

FEEDING CORRELATES OF BREEDING AND SOCIAL ORGANIZATION IN TWO GALÁPAGOS FINCHES

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ABSTRACT.—Several aspects of breeding and social behavior in two Galápagos finches are related to food supply. *Geospiza fuliginosa* is largely granivorous, and *G. difficilis* is largely insectivorous. Measurements show that breeding of both species occurred when arthropod abundance was high. Breeding stopped when arthropod abundance was declining but before it was low. Breeding-territory size in *G. difficilis* varied inversely with food supply. Territory size in *G. fuliginosa* was similar across sites and was not correlated with food supply. This difference between species may be attributed to differences in the effects of invertebrate and seed resources on the functional response of consumers: feeding rate of *G. difficilis* on invertebrates increased linearly with their supply, whereas feeding rate of *G. fuliginosa* on seeds was essentially independent of seed abundance. In the nonbreeding season, the granivore *G. fuliginosa* moved in flocks, whereas *G. difficilis* was more stationary and solitary. Data indicate that seed supply was temporally more variable than invertebrate abundance, and this helps account for dry-season behavioral differences between the species. Functional response and/or renewability of seeds and invertebrates may also have influenced behavior at that time. Received 18 April 1983, accepted 19 September 1983.

ECOLOGICAL studies of birds have suggested that food is a major determinant of breeding and social behavior. For example the degree of gregariousness in a species is often associated with diet (Crook 1965, Lack 1968, Brown and Orians 1970, Newton 1972, Wiens and Johnston 1977, Pulliam and Millikan 1982). Also, the onset of breeding and nonbreeding seasons may be accompanied by changes in diet and/or food supply (Marchant 1959; Ward 1965, 1971; Lack 1968; Cody 1971; Newton 1972; Fogden 1972; Maclean 1976; Myers et al. 1979; Price 1979; Grant and Grant 1980). With the exception of recent studies on territoriality, however (Ewald and Carpenter 1978; Davies 1978, 1980), the critical properties of foods have rarely been measured. As a result, current views on the role of food in determining breeding and social organization in birds remain largely untested.

The purpose of this study is to evaluate whether or not food characteristics determine breeding and social behavior in two Galápagos finch species. The diets of the two species vary seasonally, but one, *Geospiza difficilis*, feeds much

more on insects and other invertebrates than does the second, *G. fuliginosa*, which is largely granivorous (Schluter 1982a, b). For both species I evaluate the degree to which timing of breeding and nonbreeding is determined by seasonal changes in food abundance. Additionally, I compare territorial behavior in the breeding season and the degree of gregariousness in the dry season in *G. fuliginosa* and *G. difficilis* in relation to differences in abundance and variability of their major foods.

METHODS

I describe most of the methods in detail in earlier works (Schluter 1982a, b, and references therein) and only summarize them here. The study was conducted over 2 yr (Table 1) at a series of six 1-ha sites along Isla Pinta's south slope. Each of the major vegetation zones was represented, including the coastal arid zone (site 1), the mid-elevation transition zone (sites 2-5), and the highland forest zone (site 6; Wiggins and Porter 1971). I established five sites in 1978 (1-3, 5, 6) and added the sixth (4) in 1979.

An assistant and I quantified finch diets by walking systematic routes through a given site and recording with a stopwatch the amount of time that individual birds fed on identified food items for up to a maximum of 300 s per bird. When visibility allowed, we also recorded the number of individual food items consumed by a bird per unit time. Mean

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TABLE 1. Dates and seasons of visits to Pinta.

Year	Dates	Season
1978	6 January-1 April	breeding (wet)
1978	10-29 May	early nonbreeding (dry)
1979	20 January-28 February	early breeding (wet)
1979	26 April-29 May	early nonbreeding (dry)
1979	9 August-15 September	middle nonbreeding (dry)
1979	28 October-3 December	late nonbreeding (dry)

foraging rate on specific food types could then be estimated using a weighted average of observed rates (cf. Schluter 1982a).

We measured food abundance at all sites during all visits except May 1978, when time was insufficient for measuring. At each site, 25 random 1-m² quadrats were located; we increased the number to 50 at site 1 later in 1979, which was required by another study (Schluter 1982a). In 1978 we counted the total number of seeds on stems of the perennial grass *Paspalum galapageia* in quadrats; this is the most abundant seed type in the diet of nestling *G. fuliginosa*. Additionally, we removed all arthropods from litter and surface soil in two subquadrats of 0.125 m²; this food type predominates in the diet of *G. difficilis*. Arthropods were stored in vials and later dry-weighed in the laboratory. In 1979 the basic procedure was the same, except that we counted seeds of all plant species, both on the vegetation and in the litter/soil. In the latter two visits of 1979 we also sampled litter gastropods, a major dry season food for *G. difficilis*.

Caterpillars removed from the foliage comprised most of the arthropod portion of the diet of nestling *G. fuliginosa*. I sampled caterpillars at sites 1-3 and 5 at about 1-week intervals in 1978 on those plant species where adult finches concentrated their effort. Sampling consisted of searching each plant species separately for 25 min, 5 min at each of five different locations within a given study site. I searched leaves and stems at a constant rate, collecting all caterpillars encountered; these were later measured, counted, and dry-weighed. While foraging for caterpillars, *G. fuliginosa* spent most of its time searching the foliage of *Bursera graveolens* and *Rynchosia minima* throughout the breeding season. The rate at which I encountered caterpillars on these plants was correlated with capture rates by *G. fuliginosa* on the same day ($r = 0.86$, $P < 0.01$, $n = 13$, and $r = 0.68$, $P < 0.05$, $n = 9$, respectively).

I estimated breeding densities of finches in February of both years by using observed territory density at sites. Territories were mapped as convex polygons enclosing singing positions of all adult males present at sites. The size of each territory was based on approximately the same number of data points (20-25). For each territory, I computed the fraction

of its total area that overlapped a given site. These fractions were then summed within a site to yield territory density for both species separately.

I estimated finch abundance using two methods. In the first, mist nets were opened at each site on two successive days for 2.1 h each, and the total number of finches captured was recorded. Adult finches captured in the breeding season were uniquely color banded before release. Two 12-m nets were used per site in 1978 and during the first visit in 1979; three nets were used thereafter. In the second method, used only in the dry season, I estimated finch abundance by means of census walks, wherein the number of finches encountered within 10 m of the observer along a predetermined transect was counted. Results from the netting and census-walk procedures were positively correlated (*G. fuliginosa*, $r = 0.67$; *G. difficilis*, $r = 0.64$; $n = 12$; $P < 0.05$).

Active nests were marked nearby with flagging and visited every 2 or 3 days. Nest visits were terminated when nestlings were 8 days old, because by 9 days nest disturbance may induce premature fledging. Diets of nestlings were sampled in 1978 by extracting the "crop" contents using a modified eyedropper. Contents were stored in alcohol for later analysis.

I used a rain gauge situated near the coast (arid zone) to record precipitation throughout the study.

RESULTS AND DISCUSSION

Breeding phenology.—The first rains in 1978 fell on 15 January, and the first clutches of eggs appeared approximately 12 days later (Fig. 1). The breeding response of both finch species was similar at all sites. The normal interval between broods is about 30 days in Galápagos finches (Grant and Grant 1980). The two "waves" of clutch initiations about a month apart at most sites thus suggests two successive broods (Fig. 1). Breeding records for pairs of banded finches are consistent with this suggestion. The pattern for *G. fuliginosa* at sites 1 and 2 is somewhat different, resulting from the virtual destruction of all early clutches by Galá-

pagos Mockingbirds (*Nesomimus parvulus*) at these two sites and a probable subsequent earlier renesting.

No rain was recorded between 8 March and 1 April in 1978 (Fig. 1), and the May vegetation indicated that none fell in April. I cannot be sure that the last clutches recorded indicate the end of the breeding season, because the study ended on 1 April and efforts to locate new nests declined by about 50% after 24 March. Breeding was declining, however, and it probably ended close to this date. *Geospiza fuliginosa* had certainly ceased breeding by 24 March at site 5, and territories were no longer being defended. Additionally, fledglings were usually fed by parents for more than a month after leaving the nest, and those arising from eggs laid beyond 24 March would certainly have been dependent on their parents in May. Yet, of 18 banded adults of both species seen in May only two were feeding fledglings. The history of one (a *G. difficilis*) is unknown, but the second, a female *G. fuliginosa*, initiated her last known clutch on 23 March. No active nests were found in May.

Diet in both species was different in the breeding season than in the nonbreeding season (Table 2). The most conspicuous change occurred in *G. fuliginosa*, which took invertebrates, especially caterpillars, more frequently when breeding. Both caterpillars and seeds are fed to the young (Table 2). The change in *G. difficilis* was more subtle: of the invertebrate portion of the diet, large caterpillars and pupae taken from the litter and low vegetation replaced the nonbreeding diet of snails and hard-bodied arthropods. *Geospiza difficilis* also took seeds more frequently in the breeding season, although it was considerably less granivorous than *G. fuliginosa*.

Timing and duration of breeding, and the accompanying changes in diet, paralleled changes in food supply. Figure 1 documents changes in the rate at which foliage caterpillars were harvested by *G. fuliginosa* in the breeding season, revealing changes in the availability of caterpillars (see Methods). Rates were generally much higher in the breeding season than during and after May, with a peak in mid-March at all sites. Soft-bodied litter invertebrates, food for nestling *G. difficilis*, were also about twice as abundant in the breeding season as during other times. Caterpillar biomass was actually

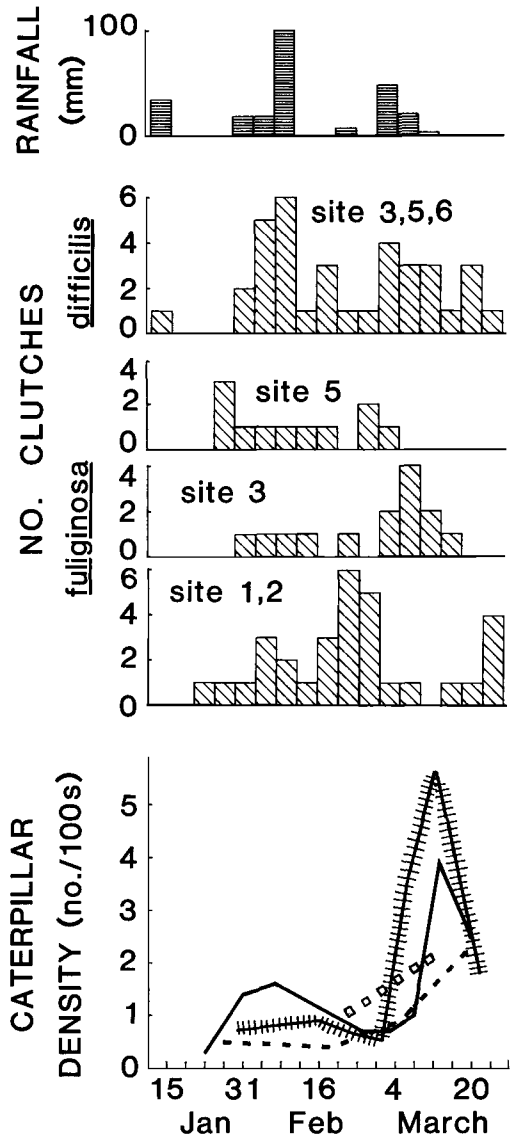


Fig. 1. Clutch initiations (1978) in relation to rainfall and caterpillar abundance. Initiation dates are the recorded or estimated days on which the first egg of a clutch was laid, in nests within sites and within the neighboring 20 m ($n = 91$ clutches total). Caterpillar density is measured as the observed success rate of *G. fuliginosa* searching for food in the foliage. Symbols are for sites 1 (—), 2 (###), 3 (---), and 5 (□).

TABLE 2. Seed and invertebrate proportions (in parentheses) in adult and nestling diets, averaged over sites. Adult values are the proportions of feeding time allocated to these two food types. Nestling values are calculated from the mean dry weights of food found in their crops. Breeding-season values are from February and March 1978; nonbreeding-season values are from August to November 1979.

Season	<i>G. fuliginosa</i>		<i>G. difficilis</i>	
	Adults	Nestlings	Adults	Nestlings
Breeding	0.56 (0.40)	0.52 (0.47)	0.30 (0.70)	0.37 (0.63)
Nonbreeding	0.90 (0.04)	—	0.08 (0.82)	—

higher in mid- to late March than is indicated by harvest rates (Fig. 1), because their mean size was also greater then. The pattern was different for seeds, where production rose following the rains, and abundance remained high well into the dry season (Schluter 1982b, unpubl. data). While seeds are thus important, especially to *G. fuliginosa*, breeding in both species was limited to the period of relatively high invertebrate abundance. It may be concluded that finch breeding is ultimately timed to coincide with the production of this food type (see also Lack 1950, Grant and Grant 1980, Boag 1981, Millington and Grant MS).

Nest predation increases in some species as the breeding season progresses, and it may therefore cause the termination of breeding (Lack 1966, Caccamise 1978, Ewald and Rohwer 1982). This hypothesis is unlikely for *Geospiza*, however: all 15 clutches in which eggs disappeared before hatching were initiated before 28 February. Only 5 of the remaining clutches were without young at 8 days of age, and 4 of these were initiated before 12 February. Thus, the breeding season ended when predation rates were lowest, indicating that some other factor besides predation was responsible (e.g. food supply).

Note that caterpillar abundance was still quite low when the first clutches appeared (Fig. 1). Also, the last clutches of the season coincided with fairly high caterpillar levels, much higher than when the first clutches were laid. This pattern makes sense if the "goal" is to ensure rapid growth of nestlings, whose energetic demands peak 2 or more weeks after the egg hatches (Lack 1968). For example, the steep decline in caterpillar density in March (Fig. 1) was probably a reliable predictor of low future caterpillar levels.

Territorial behavior.—In both years males defended nonoverlapping areas against conspecifics. Territories were approximately equal in

size within a site for each species. The density of territories of each species is shown in Fig. 2. Territory size is not shown, but, because territories were approximately contiguous within species, territory size for a given site is the inverse of density, where this is positive. Figure 2 shows that in each year the number of *G. fuliginosa* territories was similar across sites where the species bred. In contrast, territory density in *G. difficilis* varied dramatically across sites. This difference in the variability of territory density, and hence size, is the most conspicuous difference between the two species in social behavior in the breeding season.

Observations of banded birds indicate that adult finches concentrated their feeding effort within the bounds of the territory. If territory size in these finches is influenced by food availability, then size and availability should be positively associated. Food supply data for *G. difficilis* (Table 3) support this: territory density at a site was directly correlated with the density of "preferred" invertebrates in the litter (1978, $r = 0.96$, $n = 5$, $P = 0.01$; 1979, $r = 0.87$, $n = 6$, $P < 0.05$). Preferred invertebrates are those whose proportional representation in the nestling diet exceeded their proportional availability in litter samples (cf. Schluter 1982b). In contrast, territory size in *G. fuliginosa* did not vary greatly despite variability in food supply. Small seed density varied at least five-fold across the five sites where *G. fuliginosa* bred (Table 3), as did caterpillar density. This latter variable was estimated by means of encounter rates (see also Fig. 2); when scaled by the abundance of the respective plant types, the range of variation in caterpillar density was greater. Instead, territory density in *G. fuliginosa* appeared to be an "all-or-none" response to varying food levels; even though foliage caterpillars were present at all sites, *G. fuliginosa* bred only where small seeds were abundant, at sites 1–5 (Fig. 2; Schluter 1982b). This dependence

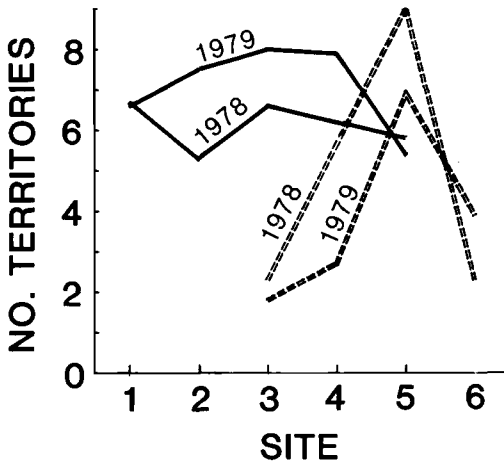


Fig. 2. Territory density of *G. fuliginosa* (solid line) and *G. difficilis* (dashed line) in 1978 and 1979. Site 1 is in the low-elevation arid zone, and site 6 is in the highland forest.

on small seeds was further illustrated outside of study sites: in several places the species was found breeding in the highland forest but only next to open areas of *Paspalum* seed production.

It could be argued that seed and caterpillar densities complement each other, rendering total food supplies for *G. fuliginosa* more equal across sites. This possibility is unlikely: summing the supplies of seeds and caterpillars within sites (Table 3) decreases the variability among sites only slightly. Another possibility is that territory size is adjusted to average food

levels in sites over many years (Seastedt and Maclean 1979) or to food conditions at the very outset of breeding, if food abundance is approximately equal over sites. I cannot test this for caterpillar abundance, but seed abundance does not support this explanation, because it is consistently variable among sites, being greatest at some higher elevations (Table 3; Schluter 1982b).

Hence, either food does not determine variation in territory size, or it must be assumed that the benefits of defending a given area cannot be summarized merely by the amount of food it contains. To test this latter idea, I examined the way in which food density is translated into feeding efficiency and diet in the two species. Distributional evidence suggests that *G. fuliginosa* is more dependent on seeds in the breeding season than is *G. difficilis* (see above). Additionally, in not one of 51 *G. fuliginosa* nests sampled did seeds fall below 25% of the nestling diet. In contrast, the seed fraction was frequently lower than 25% in the crops of nestling *G. difficilis*, and at site 6 seeds were virtually absent from the nestling diet. Differences between *G. fuliginosa* and *G. difficilis* in territorial behavior might therefore be linked to differences in the benefits derived from a given supply of seeds and invertebrates, respectively.

Figure 3 contrasts seeds and invertebrates in terms of the effects of food abundance on feeding rates. *Paspalum galapageia* was the most important seed in the diet of nestling *G. fuliginosa* (70–90% of the seed portion by weight at sites 2–5, 50% at site 1). Figure 3a illustrates that the

TABLE 3. Food supply in the wet season. Estimates of seeds in 1979 and invertebrates in both years were made in mid-February. Seed density in 1978, determined in March, includes only *Paspalum*. Caterpillar density is the mean harvest rate by the author over the period 24 February to 31 March 1978, in the most important foliage types (within the range of sizes found in the nestling diet). Caterpillars were present but not enumerated at site 6. Variation among sites was significant for all estimates (Kruskall-Wallis, $P < 0.05$).

Site	Density of small seeds (mg/m ²)		Density of foliage caterpillars (mg/25 min)		Density of preferred litter invertebrates (mg/m ²)	
	1978	1979	<i>Bursersa</i> ^a	<i>Rynchosia</i>	1978	1979
1	81.7	426.6	523.5	40.9	3.5	3.5
2	498.2	254.8	763.4	83.8	3.9	4.5
3	1,056.3	745.7	94.9	26.1	17.6	10.2
4	—	623.7	—	—	—	10.9
5	2,235.9	1,284.1	79.2	143.4	88.1	35.8
6	0.0	44.9	—	—	45.5	6.3

^a *Zanthoxylum* at site 5.

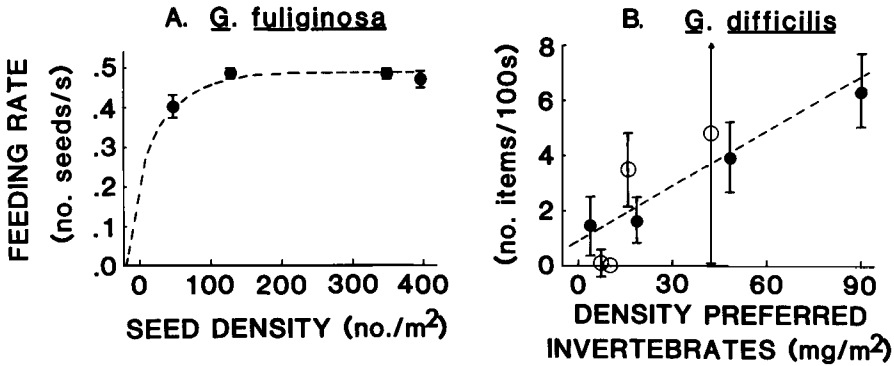


Fig. 3. Observed rates of foraging as a function of food abundance. (A) *G. fuliginosa* feeding on *Paspalum*. Data are from sites 2-5 in August 1979. The curve was fitted by eye to pass through the origin. (B) *G. difficilis* feeding on litter invertebrates in the breeding seasons of 1978 (●) and 1979 (○). Means are based on at least 1,000 s of observations from sites. Vertical bars denote standard errors. The regression line is based on mean rates ($r = 0.87$, $n = 8$, $P < 0.01$).

harvesting efficiency of this food type was independent of seed abundance over recorded densities. Data are from the dry season, but wet-season abundance of this food type was at least as great (Table 3), and production was higher. Abundance has little influence on rate, because the seed is produced in dense rows on tall conspicuous racemes. The proportion of feeding time spent searching is thus low over most densities, producing the classic type 2 functional response curve (Holling 1966).

This situation contrasts with that of the major food of breeding *G. difficilis*. Litter invertebrates are less conspicuous than seeds and may be more evenly dispersed. The proportion of feeding time spent searching for items is correspondingly larger and, hence, is sensitive to the abundance of those items. Figure 3b indicates that foraging rates were an increasing function of invertebrate abundance over the entire range of densities available. If territory size is adjusted to food levels, then variation in territory size in *G. difficilis* may compensate for elevational variation in feeding rates. For *G. fuliginosa*, where *Paspalum* seeds are an important territory resource, "perceived" food density (i.e. feeding rate) is largely independent of seed abundance, beyond some critical level, and this may help explain constant territory size.

Gregarious and solitary behavior.—Changes in social organization accompanied the termination of breeding in both finch species. Adult *G. fuliginosa* no longer defended territories in May, and by August most had joined juvenile birds

in flocks. Flocks varied in size, being largest in the open highlands (up to 200 birds), where the overall density of food and individuals was greatest (sites 4 and 5; Schluter 1982b).

Geospiza difficilis behaved differently. Territories were not actively defended in the dry season, but banded males were repeatedly sighted from May to December on or near their previous territories. They apparently foraged more widely in the dry season than in the breeding season, but not in flocks. The elevational distribution of males was therefore similar in the wet and dry seasons (e.g. Fig. 2 and Fig. 4). The distribution of adult *G. difficilis* in brown (female) plumage, however, was shifted slightly downhill from that of the males (Fig. 4). Juveniles, recognized by their brown plumage and pale beaks, were most common at the lower sites. Unlike males, females and juveniles were often found in small flocks of 2-5 individuals, though solitary individuals were also frequent.

The pattern of altitudinal separation of age and sex classes in *G. difficilis* probably resulted from avoidance, because overt aggression was generally uncommon. The preferred foods of *G. difficilis* in the dry season were most abundant at sites 5 and 6, and this region was used almost exclusively by adult males. Food abundance was considerably lower at those sites where juveniles were most abundant (Fig. 4), and, perhaps as a consequence, few juvenile *G. difficilis* survived between May and August 1979 (Schluter 1982b).

Temporal dispersion of foods is thought to have a major influence on the relative benefits of solitary and gregarious behavior (Crook 1965, Brown and Orians 1970, Newton 1972, Wiens 1976, Caraco 1981, Pulliam and Millikan 1982). Flocking should generally be favored when resource unpredictability is high for two main reasons. Individual control of resources is more costly and yields fewer benefits when unpredictability is high. Flocking increases the individual's chances of locating profitable food patches and may improve the efficiency of patch exploitation.

Thus, food abundance for *G. fuliginosa* is expected to be more variable in time than for *G. difficilis*, if food dispersion is responsible for their different behaviors. *Geospiza fuliginosa* is almost entirely granivorous in the dry season (Table 2), *Paspalum galapageia* and *Rynchosia minima* being the predominant food items in the diet at most sites. Figure 5 shows patterns of variation in the feeding rate of *G. fuliginosa* on *Paspalum* grass seeds at four sites, reflecting changes in seed abundance. Rates were indeed variable over the course of the dry season, ranging from a rate of near zero to the maximum possible rate (Fig. 3a). Changes could be sudden: at site 4 in October–November, feeding rates jumped four fold in as little as two days, a result of new seed production. Recorded rates were either very low or very high, an effect of rates being sensitive to seed abundance over only a narrow range of food densities (Fig. 3a). Some spatial variation in feeding rates was also recorded (Fig. 5), but in general rates varied synchronously across sites. Foraging rates on *Rynchosia minima* were also apparently temporally variable in the dry season, but the sample size of observations is small.

Geospiza difficilis fed mainly on litter invertebrates in the dry season (Table 2), especially in the highlands. In contrast with feeding rates on seeds, there was no evidence that feeding rates on invertebrate prey varied greatly over the dry season. While my sample size is smaller for *G. difficilis* than for *G. fuliginosa* feeding on grass seeds, the only detectable variation in foraging rates in *G. difficilis* within sites was a slight decline between August and November. Between-site differences in feeding rates were consistent over the year and were always much greater than within-site temporal changes. As in the breeding season, feeding rates of *G. difficilis* were correlated with litter invertebrate

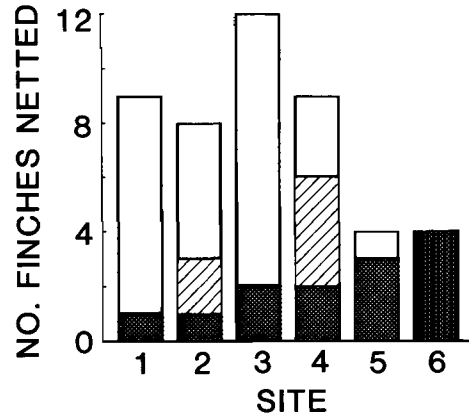


Fig. 4. Density of *G. difficilis* at sites in May 1979. Totals are the number of finches captured in nets. Categories are adult males (shaded portion), adult birds in female plumage (hatched), and juveniles (open).

densities ($r = 0.81$, $n = 12$, $P < 0.01$). These data support the view that the degree of temporal variability in food abundance has influenced the degree of gregariousness in *G. fuliginosa* and *G. difficilis* in the dry season.

A second difference between invertebrate and seed resources may also have contributed to interspecific differences in nonbreeding social organization. The hyperbolic functional response of *G. fuliginosa* to *Paspalum* reduces the potential benefits of solitary or aggressive behavior at many seed densities (i.e. above 100 seeds/m²; Fig. 3a). Any increase in food supply resulting from exclusive access at these densities would yield a trivial net increase in foraging rate (see also Gill and Wolf 1975). In contrast, the functional response of *G. difficilis* to invertebrates is linear over most densities, and hence any increase in food density resulting from control over its depletion would insure a greater feeding rate.

A third important difference between insects and seeds may be in their renewal properties after depletion. Litter invertebrates may be locally depressed in abundance during feeding (Charnov et al. 1976) and return to near-previous levels after feeding stops. Local seed replacement probably takes much longer, particularly in the dry season when production is low. Exclusive access to foods renewed quickly may pay off immediately (Gill and Wolf 1975, Davies and Houston 1981), but control of more

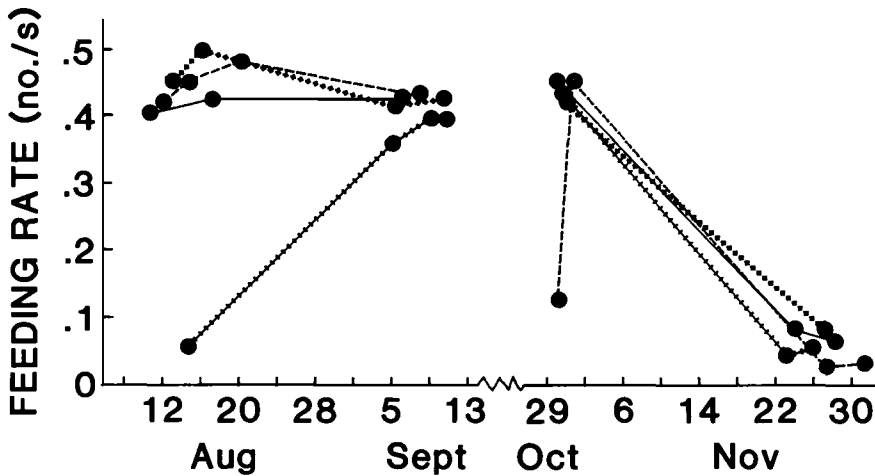


Fig. 5. Temporal fluctuations in mean feeding rate of *G. fuliginosa* on *Paspalum* seeds in the dry season of 1979. Symbols are for sites 2 (++++), 3 (++), 4 (---), and 5 (-). Rates were significantly different across October–November at all sites and across August–September at site 2 (ANOVA, $P < 0.05$).

slowly renewed resources is of benefit only in the longer term (Pulliam and Millikan 1982). In the case of seeds, such long-term benefits may be sufficiently uncertain as to favor a behavioral strategy other than resource control.

Finally, risk of predation may also favor gregarious behavior through improved predator surveillance and decreased attack-success rates (cf. Morse 1977, Caraco et al. 1980). This is unlikely on Pinta, because predation appears to be uncommon. The Galápagos Hawk (*Buteo galapagoensis*) is the only diurnal predator. Though common, it has never been observed to attack a *G. fuliginosa* or a *G. difficilis* in 2 yr of study.

CONCLUSION

That breeding and social behaviors are an adaptive consequence of feeding and food supply has been suggested for a variety of avian systems (Crook 1965, Lack 1968, Brown and Orrians 1970, Newton 1972, Wiens and Johnston 1977). The classic comparison is between insectivorous and granivorous birds. Insectivores are frequently more solitary and/or territorial than granivores, while granivores are often more gregarious and mobile, particularly in the breeding season. Quantitative analysis of some characteristics of the foods of *G. fuliginosa*, a granivore, and *G. difficilis*, an "insectivore," suggest that territorial behavior in the breeding season, and the degree of gregariousness

in the nonbreeding season, may indeed be determined by contrasting properties of invertebrate and seed resources. The results also suggest that the timing and duration of breeding and nonbreeding seasons is determined by seasonal variation in food supply.

Questions remain regarding the relative importance of different factors in determining behaviors and the details of the mechanisms involved. For example, Fig. 1 suggests that arthropod supply determines the timing of breeding. Arthropod supply *per se*, however, is not a sufficient proximate explanation for general timing, because caterpillar abundance was higher near the termination of egg laying than at its beginning. Rainfall may be used as a cue: the first rainfall is certainly a reliable predictor of high future food levels (see also Marchant 1959, Immelmann 1971, Stiles 1973, Kemp 1976, Maclean 1976). But rainfall is probably a poor predictor of when food supply will decline. The finches may judge whether food supply is increasing or decreasing and weigh immediate food levels against this factor in deciding whether or not to continue breeding. Little is known in general about the proximate factors determining cessation of breeding in such environments, and more detailed study is needed.

Note that many of the behaviors of these finches vary with local conditions. For example, *G. fuliginosa* on Pinta and other islands is

occasionally solitary in the dry season when it consumes seeds available in low densities. Individuals may also defend territories around sources of nectar, when available. Such flexibility in behavior might allow experimental manipulation of food supply to test precisely the influence of particular resource attributes on alternative behaviors (e.g. Ewald and Rowher 1982). Possible manipulations include reduction of seed supplies to levels below 100/m² to examine the effects of changes in density and functional response, artificial renewal of seed resources to test the importance of renewal rates, and manipulation of resource dispersion patterns.

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