The Jamaican Blackbird:
A "Natural Experiment" for
Hypotheses in Socioecology

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INTRODUCTION

The last twenty years have seen an unprecedented surge of new theory about evolutionary adaptations of social systems to different ecological circumstances. One of the clearest predictions in this literature relates the spatial relationships of individuals to the distribution of food in their environment. Specifically, when food is sparse, evenly distributed, and slowly renewing, and when individuals have fixed bases of operation, like nests or caches, then individuals expend the least effort harvesting the food if they occupy exclusive territories (Brown, 1964; Horn, 1968; Smith, 1968; Brown and Orians, 1970; Waser and Wiley, 1979). This conclusion derives from simple calculations (Horn, 1968; Smith, 1968; Waser and Wiley, 1979) and leads to a prediction that animals collecting sparse, evenly distributed food should occupy large, exclusive territories. This prediction is supported in a general way by comparative reviews of a number of taxonomic groups of

birds and mammals (Crook, 1965; Lack, 1968; Brown and Orians, 1970; Waser and Wiley, 1979).

One method for studying evolutionary adaptation is a comparison of two species that share a relatively recent phylogenetic origin but differ in their current environments. A comparison of this sort, unlike a manipulative experiment, cannot randomize subjects and controls, nor can it artificially manipulate the environments in which the subjects have evolved. On the other hand, it permits an investigation of adaptations evolved over a large number of generations in organisms not easily accommodated in large-scale genetic experiments in the laboratory. Investigations can extend to environmental conditions and behavioral responses not easily fitted into limited space. Furthermore, such a comparative study is not an undirected search for correlations, any more than a manipulative, randomized experiment is, provided the investigators begin with definite hypotheses and systematically consider possible alternative explanations for the results. The term "natural experiment" is commonly used for a comparison of individuals or populations with naturally occurring differences in order to investigate definite hypotheses.

The Jamaican blackbird *Nesopsar nigerrimus* provides a "natural experiment" to test the hypothesis relating the dispersion of food to the spacing of individuals in a population. Its closest phylogenetic relatives are blackbirds in the genus *Agelaius*, most of which nest in marshes on small territories that provide only a fraction of the occupants' food. In contrast, the Jamaican blackbird feeds on arboreal insects in montane forests (Lack, 1976; Cruz, 1978). If, like other arboreal, insectivorous birds in forests, the Jamaican blackbird experiences sparse, evenly distributed food, it should differ from its closest phylogenetic relatives in defending extensive, exclusive territories.

Among birds, sparse, evenly distributed food is also usually associated with monogamous pair bonds, which permit full dual parental care in which both parents feed the young (Crook, 1962; Lack, 1968). Forest insectivores normally have monogamous mating systems, while species of more nearly two-dimensional habitats, like grasslands and marshes, more often are polygynous (Verner and Willson, 1966; Orians, 1979b; Crook, 1962). This correlation appears notably among the blackbirds and orioles (Icteridae) and the African weaver finches (Ploceidae). The sparsely distributed and cryptic insects of forests favor the cooperation of both parents in rearing young. Furthermore, Jamaican blackbirds are almost sexually monomorphic in both plumage and size (Table I), characteristics that usually accompany monogamy in passerines (Verner and Willson, 1969). These considerations suggest a second prediction: the Jamaican blackbird should differ from its closest phylogenetic relatives in practicing monogamy with dual parental care.

TABLE I.   Sexual Dimorphism in Size for Selected Icteridae[a]

Species or subspecies	Ratio of standard wing lengths (male/female)
Xanthocephalus xanthocephalus	1.24
Agelaius	
phoeniceus (9 mainland subspecies)	1.19–1.27
phoeniceus (Cuba)	1.16
tricolor	1.14
xanthomus (Puerto Rico)	1.12[b]
humeralis (Cuba)	1.09
Icterus (14 species)	1.04–1.10
Nesopsar nigerrimus	1.05

[a] Data from Ridgway (1902).
[b] Larger sample size in Post (1980) yields 1.10.

The usual spacing of individuals in natural populations influences the nature of communication between individuals. In particular, birds with large, exclusive territories normally have long-range acoustic signals for territorial advertisement, usually advertising songs consisting of frequency-modulated tones. On the other hand, many birds that nest in colonies or in small, closely packed territories use wide-spectrum sounds for acoustic communication (Wiley, 1976a). As Nero (1963) notes, this contrast holds well for the Icteridae. For long-range communication, frequency-modulated tones resist degradation by irregular amplitude fluctuations and reverberation (Wiley and Richards, 1978; Richards and Wiley, 1980). In addition, tonal signals permit greater power per Hz bandwidth and thus improve the signal/noise ration for frequency-discriminating receptors, like vertebrate ears. On the other hand, wide-spectrum signals permit more accurate localization of the signaler (Konishi, 1973, 1977) and, thus, could counteract the "cocktail-party effect" created by closely spaced individuals on small territories (White and White, 1970; Wiley, 1976a). Marsh-nesting or colonial Agelaius with relatively small territories have wide-spectrum sounds as major components of their songs (see Orians and Christman, 1968; Post, 1980). This reasoning suggests a third prediction: the Jamaican blackbird should differ from marsh-nesting Agelaius in having frequency-modulated tonal songs.

In order to establish the basis for comparing the socioecology of Nesopsar and Agelaius, we first review the phylogenetic relationships of these genera. Also at the outset, we raise possible alternate explanations for the three predictions. Then we document the feeding ecology of Nesopsar, to establish their reliance on evenly dispersed and sparsely stocked feeding stations, and proceed to examine the social system and communication.

RELATIONSHIPS OF *AGELAIUS* AND *NESOPSAR*

Most species of *Agelaius* nest predominantly in emergent vegetation in marshes (Allen, 1914; Nero, 1956; Orians, 1961a,b, 1973; Wiley and Wiley, 1980), although most also occasionally build nests in trees adjoining marshes. During the breeding season, these birds usually feed on or near the ground or the surface of the water amid emergent vegetation. Most of the food for nestlings is collected outside the male's territory.

Marsh-nesting *Agelaius* have marked sexual dimorphism in size (Table I), and territorial males are often polygynous (Orians, 1972; Wiley and Wiley, 1980). In red-winged blackbirds *A phoeniceus*, 2–8 females on average nest in each male's territory, the ratio varying among populations (Orians, 1972). In yellow-hooded blackbirds *A. icterocephalus* and in some populations of *A. phoeniceus*, some males help to feed nestlings or fledglings at one or two of the nests within their territories, but even when the male does feed nestlings, his contributions usually start in the second half of the nestling period and never match the females' (Patterson, 1976; Wiley and Wiley, 1980).

Two closely related species of *Agelaius*, *xanthomus* and *humeralis*, of Puerto Rico and Cuba, respectively, nest in loose colonies in groves of trees where each pair defends only the immediate vicinity of its nest (Post and Wiley, 1976, 1977; Post, 1980). These species are sexually monomorphic in plumage and nearly so in size. In *xanthomus*, males and females form monogamous pair bonds that last at least through the breeding season, and both parents feed the young. Food for the nestlings is collected as much as several kilometers from the nesting colony. This species, thus, parallels the African weaver bird *Quelea quelea*, in which monogamy and dual parental care have evolved in conjunction with foraging at a great distance from the nest (Crook, 1962, 1964). The same pattern recurs, in less developed form, in the tricolored blackbird *Agelaius tricolor*, a close relative of the red-winged blackbird, in California. Although not always monogamous, male tricolored blackbirds average fewer mates than do male red-winged blackbirds, and they seem to participate more regularly in feeding the nestlings. More than red-wings, tricolors regularly forage for insects in grasslands at large distances (up to 5 km) from nesting colonies (Orians, 1961a,b; Payne, 1969). Presumably the participation of both parents becomes necessary for this relatively time-consuming task.

Nesopsar, a monotypic genus restricted to wet montane and lower montane forest in Jamaica, feeds primarily on insects in epiphytic bromeliads (Bond, 1950, 1963; Lack, 1976; Cruz, 1978). It is almost sexually monomorphic in size (Table I) and plumage: both sexes are entirely black. No other bird in Jamaica systematically searches bromeliads for insects,

although several other species visit bromeliads on occasion (Cruz, 1978). The West Indies lack representatives of the mainland tropical families Dendrocolaptidae and Furnariidae, both of which include species that specialize in searching for food in epiphytes (Slud, 1960, 1964; Orians, 1969a; Feduccia, 1970). Also missing from Jamaica is the specialized trembler *Cinclocerthia ruficauda* (Mimidae), which hunts for food in epiphytes on islands in the Lesser Antilles (Zusi, 1969).

Both Bond (1950) and Lack (1976) consider *Nesopsar* closely related phylogenetically to *Agelaius*, but nevertheless distinctive. In Lack's comparisons of *Nesopsar* with *Agelaius* and typical orioles in the genus *Icterus*, a number of points of comparison relate to the socioecological adaptations that this paper considers and thus might not indicate phylogenetic relationships. The morphology of *Nesopsar* offers few definite clues of phylogenetic relationships, owing to the species' entirely black plumage. The beak is similar in shape to that of *Agelaius* but longer (Cruz, 1978), a difference that probably relates to its feeding behavior, discussed below. The external nares also resemble those of *Agelaius* (Ridgway, 1902). One South American species of *Agelaius* (*xanthophthalmus*) is sexually monomorphic with entirely black plumage. Of greater significance, the subspecies of the red-winged blackbird in Cuba, the probable origin of ancestral *Nesopsar*, is much less dimorphic in plumage than mainland races. The females of this subspecies have entirely black plumage; they resemble males but lack the red wing patches.

More than morphology, the structure of the nest points to a close relationship of *Nesopsar* with *Agelaius*. The nest is a bulky cup, entirely unlike the neatly woven, slung nests of *Icterus*. The vocalizations of *Nesopsar* are also almost completely typical of *Agelaius*, as described below, and unlike those of *Icterus* or other forest blackbirds. Since most of the other similarities between *Agelaius* and *Nesopsar* might represent preadaptations for the specialized foraging of *Nesopsar*, the resemblance of songs and nests in the two genera provides the strongest evidence for a close phylogenetic relationship.

ALTERNATE EXPLANATIONS

Before *Nesopsar* can provide an interpretable test of socioecological hypotheses, it is necessary to consider whether or not other features of its ecology, in addition to the distribution of food, might provide alternate explanations for the divergence of its social behavior from that of related species. In particular, biological communities of islands are known to differ systematically from similar mainland areas. In the first place, the reduced

species diversity on islands would mean fewer competitors. However, the arguments for the evolution of exclusive territoriality and monogamy should follow equally from intraspecific competition as well as interspecific. Either should favor the evolution of an optimal strategy for feeding nestlings.

Another common feature of oceanic islands, and in particular Jamaica, is an absence of large predators. Jamica is unusual among the islands of the Greater Antilles, in having no major predator on adult birds. None of the four resident raptors (two owls, the red-tailed hawk *Buteo jamaicensis*, and the kestrel *Falco sparverius*) normally preys on birds in forests. The kestrel regularly takes small birds but does not inhabit continuous forests (Cruz, 1976). No species of the genus *Accipiter*, a specialist on birds, occurs in Jamaica. Predators on nests are also probably scarcer than in mainland habitats. Snakes are extremely rare in Jamaica. Introduced mammals, particularly the mongoose and the rat, at least the former of which now occurs in native montane forests, probably represent the greatest threat to birds' nests. High risks of nest predation could favor single parental care, in order to draw the least possible attention to a nest. Conversely, low risks of nest predation could permit dual parental care, and thus favor monogamy.

The absence of predators on adult birds is likely to have a major effect on the evolution of long-distance communicatory signals. It is generally accepted that increased exposure to predators constitutes an important risk for individuals engaged in conspicuous communication. The absence of serious predators on adult birds will require consideration when we examine long-range communication.

HABITAT

Jamaican blackbirds breed only in relatively undisturbed forests in areas of high rainfall (Lack, 1976; Cruz, 1978). Our study areas lay within 1 km of Hardwar Gap, St. Andrew Parish, in native montane forests at elevations of 1200–1300 m along the crest of the deeply dissected Port Royal Mountains. Rainfall here exceeds 2000 mm annually; the mountains are often shrouded in mist. In Jamaica, a dry season extends from January through March; May and October are, on average, the rainiest months (Asprey and Robbins, 1953). Wiley's field work extended from May 17 through June 24, 1977, a total of 33 days in the field, in Hollywell National Park, northwest of Hardwar Gap. Cruz studied breeding Jamaican blackbirds at intervals from early April to late August for three years, 1970–1972, in the area east of Hardwar Gap. Native montane forest near Hardwar Gap is easily divided into three categories: ridge, slope, and mist forest (corresponding roughly with "elfin forest," "lower montane rain

forest," and "mist forest" in Asprey and Robbins, 1953). The blackbirds entered ridge forest infrequently and then only briefly. The blackbirds' territories included most of the areas of slope and mist forest. Owing to the blackbirds' specialization on bromeliads, and to a lesser extent tree ferns, we could estimate the distribution of feeding sites in their habitats by sampling vegetation.

Ridge forest occupied narrow, exposed ridges and peaks. The canopy, composed of tiny leaves, seldom exceeded 9 m in height. Most tree trunks were less than 15 cm in diameter. Bromeliads grew only in the lower canopy and on tree trunks, up to 6 m above ground. Most were the same common species *Vriesea sintenisii* that grows in slope forest, but they were less abundant and smaller on average. Epiphytic moss and ferns were also less abundant in ridge forest in comparison to the more protected slope forests. The infrequent use of ridge forest by the blackbirds seemed related to the paucity of epiphytic vegetation.

Below the ridge lines, the slopes of the mountains fell 50–80 m with progressively increasing gradients to the creek beds. These slopes supported forests characterized by a continuous canopy, rather open understory, and numerous ferns on the gound. About 20 species of trees occurred regularly in the canopy of these forests, including *Cyrilla racemiflora*, *Alchornea latifolia*, *Haenianthus incrassatus*, and the cedar *Podocarpus urbanii* (nomenclature follows Adams, 1972). Epiphytic vegetation grew abundantly in the canopy. These forests seem to combine features of the "wet slope" and "gully" forests of Grubb and Tanner (1976). In particular, the liana *Marcgravia brownei*, characteristic of "gully" forests, occurs commonly in slope forests in our study areas.

In order to characterize slope forest, we used the point-centered quarter method (see Mueller-Dombois and Ellenberg, 1974) to sample vegetation of four short transects across sheltered slopes (n = 30 points at intervals of 20 m) northwest of Hardwar Gap. The transects were 200–500 m apart, two each in territories LB and UB (see below). The samples only included trees that formed part of the forest canopy, by the criterion that at least part of each tree's crown could have no other tree directly overhead. With the exception of tree ferns, whose crowns usually just reached the lower edge of the forest canopy, most trees with foliage in the canopy satisfied this criterion. Stratification of trees within the canopy was not a regular feature of this habitat. For each tree, we measured its distance to the arbitrarily positioned sampling point, classified it by diameter (dbh), estimated by eye the height above ground of the lowest and highest foliage in its crown, and counted the number of bromeliads in its canopy. At two-thirds of the sampling points, the terrain sloped between 30° and 60°; at a third, the slope exceeded 60°. Fifty-three percent of the 120 canopy trees were less than 30 cm in diameter. The lower limit of the canopy at the four locations averaged

7.8–10.4 m; the upper limit averaged 12.6–15.4 m. The most common tree, *Podocarpus*, comprised only 7% of the total.

The average number of bromeliads in the crown of a canopy tree ranged from 6.2 to 8.1 (overall mean, 6.72; S.D., 4.18). The mean distance of trees from the sampling point ranged from 4.4 to 5.3 m in the four samples. The overall mean distance, 4.81 m, corresponds to an average of 431 canopy trees per ha. There were, thus, about 2900 bromeliads per ha in these forests. The low variation in the number of bromeliads per tree both within and between the four transects (Table II) confirms that this major feeding site for Jamaican blackbirds has a comparatively even and fine-grained distribution throughout the habitat. In slope forest, by far the most abundant bromeliad was *Vriesea sintenisii*, which comprised 80–90% of all bromeliads in the forest canopy.

On one of the four transects, we also counted the number of tree ferns at least 2 m tall and the number of bromeliads on the ground and other locations below the canopy within an 8-m radius of each sample point (0.02 ha). The number of tree ferns averaged 5.7 (n = 10, S.D. = 4.6) and the number of bromeliads below the canopy averaged 1.5 (S.D. = 1.7); these figures correspond to 285 tree ferns and 75 bromeliads below the canopy per ha.

Mist forest in this area occurred only on nearly flat terrain well-sheltered from the wind. The usual site was a small spur ridge or saddle deep in a large basin surrounded by high ridges. Mist forest had a staggering profusion of epiphytic growth from the bases of the tree trunks to the top of the canopy. Tree trunks often leaned at low angles in irregular directions. The soil consisted of deep mor (Grubb and Tanner, 1976), often covered with large patches of filmy ferns. Although mist forest was much more restricted in distribution than slope forest, most blackbird territories included a substantial patch of this kind of forest.

In view of the profusion of epiphytes in these forests that might serve as feeding sites for blackbirds, we undertook point-centered quarter

TABLE II.   Hierarchical ANOVA for Number of Bromeliads in Trees at Six Points in Each of Four Transects in Slope Forest[a]

Source of variation	df	SS	MS	F	P
Among transects	3	161.6	53.86	1.417	.25
Among points within transects	20	760.2	38.01	0.751	.75
Within points	72	3641.5	50.58		
Total	95	4563.3			

[a] Analysis based on six points selected at random in each transect; four trees recorded at each point.

analyses along two transects in different patches of mist forest (a total of 16 points). At all but two points the terrain sloped less than 30°. The canopy trees in mist forest were somewhat smaller in diameter and height than in slope forest. Trees less than 30 cm in diameter constituted 62.5% of the total sample. On the two transects, the lower limit of the foliage of canopy trees averaged 8.6 and 9.6 m; the upper limit averaged 11.5 and 13.7 m. Canopy trees lay at mean distances of 3.3 and 3.7 m from the sample points. The overall mean corresponds to a density of 813 trees per ha. Mist forest included a lower diversity of trees than slope forest. Of the 64 sampled, *Podocarpus* comprised 14%, *Haenianthus* 9% and *Cyrilla* 8%.

The number of bromeliads per canopy tree varied much more than in slope forest both within transects and between transects; the averages (and S.D.) for the two transects were 3.6 (7.2) and 9.7 (10.9). The overall mean of 6.6 bromeliads per tree does not differ greatly from that in slope forest. In mist forest, in effect, many smaller trees reached the canopy and often had few or no bromeliads. The largest trees, on the other hand, had epiphyte loads that exceeded any observed in slope forest.

A characteristic of mist forest was the abundance of bromeliads below the canopy, even on the ground. Counts of bromeliads below the canopy in the two transects yielded estimates of 800 and 2600 per ha. Almost all of these bromeliads were the giant species *Guzmania fawcettii*, which occurred only rarely in slope forest.

FORAGING ECOLOGY

Epiphytic bromeliads constitute the predominant feeding sites for Jamaican blackbirds. From records of the foraging sites of this species in a variety of forest habitats throughout the year, Lack (1976) and Cruz (1978) report that bromeliads make up 46% and 58%, respectively, of all feeding sites. Ferns, including tree ferns, constitute 18% and 14%, respectively, of feeding sites. Cruz reports the following foods taken by blackbirds from bromeliads: snails, spiders, insects (including Orthoptera, Coleoptera, and larval Lepidoptera) and small frogs. Additional items found in the bases of bromeliads included millipedes, sowbugs, and insects (Tettigoniidae, Acrididae, Blattidae, Formicidae, Hemiptera, and larval Coleoptera).

In the area northwest of Hardwar Gap from which our vegetation samples come, we documented the feeding behavior of Jamaican blackbirds during the nesting season. The single species *Vriesea sintenisii*, which dominated the bromeliad flora in this area, provided most of the blackbirds' feeding stations. Altogether, we recorded 178 feeding sites for Jamaican blackbirds in this area. Usually, we could observe a blackbird for no more

than a few minutes before losing it, since the rugged terrain made it impossible to move quickly from one place to another within a blackbird's territory. The blackbirds did little foraging in the immediate vicinities of their nests, so that less than 20% of our observations on foraging pertain to birds near their nests. These data show the same trends as those obtained farther from nests or by birds not actively nesting. Foraging birds were just as easily lost from view in observations near nests as farther away. Foraging birds, virtually always in the canopy of the forest, never showed signs of reactions to us.

Blackbirds foraged at heights of 3–12 m above ground, although on one occasion a blackbird fed a fledgling, which had tumbled into shrubs near the ground, by collecting items nearby at heights of 0.5–3 m. Blackbirds usually searched for food in the lower canopy of slope forest, 6–10 m above ground.

Feeding stations in the area northwest of Hardwar Gap included bromeliads in the forest canopy (77%), other epiphytic vegetation in the canopy (usually moss on limbs, but also clumps of ferns, lichens, and dead bark; altogether 13.5%), and tree ferns (7.9%). In addition, a blackbird once probed briefly in the leaf litter on the ground, and twice a blackbird plucked an *Alchornea* berry and ate it. Note that bromeliads were searched about 10 times more frequently than tree ferns, a ratio that corresponds closely to the densities of canopy bromeliads and tree ferns in slope forest. In 67 instances, we identified the bromeliad that a blackbird searched: *Vriesea sintenisii* comprised 85% of these identifications. Only once was a blackbird observed investigating a *Guzmania fawcettii*. Thus, the one species of bromeliad *V. sintenisii* in this study area accounted for 65% of the feeding sites of Jamaican blackbirds.

When foraging on bromeliads, the blackbirds investigated particularly the hanging dead leaves around the base of the plant. An abundance of dead leaves is characteristic of *V. sintenisii*. In contrast, *G. fawcettii*, the abundant bromeliad below the canopy in mist forest, almost never retained dead leaves. A foraging Jamaican blackbird used techniques similar to those of related blackbirds searching for food in emergent vegetation in marshes. They ceaselessly hopped around the base of a bromeliad probing at the dead leaves. Blackbirds seemed to use nearby twigs for perches when available. Otherwise, the blackbirds often clung in a vertical sideways orientation from the hanging leaves of the bromeliad. Form this position, with the feet one above the other and the body about horizontal, the bird would reach upward and downward diagonally to probe the base of the plant. Birds much less frequently adopted a vertical upward position, with the feet side by side on vertical supports and the body more or less vertical (11 instances). Very rarely, they adopted a vertical downward orientation (3 instances) or clung upside down from a leaf (once). In these awkward posi-

tions, the bird usually cocked its tail ventrally, but in only one instance did a bird support itself with its tail, in the manner of a woodpecker or dendrocolaptid.

In probing a bromeliad, a bird pushed its head underneath the dead leaves at the base of the plant repeatedly. Often a bird pulled a dead leaf out of the base of the plant and threw it aside. On one occasion a bird repeatedly used the specialized gaping movement of many icterids (Beecher, 1951) to spread the longitudinally curled leaves of a *Tillandsia*.

Actual captures of prey were observed infrequently. On five occasions, a bird quickly snatched a small insect or other arthropod that probably had been flushed from the base of a bromeliad by the bird's rustling. Such movements were too inconspicuous to allow reliable recording of instances. On 11 occasions, a bird suddenly fluttered downward, as far as 8 m and even to the ground, apparently pursuing some item that had fallen from a bromeliad. Once a bird captured a large item, a 3-cm brown insect pulled from the very base of the dead leaves of a bromeliad. These observations of foraging blackbirds totaled about 60 min, although the birds were not in clear view for much of that time. Birds feeding nestlings usually bring large items ($\geq$ 3 cm) at rates of 1-3/hr (see below).

After finishing its investigation of one bromeliad, a blackbird often hopped along the branches of the tree toward the next one. Along the way it pecked and gaped in epiphytic moss and ferns. When ascending steep branches, a bird switched from side to side with each hop; none ever used its tail for support.

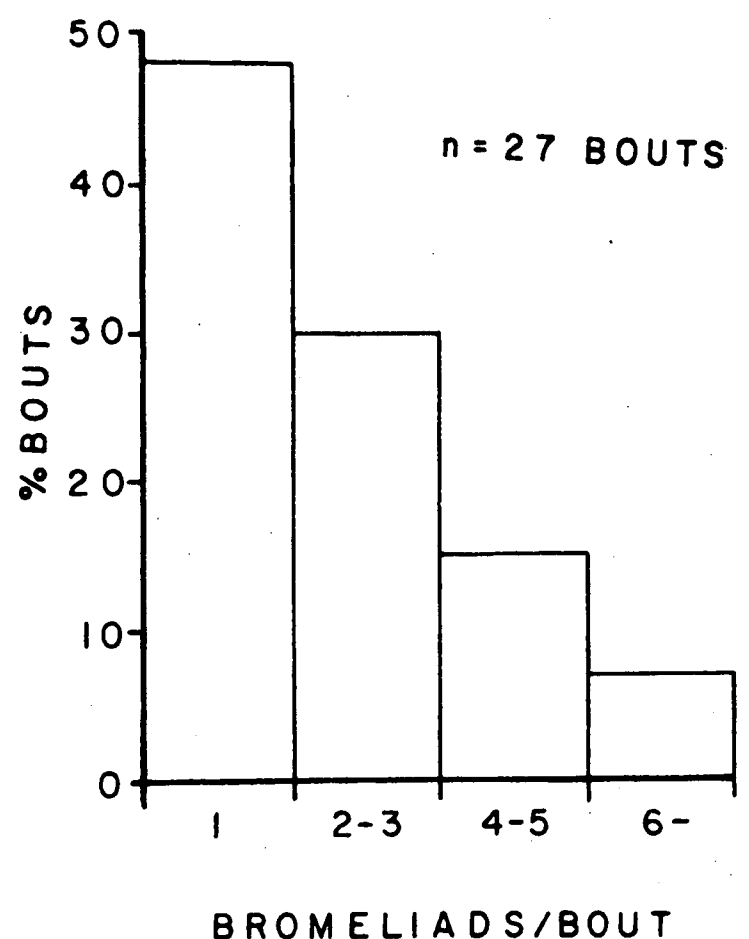While foraging on tree ferns, blackbirds used many of the same tech-

FIG. 1. Number of bromeliads visited during bouts of foraging by Jamaican blackbirds. A bout of foraging (see text) includes no flights greater than 4 m.
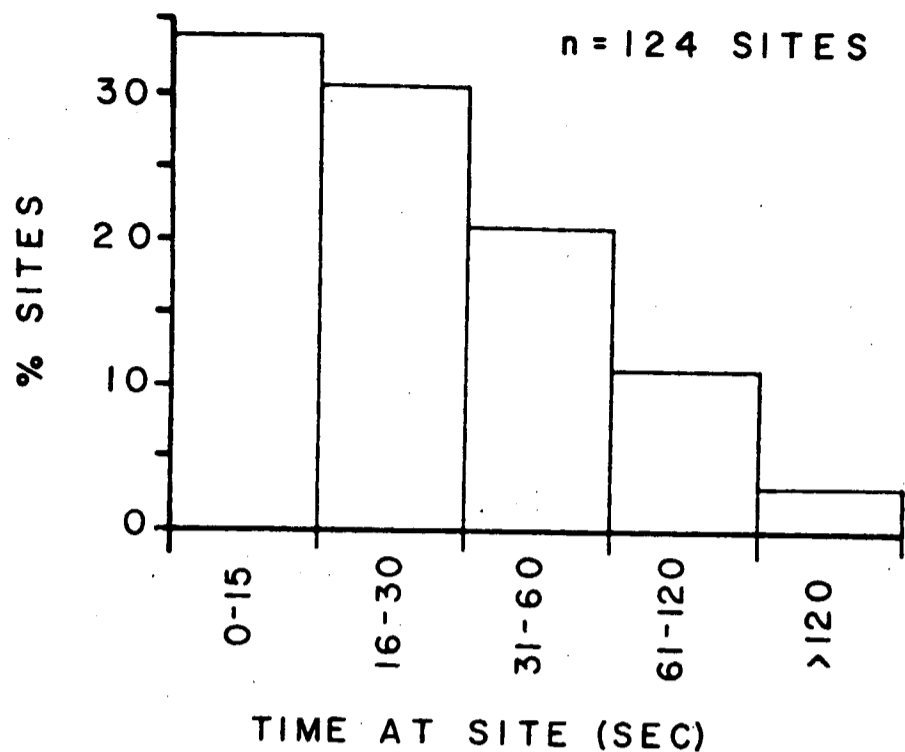
FIG. 2. Time spent at feeding sites by Jamaican blackbirds. A feeding site is one bromeliad, tree fern, or patch of epiphytic moss and ferns.

niques that they employed on bromeliads: ceaseless hopping and probing on the hanging dead fronds beneath the crown; and clinging in the vertical side-ways orientation from the rachises of hanging fronds. Once a blackbird probed in the apex of the crown of a tree from above.

Foraging blackbirds tended to search extensively rather than intensively. They rarely stayed in any small area for long. Usually a bird would fly out of sight, more than 6 or 8 m through the forest canopy, after no more than 2 min. Generally, we could keep track of a bird if it moved less than 4 m between successive feeding stations, a flight that would usually take the bird to a new tree. If we define the initiation and termination of a bout of foraging as any flight greater than 4 m, we have information on a total of 27 complete bouts. In 78% of these bouts the blackbird visited three or fewer bromeliads (Fig. 1). Most moves from one bromeliad to the next within a bout were less than a meter in length (62%, $n = 80$ observed moves between feeding stations separated by 4 m or less). In addition, blackbirds were unlikely to spend much time at any one feeding site. Of 124 timed visits to individual feeding sites, 34% lasted less than 15 sec and only 14.5% lasted more than 1 min (Fig. 2). Thus, a foraging blackbird tended to visit one or a few nearby feeding sites in rapid succession and then to move at least 4 m to a new location. In those flights greater than 4 m, a bird invariably passed many closer bromeliads before stopping at one to initiate a new bout of searching. Over periods of 30–60 min, a blackbird would often move 20–100 m while sampling a scattered series of feeding stations.

In conclusion, our studies of the vegetation and the blackbird's foraging behavior indicate that feeding stations are relatively evenly scattered throughout the habitat, food (particularly large items) is sparsely distributed across these stations, and the blackbirds search for food extensively rather than intensively.

TERRITORIALITY AND MONOGAMY

Confirming the prediction based on the spatial distribution of their food, Jamaican blackbirds occupied large, exclusive territories (Fig. 3). The maximum diameter of 11 territories averaged 281 m (S.D. = 64.9; range = 160–370 m). Our technique for determining their movements about their territories relied on their vocal behavior. As mentioned, the blackbirds proved almost impossible to keep in sight for more than a few minutes at a time in the forest. However, birds of both sexes rarely remained silent for long. Calls and songs were uttered at intervals of a minute or less during foraging and were particularly likely to accompany long flights (10 m or more). Although the blackbird's vocalizations carried hardly more than 50 m through the forest, from high vantage points overlooking the forest we could routinely follow the general locations of vocalizing birds as far as 200 m away. Thus, we could often track the general location of a blackbird for long periods, even when we could obtain ony occasional glimpses of it. Observations of one pair of color-marked birds east of Hardwar Gap in 1972 confirmed the adequacy of our procedures for keeping track of these ,territorial blackbirds.

Neighboring territories abutted each other with little overlap (Fig. 4). We never observed a bird fly from one territory into another, nor had any indication that more than two birds were present in any one territory. Nonterritorial intruders must occasionally visit established territories. Although silent intruders would not be easy to detect, our failure to notice any indications of their presence suggests that they were not frequent during the breeding season. After the breeding season, more wandering might occur. In late November, on one occasion, a squabble between two Jamaican blackbirds attracted four others to the spot.
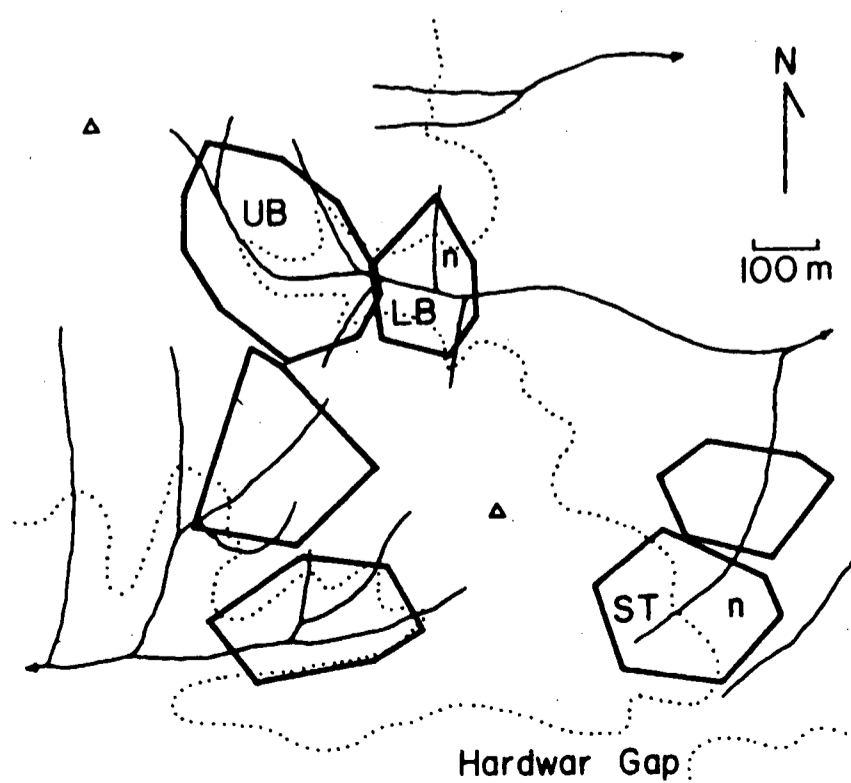

FIG. 3. Territories of six pairs of Jamaican blackbirds. Heavy lines enclose the locations in which each pair was observed. The intervening areas were not occupied by Jamaican blackbirds. Dotted line, 1220-m (4000-ft) contour. Solid lines with arrows, stream courses. Triangles, peaks. Three territories studied intensively are labeled ST, LB, and UB. n, location of nest.
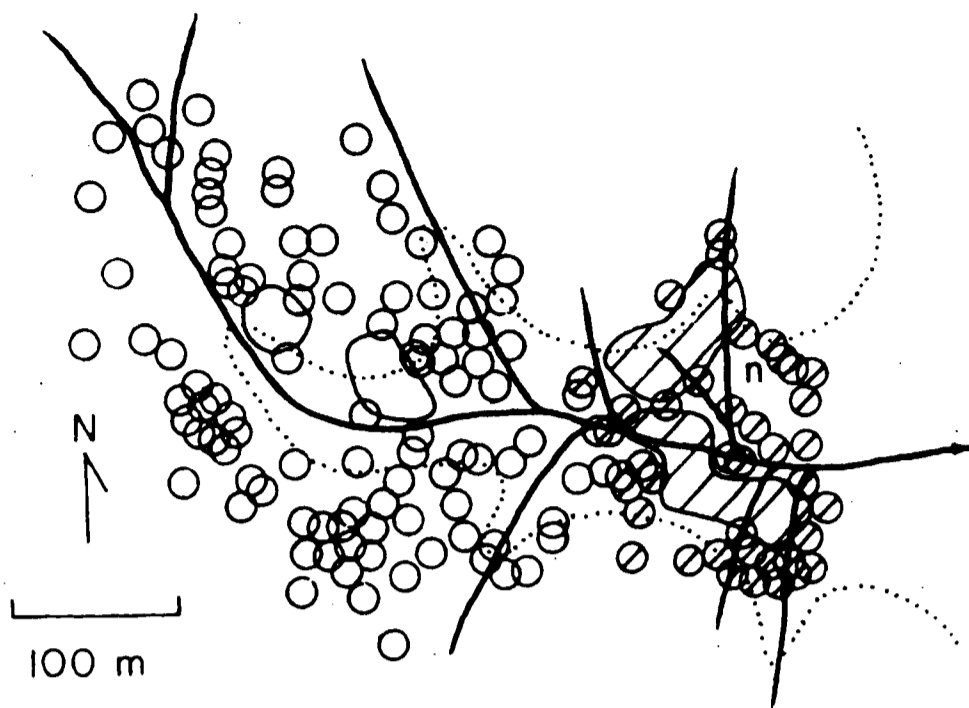
FIG. 4. Locations of resident Jamaican blackbirds in territories UB and LB. Open circles, locations of the UB birds. Open areas enclosed by a solid line indicate areas of intensive use by members of this pair. Circles with diagonal lines, locations of LB birds. Hatched areas enclosed by solid lines indicate areas of intensive use by this pair. Other conventions as in Fig. 3. Note the minimal overlap between the movements of resident birds on these two territories.

No close-range agonistic interactions were observed during our study. There were no instances of one blackbird chasing another toward its territorial boundary. Territorial neighbors never interacted at close range. On occasion in 1977, we heard a neighbor sing in immediate response to a blackbird near its territorial boundary, but on only two occasions did neighbors, in both cases about 100 m apart, sing in response to each other two or three times in succession. Thus Jamaican blackbirds avoid each other's areas and, consequently, occupy virtually exclusive territories.

Jamaican blackbirds also satisfied the expectation that they would establish monogamous pair bonds. All 11 territories investigated were occupied by a pair in each case. These pairs included five east of Hardwar Gap (one in 1970, two each in 1971 and 1972) and six northwest of Hardwar Gap in 1977 (Fig. 3). One pair in 1972 were individually marked with colored bands. Otherwise, we could keep track of the individuals in a territory by ear, as explained above. The two individuals in a territory maintained contact with each other by means of vocalizations. In addition to the regular use of calls and songs while foraging and flying through the forest, mated individuals regularly sang in response to each other (see below).

Except near a nest or young, the male and female on a territory were rarely close together. The UB pair in 1977, which had no nest during the study, were found within 20 m of each other on only eight occasions and only once for more than 10 min. Frequently this pair were separated by 200 m or more. Regularly, one member of the pair was located in the western half of the territory while the other member was in the center or northeastern portion. There were indications that the two birds tended to focus their activities consistently in these portions of the territory. At least during the first hour or two of activity in the morning, the bird that performed the special dawn patrolling (see below), presumably the male, remained in the center and northeastern portion of the territory except for

brief excursions to the west. The other bird, the female, roosted in the western portion, and tended to remain there except for brief excursions into the center. The subdivision of the territory between the two birds was not absolute, however, as birds were observed to move back and forth on occasion throughout the territory, and the pair was found together in locations both in the eastern and western portions.

Nesting pairs focused their activities around their nests. During feeding trips, the male and female often approached each other near the nest. Even during incubation, performed by the female, the male spent long periods perched quietly within 10 m of the nest. After fledglings left the nest, both parents tended to remain close to their young. Aside from association near the nest or young, however, these pairs resembled the UB pair. They rarely approached each other closely, and then only briefly. Thus, aside from activities near the nest, the pairs used vocalizations to keep track of each other's locations and avoided close spatial association.

PARENTAL CARE

Patterns of parental care in the Jamaican blackbird resembled those of many other arboreal insectivores that practice monogamy. In particular, males contributed substantially to feeding the nestlings. Our information about parental care comes from extensive observations at four nests, one each in 1971 and 1972 and two in 1977.

Seven nests, well-concealed in the lower canopy of slope or mist forest 6–11 (mean, 8.2 m) above ground, had similar locations: small trees (about 20 cm dbh) that grew on steep slopes (about 45°) and arched so that the main trunk became nearly horizontal in the lower canopy. The nests were placed against the main trunk and partially beneath it in a location where the trunk, about 10–15 cm in diameter, slanted toward horizontal. Two nests were supported on the sides by slender twigs branching from the main trunk or the slender branches of a liana; in both cases, the bottom of the nest cup was exposed below. Five nests were completely roofed by the hanging leaves of a clump of bromeliads that grew on the main trunk just above the nest. The nest materials consisted primarily of epiphytic orchids and slender dark rootlets of lianas. The structure of these nests, if not their material, resembled those of *Agelaius* species. Our dates for nest construction ranged from May 12 to June 2. The female constructed the nest alone.

In five nests, the clutch was two eggs. Incubation began after the second egg was laid, so that both eggs hatched at about the same time. The

incubation period lasted 14 days in one nest, 13–15 days in another. At nest LB two young of similar size eventually fledged within 3 hr of each other.

During the incubation period, mates had distinct behavior. As in all other Icteridae, only the female incubated. At nest ST in 1977, the female's behavior was remarkably consistent. Her periods on the nest averaged 26.5 min (S.D. = 8.2, n = 22, range = 9–41), and periods off the nest averaged 12.6 min (S.D. = 5.3, n = 26, range = 1.5–21). During 13.3 hr of observation during 1970–1972, incubating females averaged 28.5 min on their nests (7–43 min) and 16.0 min off (3–23). We detected no consistent differences in the durations of the females' periods on or off the nest during watches at different times of day. When the female left the nest she usually flew directly away at least 50 m and spent most of her time foraging 50–200 m from the nest. On returning, she often flew directly to the nest, but sometimes perched 10 m away to preen for 30 sec or a minute before entering the nest.

During the two weeks that the female incubated, her mate spent long periods perched quietly 6–25 m from the nest. Often, he preened or rested in a relaxed posture while perched in the lower portions of the canopy at about the same level as the nest. At times, particularly when other species of birds were active near the nest, he became more alert. On 20 occasions during the two weeks of incubation at nest ST in 1977, the male attacked other species of birds within 10 m of the nest (30 hr of observation). On some of these occasions he repeatedly chased the other species through the lower canopy near the nest. In 1970–1972, similar behavior occurred 41 times in 13.3 hr of observation at nests during incubation. The most frequent targets were orangequits *Euneornis campestris*, white-eyed thrushes *Turdus jamaicensis*, white-chinned thrushes *Turdus aurantius*, rufous-throated solitaires *Myadestes genibarbus*, and bananaquits *Coereba flaveola*, all common species in montane forest. During the nestling period, aggression against other species occurred less frequently (seven instances in 31.5 hr of observation at two nests in 1977).

Once the young hatched, both parents began feeding the nestlings. Since the birds spent only brief periods near the nest during this phase, they were often hard to follow individually. At one nest in 1972, with color-marked birds, the male contributed 46% of 148 feedings throughout the nestling period. In addition, during the first day on which parents fed the nestlings at nest ST in 1977, we could keep track of the two parents. On this morning, the two were simultaneously absent from the vicinity of the nest in the same direction only once. One bird, the presumed female, spent more than 2 min on the nest brooding the young on all but one of her visits; the presumed male never spent more than 2 min at the nest (mean for female 10.7 min, S.D. = 6.3, n = 14, range 0.5–25). Of 26 visits to the nest during

this morning, no bird ever arrived without food for the nestlings. The female visited the nest on 16 occasions, the male on 10 (38%).

Although during this morning the male brought food less often than the female, he tended to bring larger items than the female did. While the female never brought an item judged longer than 1 cm, the male on four of nine instances brought items estimated at 1.5 or 2 cm in length. After the first day of feeding at the ST nest, neither parent remained at the nest for more than 2 min except rarely. Both parents normally arrived and departed quickly. The same pattern held at nest LD in 1977 throughout observations there. Whenever we could identify the female by periods of brooding and could keep track of the two parents, the female consistently made somewhat more trips to the nest than the male (26 trips by females, 16 by males). In summary, the male began feeding the young on the first day after they hatched, at the same time the female began. He made fewer trips than the female but, possibly, tended to bring larger items. The parents thus shared approximately equally the task of feeding their young in the nest.

The overall rate of feeding by both parents ranged from 3–25/hr. The average rate at nest ST was 9.6 visits/hr (12 hr of observation on 6 days) and at nest LB 7.2 visits/hr (12 hr of observation on 4 days). In 26 hr of observation at nests in 1971–72, feeding rates averaged 8.3/hr. Rates were highest early in the morning and late in the afternoon. Our data revealed no consistent tendency for feeding rates to increase during the nestling period.

Food brought to the nest included a great variety of insects, including larvae. On rare occasions, the parents brought spiders, centipedes, or small tree frogs. During observations in 1970–1972, 215 items brought to nests included 37% Orthoptera, 24% Lepidoptera (larvae and adults), and 21% Coleoptera (adults). At nest ST in 1977, 40% of 110 items were identified as Orthoptera; at nest LB, 35% of 62 observed items were Orthoptera. More than half were dark brown, which suggests that they had been caught in the decaying material at the bases of bromeliads or in debris trapped by other epiphytes. In addition, a substantial number of items were dark brown insects that were too mangled to see clearly. Probably about 40% of the items brought to nest were dark brown orthopterans taken from the bases of bromeliads or other epiphytes. A few cockroaches, beetles, and centipedes probably also came from these locations. Paler orthoptera, many of them apparently Tettigoniidae, and infrequent cicadas, flies, small moths, stick insects, lepidopteran larvae, and spiders could have come from the foliage of bromeliads, tree ferns, or epiphytic ferns.

Birds brought more than one item at a time on only 5 of 172 trips at the two nests in 1977. Items ranged from less than 0.5 cm to more than 3 cm in length. At nest ST, items brought during the first half of the nestling period (June 9–13) were almost always 1 cm or less in length. During the
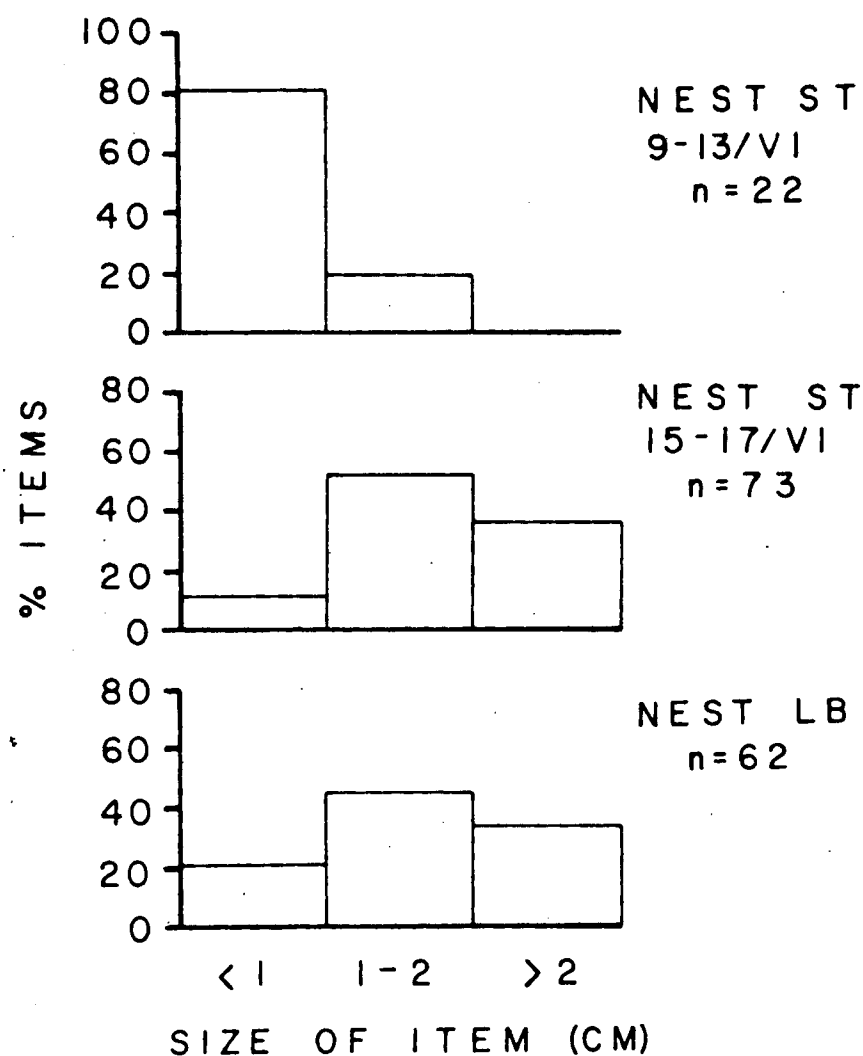
FIG. 5. Sizes of food items brought to the nest in territories ST and LB. Nest ST was observed both early (June 9–13) and late (June 15–17) in the nestling period; observations at nest LB were in the second half of the nestling period.

second half of the nestling period (June 15–17), the parents brought substantially more large items (Fig. 5): 88% of items were larger than 1 cm. At nest LB, observed predominantly during the second half of the nestling period, the items brought by the parents corresponded in size closely with those brought to nest ST during the second half of the nestling period (Fig. 5). Parents brought larger items but, in general, did not make more frequent trips as the nestlings grew older. The tendency to bring one item at a time suggests that suitable insects were sparse and scattered.

After fledging, young remained with their parents. In 1972, the color-marked pair produced fledglings around June 20. A month later, on July 29 and 30, both parents closely accompanied and still fed one juvenile; the other had disappeared. This family group persisted at least until August 29, two months after the young had fledged.

INTRASPECIFIC COMMUNICATION

The evolution of large exclusive territories and monogamous pair bonds requires concomitant adaptations in intraspecific communication. Animals with large territories standardly have in their repertoires a long-range advertising vocalization audible approximately the diameter of a territory and often delivered spontaneously, without evident releasing stimuli (Marler, 1969). For long-range communication in forests, birds standardly use tonal frequency-modulated songs. Many species in the interior of forests

avoid rapid repetitions of a given frequency in their songs, probably to reduce the effects of reverberation on the ability of receiving individuals to determine the structure of the song (Wiley and Richards, 1978; Richards and Wiley, 1980). In contrast, the songs of marsh-nesting species of *Agelaius* consist predominantly of wide-spectrum sound, buzzy or wheezy to our ears. Such sounds, optimal for ease of location by other individuals (Konishi, 1973, 1977), have advantages in crowded, noisy colonies (Wiley, 1976a). Ease of location is one mechanism by which receiving individuals can focus their attention on particular sounds in an environment with a low signal/noise ratio. Birds employing such wide-spectrum sounds include much of the information in the vocalization in the patterns of amplitude modulation, which do not propagate well in long-range communication (Wiley and Richards, 1978).

Contrary to expectation, the songs of Jamaican blackbirds resemble those of marsh-nesting *Agelaius* (Fig. 6). All of the birds in the study area northwest of Hardwar Gap sang three basic types of songs and a variant of each that lacked the last note. All of these songs consisted primarily of wide-spectrum notes with limited frequency modulation. The remaining notes in the songs were brief tonal sounds. All birds, including both sexes, used essentially identical songs. Slight variation in the durations of the noisy components in the songs occurred in successive performances of any one individual. No variants were specific to particular individuals.

As expected for songs with this structure (Wiley, 1976a), they were not easy to hear farther than 50 m away through the forest, much less than the typical dimensions of a territory. The dense vegetation within the forest not only obscured the structure of the songs by reverberations, it also attenuated the sound by scattering. The precipitous terrain helped to increase the range somewhat, because a song could often be heard on the opposite slope of the steep-sided valleys, sometimes 100–200 m away, even though they could hardly be heard 50 m away through the forest on the same slope. Nevertheless, the propagation of sound across valleys had little significance for territorial advertisement, since territories in the same valley tended to be arranged along the axis of the valley (Fig. 3). Although birds on islands often have simpler vocalizations than their mainland relatives (Marler, 1960), including some species in Jamaica, this consideration alone does not explain the Jamaican blackbirds' unexpected vocalizations. No other passerine bird in the Jamaican montane forests uses wide-spectrum sounds for long-range territorial advertisement; all use tonal, frequency-modulated songs.

Songs by Jamaican blackbirds were not usually accompanied by visual displays, like the wing spreading and feather ruffling in the song-spread displays of *Agelaius* (Nero, 1956, 1963; Orians and Christman, 1968; Post, 1980). This rarity of visual display, like the absence of colored patches in
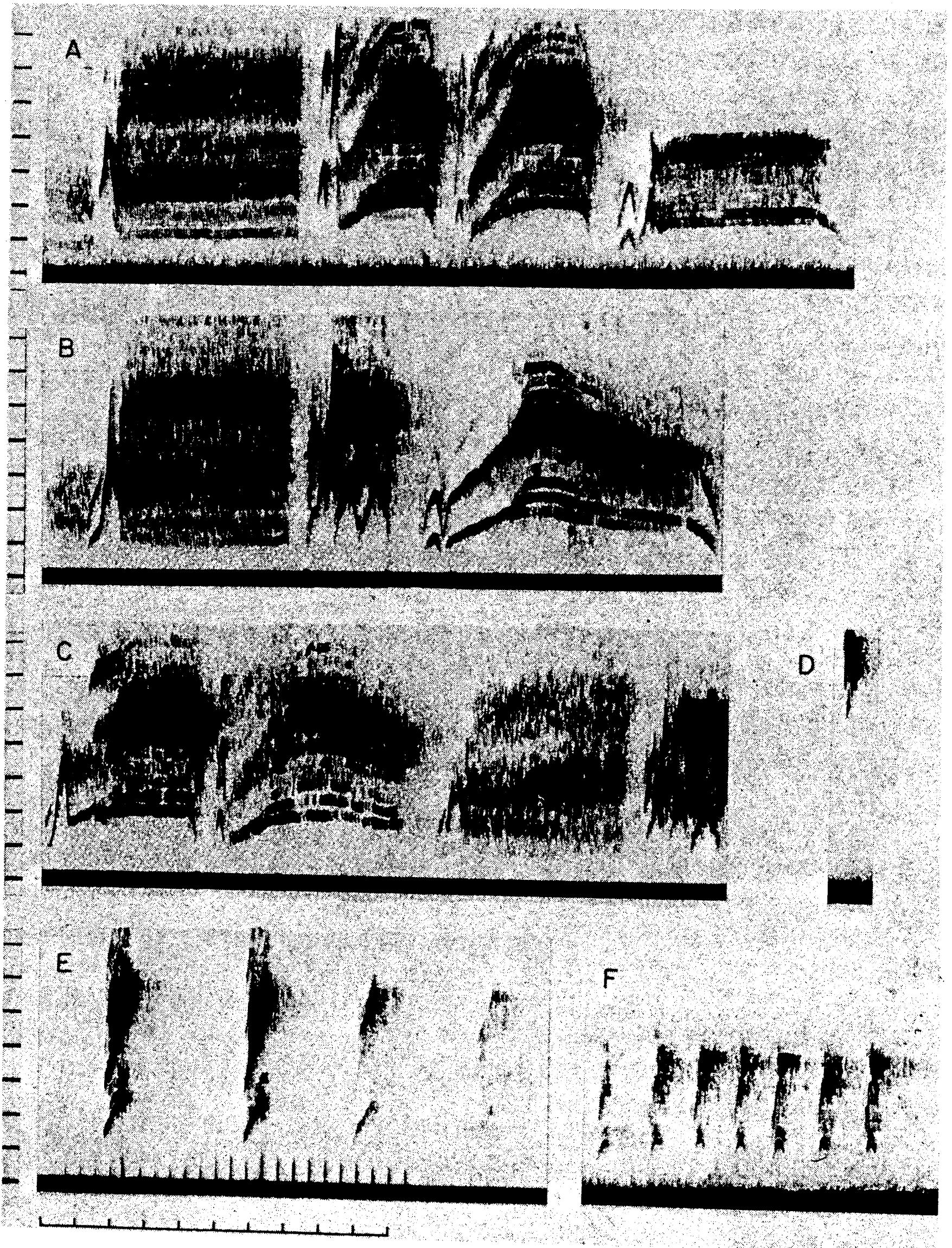
FIG. 6. Spectrograms of vocalizations by Jamaican blackbirds. A, B, and C, three song patterns. Pattern C often included an additional final segment identical to the final segment of B; patterns A and B sometimes lacked the final segment. Note that the first segments of A and B are identical, as are the second segment of B and the fourth of C. D, zeenk. E, a train of four dziks decreasing in amplitude and coinciding with an audible whir produced by the wings. F, a train of chets. Vertical scale, 0–7 kHz in 1-kHz intervals; horizontal scale, 1.0 sec in 0.1-sec intervals.

the plumage, is no doubt a result of the infrequent visual contact between birds, even partners, in this habitat. Usually, the only movements during singing consisted of elevating the beak to about 45° and pivoting the head irregularly from side to side. However, on four occasions in 1977, a bird performed a song-spread display near its nest before feeding the nestlings. On two of these occasions, the partner was 1–2 m away, but on two other occasions, with less intense display, the bird was alone near the nest. Similar displays were noted on six occasions in 1970 and 1972, when birds were 0.5–3 m from their partners. On all of these occasions, the singing bird extended its wings to varying degrees; in the extreme form, the wings were fully spread, raised about 30° above horizontal and moved slowly and irregularly during the song. In all performances, the head, body, and tail were horizontal and the tail fanned. In one extreme instance, the bird extended its wing more on the side away from its mate than on the nearer side. All of these features of the song-spread display resemble the homologous action in *Agelaius*.

Apparently in order to enhance territorial advertisement, Jamaican blackbirds have two kinds of behavior unusual for forest birds. One of these actions is presumably retained from ancestral marsh-nesting *Agelaius:* spectacular song flights high above the vegetation. Unlike almost all other forest birds, temperate or tropical, Jamaican blackbirds fly high above the forest canopy, deliver one of the usual songs, and then swoop back into the canopy below.

The following notes describe a typical instance: the bird ascended from the canopy on the slope of the valley and began to sing as it approached 40 m above the bottom of the valley; as it sang, it ascended slowly at a shallow angle with slow, exaggerated wing beats; the moment it finished its song, it closed its wings and fell head-first like a rock toward the canopy below, opening its wings for several stop-and-glide maneuvers as it approached the trees. The slow, exaggerated wing strokes are closely similar to those in song flights by marsh-nesting *Agelaius* (Orians and Christman, 1968; Nero, 1956, 1963). We know of only one other forest-dwelling passerine that sings in flight above the canopy, the North American ovenbird *Seiurus aurocapillus*, which sings in this way only after dark (Bent, 1953).

Jamaican blackbirds performed song flights, easily audible for several hundred meters up and down the valley, at irregular intervals throughout the day. On a few instances a bird performed twice within 15 min; but usually an hour or two separated these performances. Although these displays permitted long-range advertisement up and down valleys, they also served for communication between partners within territories, as discussed below.

Unlike most territorial passerines, Jamaican blackbirds did not sing repeatedly at dawn. Instead, the male of each pair performed remarkable

patrolling behavior. The male became active at about 6:05–6:15 a.m., some 15–30 min before his mate. In three intensively studied territories, the male roosted 50–100 m from the female. For about half an hour, the male repeatedly flew 3–20 m as he doubled back and forth on a beat more or less in the center of the territory (Fig. 7). During these flights he repeated a call, dzik (Fig. 6), which both sexes used regularly throughout the day. During the dawn patrolling, the male uttered a train of these calls on almost every flight. In addition, each flight was accompanied by a sharp whirring of wings, only rarely heard at other times. During whirring flight, the male flew with unusually rapid wing beats, while the flight seemed slower than normal. These flights recurred on average more than 2.5 times/min and reached maximum rates of 5/min. Thus for about 20–30 min each morning, the core of each territory was the site of almost continuous dzikking and whirring.

Eventually the female became active, uttered one or two dziks as she flew, and soon one or both birds would sing for the first time. Thereafter the male's peculiar patrolling behavior subsided, sometimes rather abruptly. Both partners used the dzik call throughout the day, usually one or two during flights through the forest or at intervals while foraging. The dawn patrolling, even with the repeated trains of dziks, could not be heard from one territory to the next through the forest. The male's beating back and forth through the core of the territory, however, would alert any intruding birds to the male's presence. This elaborate patrolling behavior is unlike anything we know in other passerine birds, including the marsh-nesting blackbirds.

Jamaican blackbirds thus advertise their territories by means of two forms of behavior peculiar for a forest bird: song flights high above the forest canopy probably permit the only reliable communication between territories; each territory is advertised further at dawn by means of a simple vocalization used in conjuction with flying back and forth through the forest.

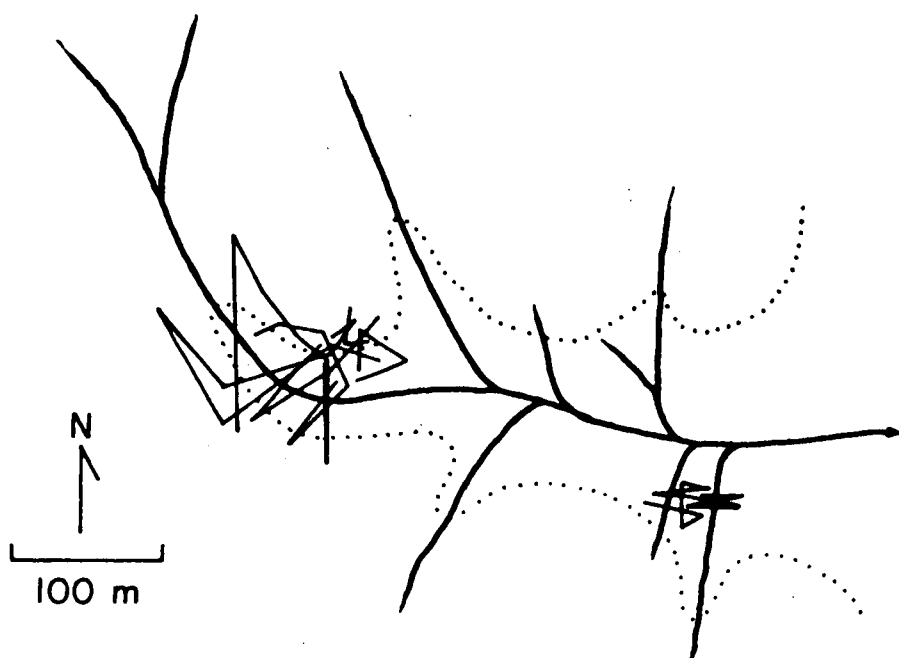Monogamous pair-bonds standardly require communication that serves

FIG. 7. Dawn activity of male Jamaican blackbirds in territories UB and LB. Solid zigzag lines, paths taken by male blackbirds during repeated calling and whirring flights in the first half hour of activity. Left-hand cluster of paths, male in territory UB (six mornings); right-hand cluster of paths, male in territory LB (two mornings). Each leg of the paths plotted here involved repeated short flights with trains of dzik calls and whirring wings. Male ST exhibited similar behavior in the region from 50 m north to 50 m southwest of its nest (see Fig. 3).

N

100 m

to maintain contact between the partners or to reestablish contact after absences. In common grackles *Quiscalus quiscula*, for instance, mated partners answer each other's songs; in addition, the male frequently follows the female, and the female regularly utters sharp calls when taking flight (Wiley, 1976a,b,c). In the polygynous marsh-nesting blackbirds, a male associates with his mates much less consistently, even during the period of copulation. Females forage independently of their mates. Females employ an elaborate vocalization when they leave their nests, probably to attract the male's attention, but the male rarely follows the female (Nero, 1956; Orians and Christman, 1968).

Jamaican blackbirds communicate with their partners primarily by means of vocalizations. As already described, partners spend little time in close association and following is not a major feature of their interactions. At moderate distances through the forest, the use of dzik calls, particularly during flights through the forest, serves to notify the partner of movements. Both sexes also sing at intervals. At a nest the pair often exchanged vocalizations in order to notify each other of departures and arrivals near the nest during the incubation period. Thus, after an absence, the male usually sang within a minute of arriving near the nest. The female, on departure from the nest, would usually utter several dziks or, particularly when her mate had not been heard for some time, a song as she flew away to feed. On her return, if the male was near the nest, he usually sang as she approached. In other typical responses, the male sang immediately after the female left the nest; the female sang from the nest as the male arrived silently nearby; or the female left the nest immediately after her mate sang nearby. In all of these situations, one partner notified the other of its own movements or acknowledged the movements of its partner.

Both partners answered each other's songs as well. At nest ST, the female on the nest often answered her mate's songs from nearby. The male also answered the female's songs. When the pair met near the nest after they had been separated and silent for a while, when one sang often the other answered so promptly that it overlapped the first's song. Answering also occurred away from the nest in all of the pairs observed intensively. On an occasion when the UB pair visited their southeastern boundary, the two repeatedly answered each other's songs for 20 min while they remained 5–20 m apart near the boundary.

Although both sexes sang frequently, the female at nest ST answered her mate much more frequently than vice versa. During the incubation period the male sang 2.0 times as often as the female, while during feeding of the young the female sang 1.3 times as often as the male. Overall 37% of the female's songs were answers to her mate, while only 5% of the male's songs were answers ($n = 598$). Similar patterns were noted qualitatively for other pairs.

Song flights also served to notify partners. Song flights above the

canopy were usually performed by males. For the color-marked pair in 1972 and nest ST in 1977, we recorded none by the female. However, both partners in territory UB did perform song flights in quick succession on one occasion, and a similar event was observed in one of the less intensively observed territories. On several occasions, we observed song flights after an extended period of silence by the partner; on one occasion the partner immediately sang in answer. On seven instances, song flights accompanied long flights toward or away from the partner (three times toward the partner, four times away). The possibilities for long-range communication by means of song flights were thus exploited for communication between partners as well as between territories.

A special, quiet vocalization served for communication at close range. These calls, a slightly trilled zeenk (Fig. 6) uttered at an even rate of about 2/sec in flight, accompanied arrival at the nest with food during the nestling period. In addition, on four occasions both partners repeated these calls when they were within 10 m of each other away from a nest.

Jamaican blackbirds used four other vocalizations, all very similar to calls of *Agelaius* species. During the episodes of interspecific aggression near nests, the attacking blackbird produced a guttural staccato train. Once, when a male approached an incubating female, we heard rapid high-pitched notes like those uttered by females in the solicitation posture of many passerines. Two vocalizations seemed to serve as alarm calls. One was a train of sharp, harsh notes, chet (Fig. 6), usually 5–15 in a bout with a regular rhythm or slight acceleration in the middle. Occasionally, birds uttered these calls near us when we approached too close. In most cases, they were not directed toward us, nor could we identify the referent if any. Finally, a high intensity alarm consisted of two high, thin notes, seee seee.

Thus, in the acoustic structure of their vocalizations, Jamaican blackbirds clearly resemble *Agelaius* species. In the use of similar songs by males and females and in the regular answering by mates, Jamaican blackbirds resemble the behavior of other monogamous icterids, in particular the common grackle *Q. quiscula*.

SOCIOECOLOGY OF THE JAMAICAN BLACKBIRD

The first task in this comparative study was to establish that Jamaican blackbirds do indeed exploit a sparse, evenly distributed resource. Owing to their use of discrete, easily recognized feeding stations, principally bromeliads, we could document the density and distribution of feeding sites in the habitat of blackbirds in more detail than other studies of insectivorous birds. The analyses of the vegetation of the slope forest occupied by

blackbirds indicate that feeding stations are evenly distributed. Although we could not measure the depletion of the insect fauna in a bromeliad as a result of a blackbird's visit, nor the renewal rate after a visit, it seems probable that the blackbirds do not search thoroughly enough in any one bromeliad to deplete the insects substantially. Thus the foraging ecology of Jamaican blackbirds satisfies the necessary conditions for the predictions.

The first prediction for Jamaican blackbirds was occupation of extensive, largely exclusive territories. The exclusiveness of territories is the salient adaptation to evenly dispersed food; even when females of marsh-nesting blackbirds feed entirely within the marsh, they do not occupy exclusive areas (Willson, 1966). Predation on nests, depending on the mechanisms by which predators locate nests, could favor either dispersed, cryptic nests or clumped nests (Kruuk, 1964; Hamilton, 1971; Robertson, 1973; Hoogland and Sherman, 1976; Waser and Wiley, 1979; Wiley and Wiley, 1980). Marsh-nesting blackbirds, in general, experience high rates of nest predation (Ricklefs, 1969; Wiley and Wiley, 1980). A relaxation of predation should permit fuller adaptation of spacing to the demands of foraging. Wide availability of adequate nest sites is another necessary precondition. The evolution of large, exclusive territories by Jamaican blackbirds seems clearly explained by adaptation to an even dispersion of food.

The prediction of exclusive territories pertains only to the spacing of pairs that forage from a base of operations, such as a nest (Waser and Wiley, 1979). Nonbreeding Jamaican blackbirds, therefore, do not fulfill this condition. As Waser and Wiley (1979) argue, the specific deductions for individuals with bases of operation, like nests or caches, can be generalized to individuals that receive any advantage from returning to former foraging areas rather than constantly proceeding ahead. In particular, an advantage of familiarity with foraging sites, such as increased efficiency in exploiting a renewing resource, could favor the evolution of exclusive territories. Whether or not such an advantage of familiarity with foraging sites accrues to individual Jamaican blackbirds is unknown.

As a corollary to the prediction of exclusive territories for individuals that forage from a base of operations or experience some advantage in returning to former foraging sites, one can predict that a mated pair should tend to separate into two distinct territories except during a nesting cycle, when both individuals use the same base of operations, the nest. In fact the pair in territory UB appeared to practice some separation of foraging areas.

The second prediction for Jamaican blackbirds was monogamy with full dual parental care. This prediction is based on strong correlations in passerine birds among arboreal insectivory, monogamy, and feeding of the young by both parents (Lack, 1968). In addition, a certain amount of theory supports this prediction, although the deductions are not so clear as in the

case of the preceding prediction. Some authors have argued that monogamy and dual parental care evolve when food supplies are sparse and/or distant from suitable nest sites, so that the participation of both parents in feeding the young substantially improves the chances of survival for their progeny (Crook, 1962, 1964, 1965). The amount of food delivered to the nest must, of course, be considered in relation to the clutch size and growth rate of the young; supply and demand can be made commensurate either by adjustments in the requirements of nestlings or the contributions of parents. Other authors have pointed out that frequent visits to a nest might increase the chances of predation so that the increased risk of predation might not balance the increased benefit of more food (Snow, 1962, 1970; Lill, 1974). Reductions in clutch size and increases in the amount of food transported in each trip to the nest would reduce the number of feeding trips required and, thus, the risk of predation. For some tropical frugivorous birds, clutches are apparently reduced to the extent that obtaining the food necessary for feeding the young presents little difficulty for one parent. Other theory argues that spatial variation in the quality of males' territories would result in some males' obtaining multiple mates while others obtained none (Verner, 1964; Orians, 1969b; Wittenberger, 1976; Altmann et al., 1977). If differences in the food available or the risks of predation were sufficient, a female choosing a nesting site might expect to fare better when mated bigamously with a male in a good location than when mated monogamously with a male in a poor position. This theory requires an independent explanation for the regulation of the sizes of males' territories, in order to explain why more males do not subdivide the optimal locations. Finally, a number of authors have argued that mating systems depend on whether or not resources critical for females or the females themselves are "defensible" (Emlen and Oring, 1977; Bradbury and Vehrencamp, 1977). When receptive females occur in groups or use localized resources, individual males might defend more than one female. This theory, in common with the preceding one, requires an independent explanation for the limits of a male's perimeter of defense, in order to explain why more males do not subdivide resources or females. The Jamaican blackbird seems to fit predictions of monogamy from all of these theories: its food is sparsely distributed; nest predators are probably less frequent in Jamaica than on the mainland; the distribution of food is relatively even across territories; and neither females nor resources occur in discrete clumps.

The third prediction for Jamaican blackbirds, tonal, frequency-modulated vocalizations for long-range communication, is unequivocally contradicted by the results. The Jamaican blackbird has retained from its phylogenetic ancestors wide-spectrum vocalizations with little frequency modulation. Long-range communication and territorial advertisement are accomplished by behavior unusual for a forest bird. Song flights, also

apparently retained from agelaiine ancestors, extend the range of their songs. Advertisement of the territory at dawn involves continuous repetition of a simple call while patrolling a beat in the core of the territory. Although birds that inhabit grasslands, fields, and marshes often perform song flights high above the vegetation, birds of forests practically never do. No other bird, so far as we know, advertises extensive territories primarily with behavior like the dawn patrolling of Jamaican blackbirds.

Song flights are advantageous in habitats with low vegetation because the range of an acoustic signal near the ground is limited by interference from ground reflections and refraction of sound by temperature and wind gradients (see Wiley and Richards, 1978). In such habitats, singing from an elevation above the vegetation greatly extends the range of a vocalization. Neither of these advantages accrues to birds in the canopies of forests. Since song flights require steep ascending flights, they entail expenditure of considerable energy. The dawn patrolling of Jamaican blackbirds, which consists of repeated flights for a period of half an hour, also requires considerable expenditure of energy. Exposed or repeated movement accompanied by conspicuous vocalizations is also likely to attract predators. Birds of open country often have little alternative to increase the range of their vocalizations, but birds of forests would probably reduce risks of predation as well as conserve energy by avoiding song flights.

The absence of predators on adult birds in Jamaica might, thus, partly explain their peculiar forms of territorial advertisement. It still seems remarkable that the energetic savings that would come from reducing the amount of locomotion in territorial advertisement have not resulted in the evolution of tonal, frequency-modulated signals that would propagate with less distortion and better signal/noise ratios in forests.

"NATURAL" EXPERIMENTS

This study of the Jamaican blackbird is a "natural" experiment in the sense that we have used a naturally occurring difference to examine three predictions from current hypotheses in socioecology. Unlike a manipulative experiment, a "natural experiment" involves no direct manipulation of the experimental variable nor randomization and, thus, demands particular attention to the possibility of alternative hypotheses. This study proceeded by documenting the dispersion of feeding sites, the experimental variable, examining the social behavior of Jamaican blackbirds with reference to the three predictions, and evaluating possible alternative explanations related to peculiarities of island ecology.

Manipulative experiments are often impossible in studies of evolu-

tionary adaptation. The experimental variables of concern are features of a population's environment, such as the nature of predation or food resources. The responses consist of alterations in the population's gene pool and the consequent changes in phenotypes. With few exceptions, the spatial and temporal dimensions of such a study, particularly for adaptations in social behavior of relatively long-lived animals, in practice eliminate the possibility of manipulative experiments. Many manipulative experiments under field conditions, such as playback of tape recordings, use of taxidermic models, or manipulation of food supplies and clutch sizes, reveal the developmental and phenotypic plasticity of individuals in populations, the limits to the conditions that evoke normal or adapted behavior. Although such information can clarify the mechanisms of the current adaptations of animals, it does not directly reveal the operation of natural selection in the evolution of adaptation. In many cases, "natural experiments" are the only practical recourse for investigations of evoultionary adaptation.

Although "natural experiments" lack the full force of manipulative experiments with randomization, the advantages of manipulation and randomization are not absolute. Randomization in manipulative experiments serves two purposes (Webb et al., 1966). By randomizing the selection of subjects from a larger, defined population, the investigator assures the "external validity" of his experiment. In other words, he establishes the conditions for generalizing the results of his observations on the selected subjects to the larger population. By randomizing subjects with respect to treatments within the experiment, he assures the "internal validity" of the experiment. In other words, he reduces the possibilities for extraneous variables, related to unknown sources of variation among the subjects, that might explain the observations.

The validity of a manipulative experiment can founder for two reasons. First, randomization can fail. Unsuspected systematic differences between subjects and the population at large or between subjects assigned to different treatments can compromise respectively the external and internal validity of the experiment. Second, manipulation of the experimental variable can have unsuspected, correlated side effects. Manipulations often include matching the conditions, other than the experimental variable, for subjects in different treatments, and imperfect matching of conditions can leave unsuspected differences between treatment groups. Probably no experimental manipulation is ever absolutely free of correlated side effects or ever achieves perfect matching of extraneous variables. Although manipulative, randomized experiments have clear advantages in narrowing the field of alternative explanatory hypotheses, in the end their validity is subject to the same sort of scrutiny necessary in a "natural experiment."

"Natural experiments," although lacking some advantages of manipulative experiments, are nevertheless on firmer ground than correlational

studies. Correlational studies lack antecedent hypotheses from basic theory. The interpretation of correlational studies is, thus, ambiguous, owing to possibilities for multiple explanatory relationships among the observed variables. In the worst case, it is impossible to decide which of two correlated variables is the independent one, if either. The variables might have reciprocal dependencies or both depend on a third, unmeasured variable (Campbell and Stanley, 1966). The situation is much stronger, however, when basic theory restricts the possible alternate explanations. For instance, in the case of the first prediction for Jamaican blackbirds, concerning exclusive territories, the prediction derives from a specific, formalized hypothesis (Horn, 1968; Waser and Wiley, 1979). This hypothesis, in turn, is based on the reasonable proposition that a living organism increases its fitness by increasing its foraging efficiency, within the constraints of an optimum balance between reproduction and survival. Alternate dependencies (for instance, that the social behavior of Jamaican blackbirds determines the evolution of the dispersion of insects in montane forests or that some third variable, such as predation or the vegetation structure, independently determines the evolution of both the blackbirds' social behavior and the insects' dispersion) seem clearly of subsidiary importance.

Thus a "natural experiment" shares with correlational studies the absence of direct manipulation of experimental variables and randomization of subjects; it shares with manipulative experiments the antecedent presence of definite-hypotheses. The absence of randomization and manipulation require extra care in evaluating alternative, extraneous explanations, although even manipulative experiments cannot in practice escape completely from such judgment. In view of their importance for investigating processes that span large spatial and temporal dimensions, the characteristics and rational for "natural experiments" deserve more attention.

SUMMARY

From current hypotheses of relationships between the ecology and social behavior of birds and from information in the literature that the Jamaican blackbird (*Nesopsar nigerrimus*) feeds on insects in montane forests, we predicted that this species should have large, exclusive territories, monogamy with dual parental care, and advertising songs consisting of frequency-modulated tones, all in contrast to blackbirds in the genus *Agelaius*, the closest phylogenetic relatives of *Nesopsar*. During studies in montane forest in Jamaica, we documented that Jamaican blackbirds exploit sparse, evenly distributed insects in the canopy of montane forest. Seventy-seven percent of feeding stations were epiphytic bromeliads, in which

the blackbirds probe for insects. The density of canopy bromeliads averaged 2900/ha and showed no significant small-scale (20 m) or large-scale (200–500 m) variation in density in two adjoining territories of blackbirds. Blackbirds generally moved rapidly between bromeliads while foraging and at intervals flew long distances. Pairs of blackbirds occupied large territories (150–360 m in diameter) with no overlap between adjacent residents' movements. While the female incubated, her mate spent long periods perched nearby and attacked other species that approached the nest. At two nests, both sexes fed the young approximately equally throughout the nestling period. The overall feeding rate was about eight trips/hr. Parents brought one item at a time, most often dark brown Orthoptera from epiphytic vegetation. The songs of Jamaican blackbirds consist of buzzy, wide-spectrum sounds, not unlike those typical of *Agelaius* species, contrary to prediction. As these sounds are not well-adapted for long-range communication in forests, this species employs two unusual strategies for territorial advertisement and long-range communication between mates: spectacular song-flights high above the forest canopy, presumably behavior retained from their marsh-nesting ancestors; and dawn activity that consists of the male flying back and forth on a beat near the center of the territory while repeating short trains of a simple sharp call. Mated birds frequently answer each other's songs; both sexes use the same song patterns. The exclusive territories and monogamy with dual parental care confirm predictions from socioecological hypotheses for species exploiting dispersed, sparse resources. The unexpected from of territorial advertisement might be adapted only to island environments, like Jamaica, with no major predators on adult birds. A "natural experiment," like this study of the Jamaican blackbird, lacks certain advantages of manipulative experiments with randominzation but, nevertheless, avoids difficulties in purely correlational studies.

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