began regular trips to feed the nestlings, he usually reduced his territorial activities, in particular the frequency of singing on his territory, but none lost his territory. Males therefore had to strike a balance in their allocation of time to territoriality and feeding nestlings. Both in Trinidad and in the Venezuelan llanos, territorial defense and nest building by males varied inversely with the time devoted to feeding at nests. Males switched from territoriality to feeding young late in the nestling period, at a time when successful fledging lay within a few days' time and provision of extra food had the greatest effect on the survival of young. In Trinidad, the males had to balance the advantages of a final effort for success at one nest against the chances of starting several new nests, most of which would fail. In Venezuela, although the chances of nest success were much greater in a successful colony than in Trinidad or Surinam, by the time nests had half-grown young, few females were laying and males had little chance for starting new nests. Thus in Venezuela males made the switch at a time when they had little chance of starting new nests, while in Trinidad, males switched to feeding young once the chances for the success of the particular nest had increased sufficiently.

#### IMMATURE MALES

Many of the nonbreeding males at each study site had immature plumage. We never observed such a male holding a territory. In flocks of nonbreeding blackbirds, immature males occasionally directed bill-up displays toward other immatures and rarely displaced or chased other immatures. On three occasions we saw immature males approach females with fluttering flight in these flocks, but only briefly. They also occasionally sang in these flocks, as adult males and females did.

The plumages of these immature males are extremely variable; some resemble juveniles but with more yellow on the throat and forehead. The feathers of the head are progressively replaced with yellow, while the brown feathers of the body are replaced by sooty black feathers with yellow-brown edgings. Many immature males during the breeding season begin to acquire the deep black feathers of the adult male. These immatures have yellow heads with persistent brown patches on the nape and sometimes the auriculars, mixed black and sooty feathers on the back, and sooty feathers with narrow edgings below. They

are apparently yearlings engaged in a slow molt into full adult plumage.

In Trinidad and Surinam, one might expect more variability in the plumages of immature males at any one time than in Venezuela where the nesting season is shorter. Our observations agree with this expectation. In Venezuela at FPM, most immature males were in the late stage described above until the middle of November when many immature males in the earliest stage joined the mixed flocks of blackbirds gathering at that time. In Trinidad and Surinam, the plumages of immature males had less recognizable modes. At all sites, the proportion of immature males in flocks of nonbreeding males was  $\approx 25\text{--}35\%$ . As breeding males did not join these flocks, the actual proportion of immatures among all males must be closer to  $10\text{--}15\%$ . As described above, substantial numbers of males in adult plumage, perhaps as many as one-half of adult males, did not hold territories during the breeding seasons at all of our study sites.

#### DISCUSSION

##### *Comparisons of temperate and tropical marsh-nesting blackbirds*

Yellow-hooded Blackbirds agree in many aspects of their ecology with tropical populations of Red-winged Blackbirds in Costa Rica (Orlans 1973), which, like the Trinidad and Surinam populations of yellow-hoods, have an extended nesting season during the rainy months of the year. In temperate North America, three species of marsh-nesting blackbirds have received extensive study: red-wings, Tricolored Blackbirds, and Yellow-headed Blackbirds *Xanthocephalus xanthocephalus*. In some respects, tropical red-wings and yellow-hoods differ consistently from these temperate blackbirds.

*Nesting success and clutch size.*—Tropical red-wings and yellow-hoods lay clutches that average  $<3$  eggs. Yellow-hoods never lay  $>3$  eggs. Temperate marsh-nesting blackbirds have somewhat larger clutches. Clutches of the North American Yellow-headed Blackbird and North American red-wings usually average  $>3$  eggs per nest and include some with 5 eggs (Willson 1966, Holm 1973). Thus marsh-nesting blackbirds fit the widespread pattern among birds of lower clutch sizes in the tropics than in temperate regions.

Nest success among temperate marsh-nesting blackbirds usually amounts to  $25\text{--}65\%$ , and  $20\text{--}45\%$  of eggs fledge (Young 1963, Willson 1966, Board 1967, Francis 1971, Robertson 1972, Holm 1973, Dolbeer 1976, Caccamise 1977). Partial brood losses, an indication of starvation of nestlings, are a high percentage ( $15\text{--}50\%$ ) of mortality among nestlings in marsh-nesting birds in temperate regions (Young 1963, Willson 1966, Ricklefs 1969, Holm 1973, Robertson 1973a). Predation is also an important source of mortality for nests in temperate

TABLE 9. Masses of adult blackbirds (grams).

Location	Sex	Mean mass (g)	SD	Range (g)	N	Source
<i>Agelaius icterocephalus</i>						
Surinam	Male	35.9	1.8	32.0–37.5	9	This study
	Female			29.0–31.0	2	This study
	Male			33–39		Haverschmidt 1968
	Female			28–32		Haverschmidt 1968
Trinidad	Male	35.4	2.0	31.4–40.0	27	Snow and Snow 1963
	Female	26.6		24–31	17	Snow and Snow 1963
<i>Agelaius phoeniceus</i>						
California	Male	65				Payne 1969
	Female	44				Payne 1969
<i>Agelaius tricolor</i>						
California	Male	66				Payne 1969
	Female	46				Payne 1969

marshes: 25–45% of eggs are lost to predators before fledging (Young 1963, Willson 1966, Robertson 1972, Holm 1973).

In Costa Rica, red-wings had  $\approx 21\%$  nest success (Orians 1973), higher than our small sample for yellow-hoods in Trinidad and Surinam. Orians found clear evidence of starvation among nestlings, although some females fledged full clutches of three young. Predation after hatching, primarily by snakes and rice rats *Oryzomys*, claimed 59% of nests. This pattern agrees in general with our observations of nest success in Trinidad and Surinam, except that a higher proportion of nests was lost before hatching so that overall nest success was lower. Thus tropical marsh-nesting blackbirds in moderately seasonal areas suffer from greater predation on nests and starvation of nestlings than do temperate marsh-nesting blackbirds.

In tropical regions, complete losses of nests, an indication of predation, dominate nest mortality in humid forest environments, while partial losses, an indication of starvation, predominate in arid environments (Marchants 1960, Ricklefs 1969). The present study and Orian's (1973) are the first to document nest mortality in tropical marsh-nesting species. Both have indicated that substantial losses result from both predation and starvation.

*Feeding of nestlings.*—North American Red-winged and Yellow-headed Blackbirds feed predominantly within the males' territories in some localities but not others (Orians 1961, Willson 1966, Holm 1973, Caccamise 1977). When feeding in marshes, these blackbirds bring large numbers of odonate teneral to nestlings (Orians 1966b, Willson 1966, Robertson 1973a). In addition to bringing a number of items on each trip to the nest, these blackbirds make many more trips per hour than do tropical yellow-hoods. In Washington Yellow-headed Blackbirds delivered food 10–17 times/h on the average, more often later in the nestling period than earlier (Willson 1966).

Tropical red-wings collect most of their food within

their nesting marshes, although Orians (1973) does not specify whether birds remain within their own territories. Like yellow-hoods, they take primarily herbivorous insects, Orthoptera and larval Lepidoptera, rather than insects with aquatic larvae, like Odonata. The tropical blackbirds normally bring one item per trip to the nest and make fewer trips per hour in comparison to temperate marsh-nesting blackbirds. These observations, in conjunction with the high frequency of starvation among nestlings, suggest that blackbirds have substantially greater difficulty finding food in tropical than in temperate marshes.

Yellow-hooded Blackbirds and red-wings have about the same relative growth rates during the nestling period; both attain  $\approx 50\text{--}55\%$  of adult mass (mean for both sexes; see Table 9) by the 8th d of nestling life (Holcomb and Twiest 1970, Robertson 1973b). Absolute growth rates, however, are much lower for the smaller yellow-hoods:  $\approx 3$  g/d for nestling red-wings in comparison to  $< 2$  g/d for yellow-hoods. In combination with the smaller clutch sizes, the lower absolute growth rates mean that a female yellow-hood must provide food for no more than half as much total growth of nestlings each day, probably an important consideration for a species that depends on smaller, more dispersed food items.

*Asynchronous hatching and brood reduction.*—Temperate marsh-nesting blackbirds begin incubation with the second or later egg. As a consequence, the first two eggs hatch at about the same time, while subsequent eggs often hatch asynchronously (Willson 1966; S. Lenington, *personal communication*). In tropical red-wings also, incubation begins with the second (and usually penultimate) egg. Yellow-hoods, in comparison, always begin incubation with the first egg, so that all eggs hatch asynchronously. Consequently, yellow-hoods have greater size differences among nestlings and more regular brood reduction.

Asynchronous hatching and the consequent starvation of the youngest nestling can be advantageous

when parents confront a sparse and unpredictable food supply (Lack 1947, 1966, Howe 1976). For yellow-hoods, the variable course of the rainy season, particularly in the Venezuelan llanos, might well make the abundance of food for nestling blackbirds unpredictable. When brood parasitism is common, the early start of incubation also increases the chances that the female blackbird's own eggs will fledge. Indeed if risks of brood parasitism favored early onset of incubation, parent-offspring conflict might generate brood reduction, even if the food supply were predictable. Our data on survival of young in nests that hatched two and three young in colony GC in Venezuela suggest, according to O'Connor's (1978) arguments, that brood reduction in nests with three young had evolutionary advantages for the surviving young but not for the parents. Thus female yellow-hoods should have tried to raise three nestlings, while the oldest nestlings should have tried to exclude the youngest from obtaining food.

*Participation of males.*—Among North American populations of red-wings, the contributions of males to the nesting effort varies. In California and Washington, they rarely feed nestlings, although they often feed fledglings (Orians 1961b, Payne 1969). In an Indiana population,  $\approx 1/2$  of the males feed nestlings, particularly at the first nest in a male's territory, and thereby increase fledging success (Patterson 1976). Male Yellow-headed Blackbirds regularly feed nestlings at the first nest in their territories after about day 4 of the nestling period (Willson 1966).

Male Tricolored Blackbirds help to feed nestlings more than do male red-wings (Orians 1961b), but little quantitative information is available about their participation. Payne (1969) noted that many nests are tended only by females early in the nestling period, while later in the nestling period males participate equally, at least in some colonies. Evidently the participation of males in feeding the young increases during the nestling period, as in both Yellow-hooded and Yellow-headed Blackbirds. The greater participation of male tricolors, in comparison to red-wings, in feeding nestlings relates to a greater difficulty of providing food for the young (Orians 1961b). Nestling tricolors are fed primarily Orthoptera collected in grasslands up to 6 km from the nesting colony.

Tropical red-wings resemble populations in western North America in the extent of male participation. Apparently male red-wings in Costa Rica do not feed nestlings (Orians 1973). Male yellow-hoods, in comparison, regularly feed nestlings. The difficulty of finding food in tropical marshes, one might expect, would favor participation of males in feeding nestlings. Our study has found that feeding by males does increase the masses of nestlings, an indication that feeding rates limit the growth of young in this species. In addition, male yellow-hoods have taken over the task of nest construction. Females can thus spend all of their time

on the best feeding grounds until a few days before beginning to lay their eggs.

*Brood parasitism.*—Parasitism by cowbirds is not frequent in north temperate blackbirds (Willson 1966). In addition, the tropical red-wings in Costa Rica do not have brood parasites. The parasite of Yellow-hooded Blackbirds, the Shiny Cowbird, only reaches eastern Panama. This species is currently expanding its range in the Caribbean. In Puerto Rico it has become a serious parasite of Yellow-shouldered Blackbirds *Agelaius xanthomus* which have not yet evolved defenses against nest parasitism (Post and Wiley 1976, 1977). In addition, this cowbird parasitizes marsh-nesting *Agelaius* species in Argentina (Friedmann et al. 1977). Primarily owing to the male's vigilance against female cowbirds and the early onset of incubation by Yellow-hooded Blackbirds, cowbirds have little effect on the nest success of this species.

*Coloniality and synchrony of nesting.*—The contrasts in spacing and synchrony of Yellow-hooded Blackbirds nesting in less seasonal and more seasonal areas (Table 10) recall the contrasts between Red-winged and Tricolored Blackbirds in California. Tricolored Blackbirds, in comparison to red-wings, nest in dense colonies where each male defends  $\approx 3.5$  m<sup>2</sup> (Orians 1961a). The largest colonies of Yellow-hooded Blackbirds included <100 females, two orders of magnitude smaller than the largest colonies of Tricolored Blackbirds. Tricolors in any one colony lay their eggs within 5–10 d, while red-wings continue laying for 4–6 wk. Although the Venezuelan Yellow-hooded Blackbirds nested more synchronously than the coastal populations, they did not match the extreme synchrony in colonies of Tricolored Blackbirds.

Many colonies of Tricolored Blackbirds, particularly smaller ones, fail totally (Orians 1961b). In one sample,  $\approx 50\%$  of colonies failed completely (Payne 1969). In successful colonies, 5–80% of nests succeeded, or 40–67% in the larger successful colonies (Payne 1969). The reasons for the failure of entire colonies is not always evident. Often the whole colony deserts almost at once. In some cases, a concentration of predators might trigger desertion (Orians 1961a, b, Payne 1969). This pattern recalls that of Yellow-hooded Blackbirds in Venezuela, where many colonies, particularly smaller ones, failed completely.

Tricolors, unlike yellow-hoods, show some clear signs of coordinating their feeding efforts. Thus arriving and departing birds often stream in one direction from the colony at a particular time. In addition, many individuals in a colony often depart on mass feeding flights. Neither of these forms of interaction appear among colonial Yellow-hooded Blackbirds.

Although the differences in spacing and synchrony between populations of yellow-hoods in more and less seasonal environments parallel the differences between Tricolored and Red-winged Blackbirds, these differences are less extreme. Tricolors and colonial

TABLE 10. Summary of seasonality, spacing, and breeding ecology of *Agelaius icterocephalus* in two tropical environments.

	Coastal Trinidad and Surinam	Venezuela (llanos bajos)
Seasonality		
Seasonality of rainfall	Moderate	Extreme
Population residence near breeding areas	Continuous	4 mo
Length of breeding season (duration of laying)	>2 mo	<1 mo
Spacing		
Nests	Scattered (2–10 m apart)	Clumped (.5–2 m apart)
Territories (center-center spacing)	15–50 m	5–10 m
Breeding success		
Nest parasitism	33%	{ ≈100% (unsuccessful colony) 33% (successful colony)
Nest predation during incubation	High	15% (successful colony)
Nest success	Low	{ ≈0% (unsuccessful colony) 60% (successful colony)

yellow-hoods differ furthermore in the exposure of colonies to brood parasites and predators and in the importance of coordination in foraging activities. The parallels between these two comparisons, one intraspecific, the other interspecific, might result from different balances between advantages of aggregation and synchrony for feeding and for reducing predation or parasitism.

#### *Polygyny*

Yellow-hooded Blackbirds are comparable to redwings in their degree of polygyny, although an exact estimate of the number of females per territorial male was difficult to obtain for any of our study sites. At the successful colony GC in Venezuela, the ratio was ≈3, if we include all territorial males in the colonies in our calculations. At FPM, however, numbers of territorial males in unsuccessful colonies attracted no females. In addition, there seemed to be large numbers of nonbreeding, adult-plumaged males at any given time at all study sites.

It remains uncertain whether access to food or optimal nest substrates provide a basis for a female's choice of a male's nest and territory. Unlike females in some populations of Yellow-headed and Red-winged Blackbirds in North America, female yellow-hoods seem never to use the males' territories as a source of food. Males' territories seem not to offer different advantages in foraging for females. Our studies also revealed no clear indications that certain kinds of vegetation offered more secure positions for nests than did others, as in North American marshes (Holm 1973). However, the emergent vegetation in most tropical marshes includes a greater diversity of plants than in temperate marshes, so our samples of nests in different kinds of vegetation are too small to test this possibility. In the large colonies in stands of *Thalia* in the Venezuelan llanos, positions near the center of the

colony appeared to involve less risk of predation than those at the edge.

Nest construction by male Yellow-hooded Blackbirds recalls polygynous species in a number of other avian families, the wrens and weaver birds particularly (Crook 1964, Collias and Collias 1970, Verner and Engelsen 1970, Collias and Victoria 1978). Apparently no other species in the family Icteridae has evolved nest construction by males. The sparseness of food in tropical marshes suggests that this behavior in Yellow-hooded Blackbirds has evolved to permit females to devote full time to feeding during the intensive metabolic demands of egg synthesis.

Like many other polygynous species, Yellow-hooded Blackbirds have sexual bimaturism. Males retain immature plumage through at least their 1st yr and during this time never defend a territory; thus males breed for the first time no sooner than 2 yr of age. Females apparently breed sooner. It is difficult to ascertain whether all females breed each season in Trinidad and Surinam, since laying is distributed over several months. At FPM in Venezuela, females were noticeably absent from the flocks of nonbreeding birds during most of October and November when nesting activity was at its peak. Presumably females breed in their 1st yr, as in the North American congeners. As Orians (1961a) noted in discussing the evolution of mating systems in North American blackbirds, the deferment of breeding until age two creates a difficulty in understanding the evolution of polygyny. The advantage to a male of multiple mates is not so clear when it involves a postponement of the onset of reproduction (Wiley 1974a, b, *in press*).

As Verner (1964) and Orians (1969) have emphasized, the evolution of polygyny must result from advantages for both males and females. Since half of the progeny on average from any mating are males and half females, it is to each sex's advantage to mate with

TABLE 11. Causes of breeding failure ranked by numbers of eggs and nestlings lost at different study sites. 1 = largest losses; 4 = smallest losses.

Source of loss	Trinidad and Surinam	Venezuela	
		Successful colony	Unsuccessful colony
Predation			
Before hatching	1	3	...
After hatching	2	2	...
Starvation	3	1	...
Brood parasitism	4	4	1

partners whose behavior and life history strategies optimize the propagation of their genes in the population. One condition for the evolution of polygyny, as just discussed, is an evolutionary advantage for males that defer reproduction. Another condition is that females choosing polygynous males must have expectations of reproductive success as great as those choosing monogamous males (Orians 1969, Wittenberger 1976, Altmann et al. 1977).

Whether or not female Yellow-hooded Blackbirds nest as successfully on polygynous territories as on monogamous ones is not established. In Trinidad and Surinam, such a large percentage of nests failed that territories are unlikely to have simultaneous nests with young. We observed one such case, in which a territory had three nests with young, and only the nest at which the male helped fledged young. In view of the demonstrated effect of the males' contribution on nestling masses and survival, some compensating advantage must accrue to females from polygynous mating. At least in the dense colonies in central Venezuela females might obtain advantages from nesting near the center of a colony.

#### *Nesting adaptations of blackbirds in the llanos*

*Limitations on nesting success.*—The relative importance of predation, starvation, and brood parasitism in losses of eggs and young differed among our study sites for yellow-hoods. Predation predominated in the moderately seasonal sites in Trinidad and Surinam, starvation in the successful colony in the extremely seasonal environment in the Venezuelan llanos, and parasitism in unsuccessful colonies in the llanos (Tables 10 and 11).

The relative proportions of losses of eggs and young ascribed to different sources of mortality do not necessarily indicate their importance in limiting reproduction. The different sources of mortality occur at different times in the nesting cycle. Predation can occur throughout the cycle; starvation primarily affects nestlings during the second half of the nestling period; brood parasitism affects nests either at the very start of the cycle, when nests with too many parasitic eggs are deserted, or toward the end, when nestling para-

sites compete with the hosts for food. Since mortality affects any nestling only once, the inherent temporal relationships of the sources of mortality alone influence their relative frequencies. Thus in Trinidad and Surinam, although most nests were lost to predators both before and after hatching, partial brood losses occurred in all nests that escaped predation.

It is not justifiable to ascribe a species' nesting adaptations primarily to selection pressures created by the most prevalent source of mortality. In fact all three sources of mortality are likely to limit reproduction in the sense that lesser adaptation of the blackbirds against each source of mortality would further reduce nest success. In the Venezuelan llanos, although brood parasitism accounts for the least mortality in successful colonies of blackbirds, nevertheless its overwhelming importance in the failure of other colonies suggests that the spacing of blackbirds in the llanos has evolved primarily in response to the threat of brood parasitism and in spite of some disadvantages in gathering food to prevent starvation of nestlings.

*Temporal restriction of nesting.*—The short breeding season of Yellow-hooded Blackbirds in the Venezuelan llanos is in part a response to the short season during which food and nesting sites are available. It is possible that parasitism by cowbirds has favored even greater seasonal restrictions on nesting than demanded by the food supply. Our evidence indicates that the response of cowbirds does not track the sudden availability of blackbird nests: the temporal concentration of nests reduced the individual vulnerability of nests to brood parasites during the first few weeks. Some ungulates have also evolved synchronized birth seasons in order to reduce vulnerability to predators (Gosling 1969, Estes 1976). Whether or not Yellow-hooded Blackbirds in the llanos have evolved greater synchrony in breeding than required by the seasonality of their food supply, the temporal restriction on their nesting has an effect of temporarily reducing vulnerability to their brood parasites.

*Spatial restriction of nesting.*—The aggregation of blackbirds in the llanos in dense colonies results in part from the growth of their favored nesting substrate *Thalia* in dense patches. Almost no blackbirds attempted to build nests elsewhere. The superiority of *Thalia* as nesting substrate seems clear. The dense stands impede the entrance of predators like raccoons and snakes, the stems provide firm anchorage for the nest, and the broad leaves waving 1 or 2 m above the nest tend to screen them from searching cowbirds. Nevertheless, many patches of *Thalia* had no nesting blackbirds, and in large beds of *Thalia* the blackbirds congregated densely in a small proportion of the total area.

The restriction of nesting to dense, discrete colonies appears to have disadvantages for foraging. The insects fed to nestlings are sparsely distributed throughout vast reaches of wild-rice marsh. Since this re-

source lacks clear patchiness and since the females show few signs of following each other to and from feeding locations, widely dispersed nests would shorten the flying time and energy required to feed the nestlings.

Advantages in exploiting food supplies thus seem unlikely to explain the switch of Yellow-hooded Blackbirds to dense colonies, instead of dispersed nests, in the Venezuelan llanos. Our evidence suggests instead that the congregation of blackbird nests in dense colonies offered advantages in reduced vulnerability to predators and cowbirds. The effects of dense coloniality on these two kinds of threats for the blackbirds are not the same.

Clumping by prey can have two kinds of effects on their vulnerability to predation, both of which will depend on the predator's responses to the tactics of the prey: (1) changes in the risks of encounters between predators and prey individuals, where an encounter occurs when a predator detects a prey individual; and (2) opportunities for cooperative interactions among prey individuals in avoiding or repelling predators after detection.

Aggregation by prey reduces the risks of encounters between predators and individual prey (Hamilton 1971, Treisman 1975), provided that predators take one prey individual at a time, search independently, and do not adopt specialized searching after one prey individual is encountered. Any of these qualifications, which would represent adaptations by the predator, could render prey individuals more vulnerable in aggregations than alone. Specialized searching after encountering a prey individual could include acquisition of a search image or spatial restrictions on subsequent searching, both of which would tend to increase the vulnerability of aggregated prey. Spatial restrictions on searching after encounters with prey individuals would in addition result in the recruitment of predators to congregations of prey, even in the absence of any cooperation in searching among predators. On the other hand, such recruitment of predators would not occur if predators maintained regular spacing or individual distances.

Decreased risks of encounters with predators like raccoons and snakes might well result from the dense coloniality of blackbirds in the llanos. These predators take one nest at a time and presumably search independently. We found evidence that one or a few snakes concentrated on a colony of blackbirds once discovered, an example of spatial restriction in searching after encountering prey. Nevertheless, the difficulties of locating a colony of blackbirds precluded an aggregation of snakes at the colony. In the end, only a small proportion of the colony was lost to snakes. In contrast to the rates of predation on dispersed nests in Trinidad and Surinam, predation on colonies of blackbirds in the llanos was a minor source of mortality. Without a comparison of similarly dispersed nests in

the llanos, however, we cannot be sure that coloniality actually lowered predation rates there.

On the other hand, coloniality surely had no effect in reducing encounter rates of blackbird nests with cowbirds. The considerations for the interactions between predators and prey apply equally well to the interaction between cowbirds and nests. In the case of the cowbirds, the conspicuousness of colonies of nesting blackbirds and the possibilities for spatial restriction on searching permit the recruitment of numerous cowbirds to the colonies of blackbirds. Note that the effects of spatial aggregation on the detection of nests by cowbirds and temporal synchrony on the ability to exploit nests offset each other.

The second major effect of aggregation by prey, cooperation in evading predators after detection, clearly influences the interactions of cowbirds and blackbirds in the llanos. Cooperation among aggregated prey individuals can include more efficient detection of approaching predators, confusion of the predator (Tinbergen 1951, Hobson 1968, Walther 1969, Eaton 1970), and active repulsion of predators by collective attacks of prey (Kruuk 1964, Hoogland and Sherman 1976). Active repulsion of cowbirds by territorial male blackbirds probably substantially restricts the cowbird's abilities to locate and monitor host's nests. Recall that the success of a cowbird egg depends strongly on careful timing in laying, so that harassment of searching female cowbirds might well interfere with their chances of following individual blackbird nests with the accuracy needed to lay their eggs at the correct time. In addition, the crowded colonies of blackbirds might also create confusion for cowbirds. The closely spaced nests submerged in the waving expanses of *Thalia* would presumably strain the abilities of female cowbirds to keep track of individual nests.

*Conclusions.*—The seasonal restriction of the food supply and suitable nesting substrate in the llanos exposes Yellow-hooded Blackbirds to greater risks of nest parasitism than in less seasonal environments. The effects of nest parasitism and possibly also predation are reduced by dense coloniality and nearly synchronous nesting. The evolution of spatial congregation of nests has involved compromises. Spatial congregation probably has disadvantages for feeding and detection of nests by cowbirds but compensates by advantages in repelling cowbirds from nesting territories.

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