

ON THE EVOLUTION OF SOCIALITY, WITH PARTICULAR REFERENCE TO *TIARIS OLIVACEA*

RONALD PULLIAM, BARRIE GILBERT, PETER KLOPFER, DENNIS McDONALD,
LINDA McDONALD, AND GEORGE MILLIKAN

THE behavior of the Yellow-faced Grassquit (*Tiaris olivacea*) apparently ranges from social and nonaggressive on the Central American mainland to territorial and very aggressive on the island of Jamaica (Pulliam, 1970). Why these differences?

This paper reports observations on the population size, habitat distribution, and social behavior of the Yellow-faced Grassquit on the island of Cayman Brac, West Indies, and speculations on factors influencing social behavior. Cayman Brac is a very small island (20 square miles) and this population of grassquits is extremely isolated from other populations, the nearest being found on Grand Cayman (80 miles southwest) and on Jamaica (190 miles southeast). The third of the Cayman Islands, Little Cayman Island, is about ten miles west of Cayman Brac, but grassquits are very rare or absent there perhaps because of a lack of suitable habitat.

The observations reported here are based primarily on a two-week field study beginning 27 November, 1969. Additional observations must be made at other times of year for confirmation of our findings. However, the social organization of the species has been noted by one author (Pulliam) to be stable throughout the year in Jamaica and Skutch (1954) indicates that Costa Rican grassquits can be found in flocks during all seasons of the year.

THE EVOLUTION OF SELFISH BEHAVIOR

Hamilton (1964) has demonstrated that kinship selection can limit the expression of behavior which decreases the fitness of a neighbor more than it increases the fitness of the actor (i.e., selfish behavior). Kinship selection encompasses the notion that an individual's overall fitness includes not only the effects of his genotype on his own ability to leave descendants but also the effects of his genotype on the fitness of relatives who carry some proportion of genes identical by descent to his own. Although Hamilton's model is formally correct, it is applicable only if the selfish behavior of a population is determined by the gene frequencies at one locus. We contend that aggression or selfish behavior is not coded at a single chromosomal locus (see Klopfer, 1969) but that the degree of aggression in an individual must be thought of as resulting from the interaction of the animal's environment with the epistatic effect of a large number of genes at very many loci. Thus, in an almost

homozygous population, selfish behavior might be selected against because it decreases one's own inclusive fitness.

In this paper we argue that some forms of aggressive and territorial behavior constitute "selfish behavior" and, thus, their occurrence in natural populations must be restricted to relatively heterozygous populations.

An aggressive territory holder can decrease the fitness of a nonaggressive bird by excluding it from optimal habitat. It is less obvious that the decrease in fitness of the nonaggressive bird is greater than the increase in fitness of the aggressor. However, the territorial bird does lose some of the advantages of social behavior (whatever they are) and must spend considerable time defending his territory, time which might otherwise be applied towards maintenance and reproduction. The amount of time which the average aggressive individual spends defending his territory must necessarily increase as the proportion of the bird population which is territorial increases. Hence, the question: why are some grassquits territorial?

Suppose territorial individuals do have a lower reproductive capacity than social individuals would have in the absence of the former. This would result in a territorial population maintaining lower numbers than a social population even though the territorial individuals were superior in competition with the social individuals! If, for a given bird species, the social populations were shown to maintain a significantly higher population density than the territorial populations, we would have evidence that territoriality is a selfish behavior for that species.

Pulliam (1970) censused, during the breeding season, 11 similar habitats that appeared suitable for Yellow-faced Grassquits in both Jamaica and Costa Rica. Each habitat was visited twice. In Costa Rica, on a total of 25.9 acres, an average of 20.5 grassquits were seen. In Jamaica, on a total of 18.0 acres, an average of only 6.9 grassquits were seen. In both Costa Rica and Jamaica there were grassquits in four of the eleven habitats visited. The number of grassquits per acre in those sites containing some grassquits was 2.9 in Costa Rica, as compared to 0.7 in Jamaica. The increase in the density of the Costa Rican grassquits is especially surprising since there were many more individuals and species sharing sites with grassquits in Costa Rica than there were in Jamaica. Thus, it appears that the social grassquits of Costa Rica are able to maintain a population density two to three times as great as that of the territorial Jamaican grassquits. This accords with our supposition.

Very little is known about the degree of heterozygosity in natural populations of birds and we are not yet able to predict the degree of heterozygosity that might permit selfish traits to evolve. However, we do know that both isolation and population size exert considerable influence on the degree of genetic diversity of natural populations. In very small populations, random

drift can lead to fixation or loss of genetic variability. This decay of genetic variation is counter-balanced by the forces of mutation and immigration. Soulé (1971) presents arguments and evidence that for lizards large population size and migration between adjacent populations is necessary for the maintenance of genetic diversity. Soulé showed that lizards from small, isolated island populations showed less variation in electrophoretically detectable isozymes than lizards from large island populations. The decrease in enzyme variation was correlated with a decrease in morphological variance. This result indicates that isolation and small population size result in a decrease in genetic diversity and could, therefore, limit the expression of selfish behavior traits.

Tiaris olivacea is an abundant inhabitant of the subtropical plateau region of Costa Rica (Slud, 1969). However, the grassquit is a bird of secondary growth habitats, never found in the dense forest, and is therefore restricted in distribution to areas near human habitation and agriculture. The human population of Costa Rica is largely limited to areas in close proximity to roads or rail lines. Thus, habitat suitable for grassquits is discontinuously distributed along the few roads and railroads in eastern Costa Rica. In May of 1969 Pulliam searched for grassquits along the road from San José to Turrialba and along the railroad between San José and La Lola Farms, which is about 30 miles west of Port Limon on the Gulf of Mexico. This journey made an east-west transect across almost the entire range of *Tiaris* in Costa Rica. Grassquits were first noted along the roadsides about 5 miles east of Cartago. From Cartago to Turrialba, grassquits were frequently recorded in suitable habitats but these habitats were distributed in patches. Along the railroad, grassquits were noted from Turrialba to La Lola Farms, where they were common. Suitable habitat along the railroad was distributed in discrete patches and often interrupted by many miles of forest habitat. In addition to the patchwork character of suitable habitat, the presence of a dozen or more sympatric seed-eating finches may further limit the distribution of grassquits. This combination of a patchwork habitat and many competitor species would tend to result in *Tiaris* being found in isolated groups of small size in Costa Rica. We expect their social behavior to be related to a high degree of genetic homozygosity maintained because of the patchiness of their distribution.

Tiaris olivacea is found in all parts of Jamaica with the possible exception of the very dry Southeast. Throughout the range of grassquits in Jamaica there are numerous roads and, therefore, much more habitat suitable for *Tiaris* than in Costa Rica. This suitable habitat is virtually continuous over the entire island except in the high mountains which are sparsely settled by humans. Also, in Jamaica there is only one other species of finch which feeds exclusively on grass seeds. The two factors combine to produce a continuous

and therefore very large grassquit population. We expect such a population to be genetically more diverse than the discretely distributed Costa Rican population and, thus, to permit the occurrence of selfish behavior. In fact, the Jamaican birds, in contrast to those of Costa Rica, are territorial, as noted above.

These arguments are conjectural and were largely developed *ex post facto*, after our studies in Jamaica and Costa Rica. If, however, the argument is correct we would expect to find that any isolated, small populations of grassquits would exhibit social rather than selfish behavior, and be more similar in their social structure to the Costa Rican population than to the Jamaican population. With this idea in mind, we attempted to ascertain the population size and social structure of the isolated grassquit population on Cayman Brac Island.

ESTIMATE OF GRASSQUIT POPULATION SIZE ON CAYMAN BRAC

Data for population size estimates were collected by locating and then, only once, walking slowly through suitable habitats and recording all birds heard or seen. "Suitable habitat" was defined as those areas where trees and shrubs covered less than 80 per cent of the ground and where there was some grass growing. This definition of suitable habitat was consistent with our observations in Costa Rica and Jamaica that grassquits were found only in grassland and old-field habitats and the observations of Skutch (1954) in Costa Rica and Wetmore (1927) in Puerto Rico that the diet of grassquits consisted almost entirely of grass seeds. However, on Cayman Brac we often found male grassquits singing from the upper branches of trees and shrubs near the edges of fields. Figure 1 illustrates that the grassquits in trees were always very close to a grassy field. The data for Figure 1 were collected by pacing along a path which ran all the way across the island from North to South. The location of the bird is plotted as the location at which the bird was estimated to be at right angles to the path. Thus, those birds which appear, in the figure, to be in the fields may actually have been singing from trees and shrubs on the east or west sides of the fields. At any rate, the data presented in Figure 1 are consistent with our belief that the grassquits are found only in or near field habitats. Since the maintenance of such habitats on Cayman Brac depends entirely on their being accessible to people (due to the rapidity of successional growth), we felt confident that most such habitats could be found by traversing all roads and paths on the island.

One of the assumptions of the model (presented in the Appendix) used to estimate population size is that the probability of a call in any interval of time is constant throughout the time of observation. It is well known, however, that many birds show a pronounced decrease in singing in the middle of the

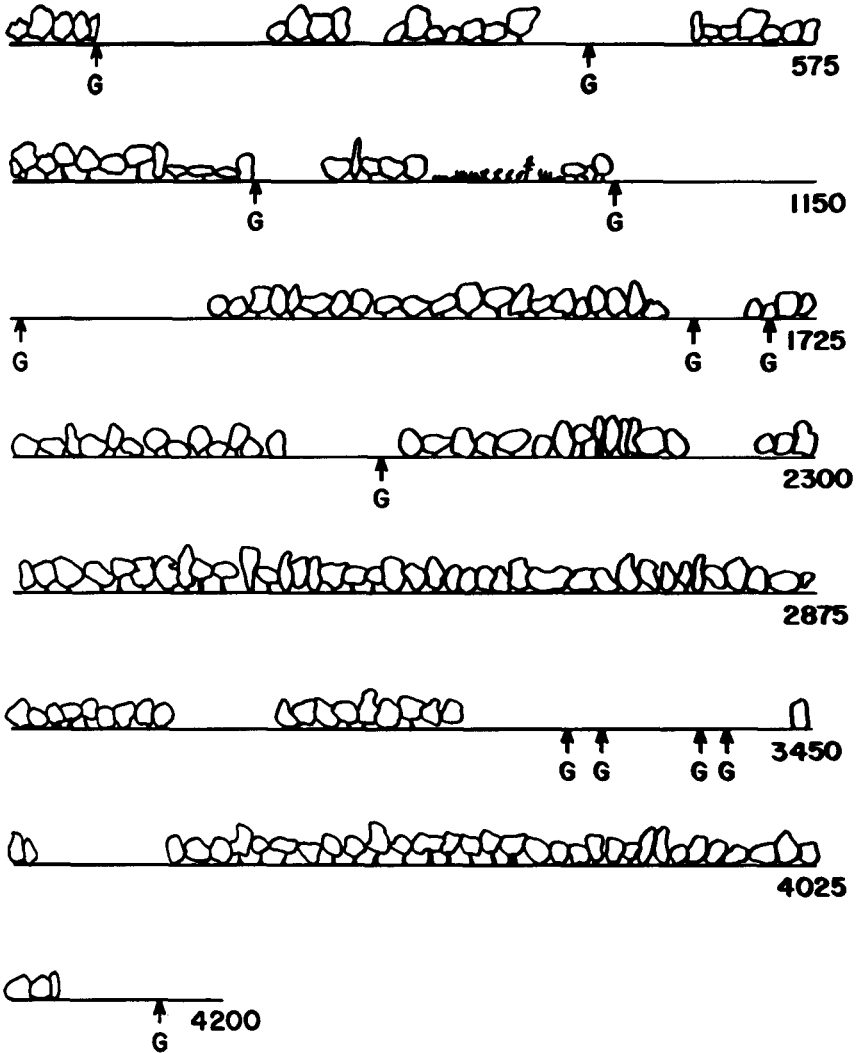


FIG. 1. Observations on the location of birds along a transect across Cayman Brac Island. The symbol G indicates the position of grassquits along the transect and the numbers on the right indicate the distance from the start of the transect. Grassy fields are indicated by the clear areas and forests and garden are indicated diagrammatically.

day. Thus, the probability of recording a bird in the middle of the day might be lower than, say, in the early morning. Table 1 shows the number of songs per thirty-minute interval for seven individual grassquits sampled at different times of the day. It appears from this sample of singing activity that there

TABLE 1

THE NUMBER OF BIRD SONGS IN THIRTY-MINUTE INTERVALS FOR SEVEN INDIVIDUAL GRASSQUITS WATCHED AT DIFFERENT TIMES OF DAY.

The times on the left indicate the beginning of each thirty minute interval.

	1	2	3	4	5	6	7	Average
7:00	60		20					40
7:30	38		18					28
8:00	48		20					34
8:30	118	3	61					60
9:00	23	17	80					40
9:30	0		82					41
10:00			85	36				60
10:30				17				17
11:00				1				1
11:30				46				46
12:00				3				3
12:30				40				40
13:00				57				57
13:30					40			40
14:00					76			76
14:30						28		28
15:00						18		18
15:30						21		21
16:00						4	43	23
16:30						9	56	32
17:00							51	51

may be a slight decrease in singing rate in the middle of the day. Since the sample size is so small, particularly for the mid-day period, this is not certain. Even if there is a decrease in singing rate at mid-day we believe it does not seriously effect our results, since the decrease appears to be small and less than 10 per cent of our censuses were taken in the mid-day period (between 10:00 and 14:00).

For three of the seven birds for which data are given in Table 1, we were able to record the occurrence of each song to the nearest second. From these data we could assess the reliability of our census technique (see the Appendix). Figure 2 indicates that the probability of recording a bird does not differ significantly from one time of day to the next.

For the total census we recorded 190 male and 24 female grassquits. Of the 190 males, 161 were heard singing and 29 were only seen. If we assume the sex ratio to be equal and that there must have been some suitable habitat which we did not locate, then we must conclude that there were at least 400 grassquits on the island. However, this is undoubtedly an underestimate since many

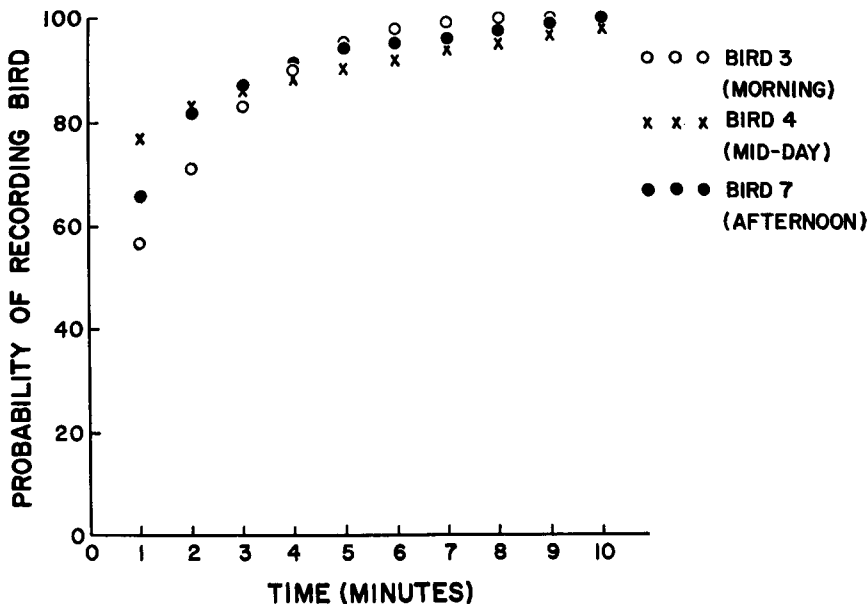


FIG. 2. The probability of recording a bird as singing as a function of the length of time that an observer is within hearing range of the bird. See Appendix for estimation procedures.

birds must not have been recorded even though we located the fields in which they resided. From the estimates of the probability of recording a bird in Figure 2 we can get some idea as to how accurate our census was. A singing male grassquit can be heard from 75 to 100 feet away. If we assume that our walking speed through the fields was between one and two feet per second, it follows that an observer was within hearing range of each bird for from one to three minutes if the field where the bird resided was actually located. Taking a very liberal estimate of the population size we assume that each bird was in hearing range for only one minute and thus, from the lowest estimated probability of recording a bird when it is within hear-range for one minute (From Bird No. 3, Fig. 2), we estimate that only 55 per cent of the male birds were recorded by being heard. Thus, a liberal estimate of population size is about 300 male birds (or approximately 600 birds, total). This estimate may still be too low since there may have been first-year male birds which were not singing. Assuming there may be as many as one non-singing male for each singing male we can boost the total estimated population size to about 1,200. Finally, there were the birds in the fields that we did not locate and assuming that we may have not found as much as 20-25 per cent of

the suitable habitat, we reach a figure of 1,500 birds. It should be realized that in arriving at this estimate of population size we took the extremes of all estimation parameters so as to give an absolute upper limit. At the other end of the scale we could assume that we observed all of the male grassquits on the island. Taking the two extremes we can state fairly confidently that there were between 400 and 1,500 Yellow-faced Grassquits on the island at the time of our census.

SOCIAL BEHAVIOR OF THE YELLOW-FACED GRASSQUIT

In Jamaica, the Yellow-faced Grassquit is strictly territorial. Nine territories in optimal habitat measured in June–July, 1968, near Treasure Beach, Jamaica, averaged only 0.25 acres each and aggressive encounters between males on adjacent territories were frequent. Although Jamaican grassquits never occur in flocks, individuals of both sexes are known to aggregate occasionally at artificial feeding stations and when this happens males seem to spend more time fighting than feeding.

Skutch (1954) describes the Yellow-faced Grassquit in Costa Rica as lacking “that pugnacious jealousy so prominent and characteristic in many members of the finch family” and as “a most pacific bird. I have never noted any fighting or discord among them.” However, males do defend a small area in the immediate vicinity of the nest from which other males of the same species are expelled. Skutch describes this defense as follows: “all the territorial male does is fly mildly in the direction of the intruder who retreats without necessity of conflict.” Grassquits which are not nesting are normally found in large feeding flocks which often contain thirty to forty individuals, with both sexes represented. Pulliam (1970) noticed no signs of aggression within flocks but did note occasional conflicts between grassquits and other seed-eating finch species during a three-week field study during the breeding season in 1969 near Turrialba, Costa Rica.

The contrast between the highly social behavior of Costa Rican grassquits and the strictly territorial behavior of the Jamaican grassquits is typical of the differences in social behavior of a number of passerine bird species from Costa Rica and Jamaica. Pulliam (1970) compared the social behavior of all resident bird species of the families Fringillidae, Thraupidae, and Icteridae for which data could be found for Jamaica and Costa Rica. He found that 18 of the 26 Costa Rican species showed some form of social tolerance (family groups or flocking) compared to only two of the 11 Jamaican species. [The definition of “no social tolerance” is that at all times of the year individuals are either alone or in the company of a single adult of the opposite sex and/or juvenile birds up until a short time after fledging.] This is consistent with the supposition that continuously distributed species are more likely to be

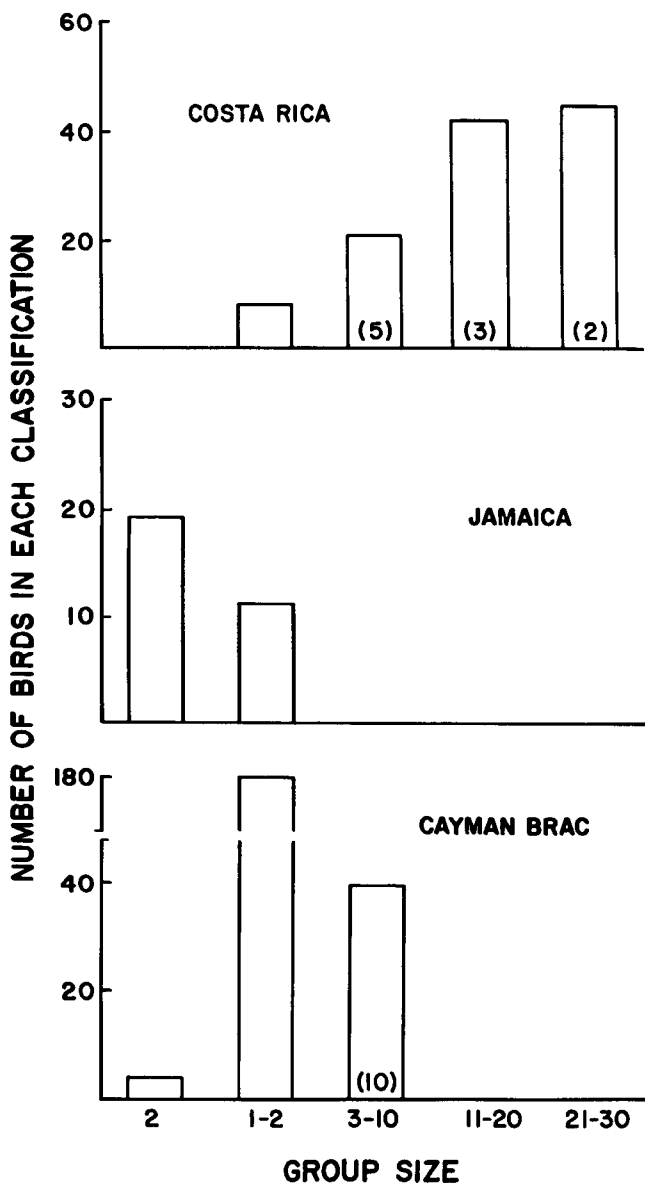


FIG. 3. The sizes of groups of grassquits observed for three different populations.

genetically polymorphic, and thus aggressive, since Jamaican birds seem to be more continuous in their distributions than Costa Rican birds.

The social behavior observed for grassquits on Cayman Brac can best be described as intermediate between the social behavior of Jamaican and Costa Rican grassquits. Adult males were typically seen singing from trees and shrubs on the edges of grassy fields. The frequency of singing appeared to increase in the presence of other adult male birds and dueting between birds on adjacent territories was frequently observed. However, chases between adult male grassquits were observed only on two occasions, whereas they were very frequent in Jamaican grassquits (Pulliam, 1970). On several occasions adult male birds were seen to sit on the same limb within a few inches or feet of each other and sing without any subsequent displacement. On at least two such occasions the birds flew together to the ground where they fed in close proximity to one another.

Figure 3 shows the group sizes observed for Cayman Brac grassquits as compared to group sizes observed by Pulliam (1970) in Jamaica and on the Central American mainland. In each case all observations during a two-week study period are recorded. However, the Cayman Brac data were collected in November–December, 1969 while the Jamaican and Costa Rican data were collected in April–May, 1968. The possibility that the observed differences are due to seasonal change will be discussed later. A total of ten groups in the category of three to ten birds (Fig. 2) were observed on Cayman Brac. These groups ranged in size from three to six and, therefore, some could be family groups. In some of these groups, one or more of the birds was identified as an immature. The category 2♂ indicates that two males were seen together and that there was a subsequent chase and displacement. While this was the most frequent category in Jamaica (perhaps because of conspicuousness), no such interactions were observed in Costa Rica and only two were observed on Cayman Brac.

HABITAT UTILIZATION

Slud (1964) describes the habitat of the Yellow-faced Grassquit in Costa Rica as follows: "it inhabits fields, plantations, pastures, clearings, roadsides, an deforested areas in general." According to Wetmore (1927) and Wetmore and Swales (1931), the grassquit in Puerto Rico is found entirely in open pastures, cultivated fields, hedges, or scanty growth of bushes. In Jamaica, grassquits are commonly found in pastures, gardens, roadsides, and plantations (Pulliam, 1970). The common denominators of grassquit habitats seem to be incomplete canopy cover and the presence of grasses.

The grassquits on Cayman Brac were found mainly along roadsides and in or near grassy fields. There were no grassquits recorded in the coconut palm

plantations on the north side of the island where there were very few grasses. However, there were grassquits in the smaller coconut palm plantations on the south side of the island where there were abundant grasses.

A large number of grassquits were found in trees and shrubs in or near grassy fields (see Fig. 1). Grassquits observed in trees were almost without exception males and only in a few instances appeared to be feeding. When the grassquits did feed in the trees they seemed to be gleaning much in the manner of a wood warbler. Skutch (1954) and Slud (1964) report the same behavior occurs in Costa Rican grassquits when food is scarce even though the normal diet consists only of the seeds of grasses.

DISCUSSION

We have argued that the maintenance of the social behavior of Costa Rican grassquits is dependent on the patchiness of their distribution which limits both effective population size and gene flow between populations and thus reduces the genetic diversity within subpopulations. If this interpretation is correct, we would expect that populations of grassquits on small isolated islands would, like the mainland grassquits, exhibit decreased heterozygosity, which would, in turn, limit the expression of selfish traits. Our census of the grassquits of Cayman Brac, indicates that there are between 400 and 1,500 grassquits on the island. A population of this size should be sufficiently large to prevent the loss of genetic diversity through random drift as might occur in smaller populations (see Crow and Kimura, 1970).

Our observations on the sociality of the Cayman Brac grassquits indicates that they are intermediate between the highly territorial Jamaican grassquits and the very social Costa Rican grassquits. However, the observations on the Cayman Brac birds were restricted to a short period in the autumn of 1969 as compared to extensive observations of the Jamaican and Costa Rican birds during all months of the year. Thus, the behavior of the Cayman Brac birds may only reflect a seasonal lull in territoriality at the end of the breeding season. However, the tolerance occasionally observed between adult male birds has not been reported from Jamaica. In Jamaica the birds breed in all months of the year, so some post-breeding males should always be in evidence.

It is clear that three further steps need to be taken to substantiate our prepared explanation: (1.) The Cayman Brac population should be studied at other times of the year to assure there are no seasonal variations in the social organization of the population; (2.) A general survey of the frequency of various forms of social organization in birds as a function of island size and isolation should be conducted; and (3.) Data specifically relating the degree of genetic variability in birds to the size and isolation of islands should be gathered.

SUMMARY

The Yellow-faced Grassquit (*Tiaris olivacea*) is discontinuously distributed and highly social in Costa Rica. In Jamaica its distribution is continuous and it is aggressively territorial. On Cayman Brac we estimate that grassquit population consists of 400–1,500 individuals which seem intermediate between Costa Rican and Jamaican grassquits in their social organization. We speculate that aggressive behavior of the sort we have characterized as “selfish” cannot arise except under conditions of considerable genetic variability.

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APPENDIX

We estimate the probability of recording the given bird as a function of the length of time (m) that an observer is within hearing distance of the bird. First, consider the probability of recording a bird given that the observer arrived within hearing distance during an interval for which the bird was silent for exactly L seconds, where $L > m$. If the observer arrives in the first $L-m$ seconds of the interval then the bird will not be recorded. However, if the observer arrives in the last m seconds of the interval, he will record the bird. Thus the probability of not recording the bird, given that the observer arrived during an interval for which the bird was silent for L seconds ($L > m$) is $(L-m)/L$. Of course, if the observer arrives within hearing distance of the bird during an interval for which the bird is silent for a period of time less than m seconds, then the observer will always record the bird.

The estimated probability that a bird will be silent for exactly L seconds is given by $(n_L \cdot L)/T$, where n_L is the number of times that the bird is observed to be silent for exactly L and T is the total length of time for which the birds' songs are recorded. Thus, the probability that a bird will not be recorded is the product of the probability that the observer arrives during a period for which the bird is silent for exactly L seconds (which is $(n_L \cdot L)/T$) and the probability that the bird will not be recorded given that the observer arrived during such a period (which is $(L-m)/L$) summed over all observed values of L greater than m , which reduces to

$$\frac{1}{T} \sum_{L>m} n_L \cdot (L-m) . \quad 1)$$

These values were calculated for the three birds for which data were available. The values plotted in Figure 1 are for the probability of recording a bird as a function of the length of time that an observer is within hearing distance of the bird. The values for the probability of recording the bird are, of course, simply one minus the probability of not recording the bird which is calculated with Formula 1. Notice that the values are very similar for the three birds indicating rather little variance in the probability of recording a bird. This probability does not approach one until after about nine or ten minutes but after one minute is already about 0.65. Bird No. 4, which was watched in mid-day, does not indicate a lower probability of being recorded despite the lower average number of

calls per half-hour period in the mid-day (as shown in Table 1.). Though there were fewer calls, they were more evenly spaced in time than was the case for the other two birds.

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ZOOLOGY DEPARTMENT, DUKE UNIVERSITY, DURHAM, NORTH CAROLINA 27706,
(PRESENT ADDRESS OF SENIOR AUTHOR, DEPARTMENT OF BIOLOGICAL SCIENCES, UNIVERSITY OF ARIZONA, TUCSON, ARIZONA 85721), 7 MAY 1971.