Feeding ecology and territoriality of the Cactus Finch *Geospiza scandens* on Isla Daphne Major, Galápagos

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Summary. In this study we investigated the relationship between food availability, feeding ecology and territoriality in a population of Cactus Finches, *Geospiza scandens*, on Isla Daphne Major, Galápagos, between 1979 and 1981.

We monitored the phenologies of the principal food types on the island and related them to changes in the feeding ecology of *G. scandens*. Feeding patterns closely tracked the availability of resources, with a similar pattern in each of the three years. Birds relied heavily on *Opuntia* fruits in the dry season.

G. scandens defends year-round territories based on *Opuntia*. Variation in *Opuntia* phenologies between individual territories and between years was documented in order to provide a measure of territory quality over the three years. A correlation was demonstrated between the area of cactus within a territory and mating success of the owner. We suggest that territory quality also affects the survival of the owners during periods of food scarcity and that the mating and survival advantage of a high-quality territory occur at different times and to different degrees in different years. Hence the importance of territorial quality can only be judged over a long-term period in these long lived and sedentary birds.

Introduction

Janzen (1980) commented, "There is no general, all-purpose method of description of resources for small, tropical terrestrial birds. To understand food resources for the birds in a habitat or for a particular species of bird, one has to determine what the bird(s) feed on and hand-tailor a census technique that collects data in a manner that correlates well with the actual resources taken by the bird." This has proved difficult because most birds feed on a wide variety of seasonally available foods (e.g. Karr 1976). However, Darwin's finches on Isla Daphne Major in the Galápagos provide an ideal subject for a detailed study of the interaction between birds and their food supply, because 1) the environment is simple, 2) the seasonally varying food supply can be relatively easily documented, and 3) the feeding behavior of the birds is readily observed.

Previous studies of the feeding characteristics of finches on Galapagos have been made during relatively short periods of time (Abbott et al. 1977; Smith et al. 1978; Grant

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and Grant 1980; Schluter 1982). Boag (1981) studied the Daphne Major finch community from 1976 to 1978 but did not quantify variations in food supply within most seasons. The purpose of the present study is to establish links between food supply, feeding behavior and territoriality in the Cactus Finch *Geospiza scandens* on Isla Daphne Major. The study was conducted for three years, 1979 to 1981, because, as is becoming increasingly appreciated, long-term studies (> one year) are necessary to understand the selective forces affecting territoriality (e.g. see MacLean and Seastedt 1979).

Methods

The physical characteristics of Daphne Major have been described elsewhere (Grant et al. 1975; Grant and Grant 1980; Boag 1981). S.J.M. and his colleagues visited this island from early January until late June in each year from 1979 to 1981. Additional visits were made in late September 1979 (two weeks) and late July 1980 (one week). Plant phenology and feeding ecology were recorded at each visit and estimates of territory size were made in 1979 and 1980.

Plant phenology

Guided by the observations of Boag (1981), we selected the four most important categories of food plants for detailed study.

a) Opuntia echios. Weekly counts of flowers and fruits were made on the same ten plants on one area of the island (the plateau; see map in Grant et al. 1975). To determine the length of time fruits remain on the plant we checked one pad on each of four bushes every two days from mid-January to early May 1980, and recorded the state of the flowers and fruits at those times. Twenty-four fruits were thus followed from flowering onwards. For each flower we noted whether or not the stigma had been snipped or otherwise damaged by a cactus finch, as described by Grant and Grant (1981).

b) Bursera malacophylla. Ten selected trees on the plateau were monitored approximately every week. On each occasion we recorded the state of leaves and flowers and the number of fruits. To quantify the availability of caterpillars on the trees we collected (with a pair of tweezers) as many caterpillars as possible (0–64) in a period of twenty minutes.

Table 1. Relationship between number of *Opuntia* flowers and percent with stigmas snipped, 1980–1981

	1981													
	Jan			Feb		March			Apr		May			Jun
Date	9	18	27	18	28	11	21	31	10	21	1	10	18	18
Buds	827	622	393	112	40	17	24	39	37	8	3	2	0	0
Total # flowers	167	106	77	24	9	5	1	0	8	5	1	0	0	0
% Flowers snipped	41	54	51	54	67	20	100	—	0	0	100	—	—	—

	1980									
	Jan			Feb			March			Apr
Date	1	16	25	4	14	28	5	16	21	16
Buds	534	291	259	140	110	70	43	40	28	0
Total # flowers	103	94	66	30	35	16	12	5	7	1
% Flowers snipped	21	23	53	43	60	38	25	60	86	100

c) Portulaca howelli. Variations in the number of flowers were quantified by counting the blooms twice-weekly on 20 plants in 1979 and daily on 50 different plants on the outer slope in 1980–1981. Flower buds are often infested by small moth caterpillars ("budworms") which destroy the buds and prevent flowering. The abundance of budworms was quantified using the same method as for *Bursera* caterpillars (collecting as many as possible in 20 min), approximately every two days during the wet season, January-May.

d) Herbs. This group of plants, mostly annuals, shows a marked response to rain. Counts of flowers and fruits were made approximately weekly on each of five to ten plants of selected species (e.g. *Tribulus cistoides, Heliotropium angiospermum, Boerhaavia erecta*). The time of appearance of other annual species (e.g. *Amaranthus sclerantoides, Cenchrus platyacanthus*) was noted.

Feeding ecology

To quantify the feeding characteristics of the birds, two observers, 50 m apart, followed a set route of approximately 1 km and recorded each bird observed feeding and the item it consumed. The birds are very tame, and most items were readily identified as they were eaten. Sometimes it was difficult to distinguish between different kinds of small seeds on the ground, and these were categorized as one item. The route was designed to cover a representative portion of the island in terms of available food types. In mid-1979, 85% of the birds had been individually color-banded, and by the end of the study the proportion had risen to 96%. This figure was obtained from estimating the percentage of unbanded birds during regular censuses. Thus it was possible to minimize recording the same bird twice. An attempt was made to obtain 25 observations each time. These "feeding walks" were carried out approximately every one to two weeks. The tameness of the birds and the openness of the terrain meant that specific feeding activities were unlikely to have been underrecorded to a significant extent.

Territories

Territories were mapped, with boundaries delineated by song, displays and chases. The area of each territory was not measured, but to obtain a comparative measure of territory quality we calculated the area of cactus in each of 20 territories by measuring axes of the larger clumps with a tape measure, and then by estimating the area of each smaller clump as a proportion of the larger ones. Six territories were chosen for intensive monitoring and all cactus buds, flowers and fruits (fertile and infertile) were counted in May and September 1979 and January and April, 1980. Flowers were also counted in the 1981 wet season. The proportion of flowers with the stigmas snipped was recorded on each count (Table 1). Finches often snip or otherwise damage the stigmas of *Opuntia* flowers or buds upon which they feed, probably to facilitate pollen and nectar removal (Grant and Grant 1981). The number of flowers and the proportion "snipped" were recorded for a number of other territories.

Rainfall

Rainfall was recorded using a plastic wedge rain gauge.

Results

Rainfall

The pattern of rainfall is shown in Fig. 1. Similar patterns occurred in 1979 and 1980, with bouts of rain in early February and mid-April, but in 1981 there was a single, high peak in late March. The annual totals for 1979–1981 were 68.6, 53.5 and 79.5 mm respectively.

Plant phenology

a) Opuntia echios. Figure 2 summarises cactus phenology. Buds first appear in September, and the peak flowering period probably occurs from December to January. A rapid decline occurs through February and few flowers are left by March. Later rainfall does not appear to stimulate further flowering (e.g. the April rain in 1979 and 1980). Individual flowers last only 2–3 days. Fruit numbers peak in February to March, coincident with the flowering decline. Thereafter numbers fall, as fruits drop off the pads, until after the next flowering in September. Relatively few old
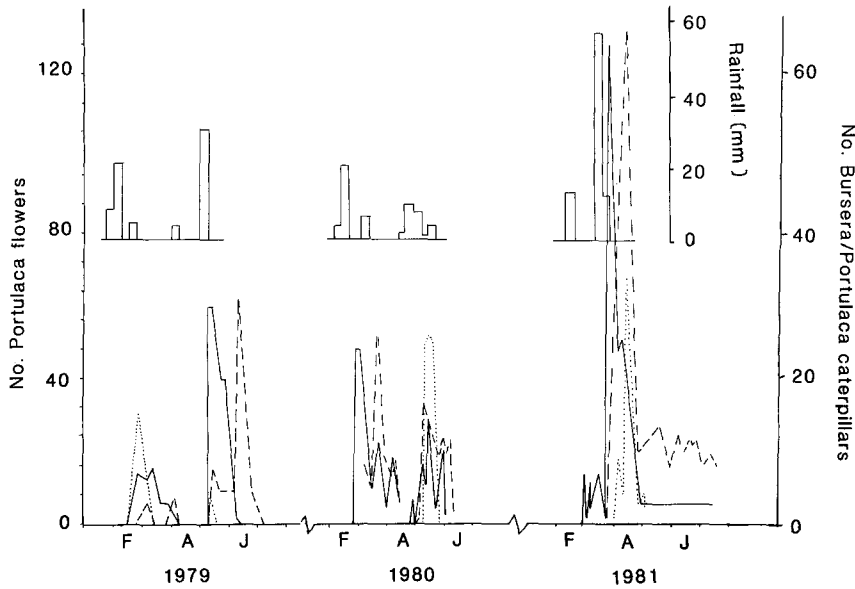
Fig. 1. Caterpillar response and *Portulaca* flower response to rainfall, 1979–1981 ⫿ rainfall; — — — *Portulaca* flowers; —— *Portulaca* budworms; ..... *Bursera* caterpillars
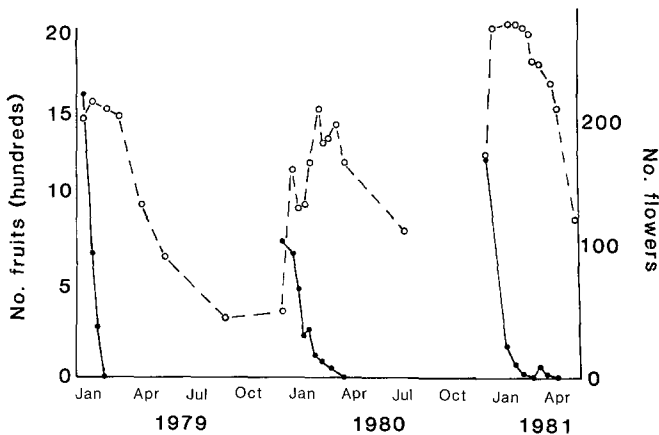
Fig. 2. Numbers of flowers and fruits on ten *Opuntia* bushes, 1979–1981 —— flowers; — — — fruits

fruits are present on the bushes at this time. It seems likely that the timing of flowering is an evolutionary adjustment to climate that results in most fruits being formed in the wet season. This is the only time that the necessary moisture is available to develop the fleshy pulp around the seeds (see Wiggins and Porter 1971).

Of the 24 fruits followed from flowering onwards, 16 fell before early May. The stigmas of all 16 had been snipped previously. These fruits stayed on the pads between 2 and 57 days ($\bar{x}$ 24.1 $\pm$ SD 20.0). They were shrivelled and presumably not fertilised. Those that were opened contained no seeds ($N=6$). The other eight fruits remained on the bush at least until early May and had thus been present for between 82 and 110 days. Six of these previously had undamaged stigmas. The fruits were fully developed and presumably contained seeds. It is possible that the two "snipped" fruits had been fertilised before snipping. Thus it appears that 1) stigma snipping results in no, or reduced, fertilisation as shown by Grant and Grant (1981) and 2) infertile fruits fall much earlier than fertilised ones. Grant and Grant (1981) showed that on Isla Santa Cruz some fruits remained on pads for up to 475 days. Few of the

fruits on Daphne appear to remain on bushes for this length of time (see p. 11 and Fig. 5).

The proportion of flowers on the ten sample bushes that had their stigmas snipped varied. However, the proportion of fruits on bushes that were judged fertile remained fairly constant between March 1979 and June 1981 at between 61% and 88%.

b) Bursera malacophylla. This tree species is patchily distributed over the island, being concentrated mainly on the plateau and southern inner slope of the main crater. The trees are leafless in the dry season, but respond rapidly to rain, coming into leaf within five days, producing flowers within the next five to ten days and 1 to 2 months later producing mature fruits. These fruits are highly edible to finches, but during the study period relatively few were produced and birds did not feed on them to a significant extent.

Bursera trees are host to caterpillars which feed on the leaves. This is an important food source for the finches. Caterpillars were observed almost as soon as the trees came into leaf (Fig. 1).

c) Portulaca howelli. This is a low, fleshy perennial (Wiggins and Porter 1971) that forms most of the ground cover over much of the island. Like *Bursera* it remains leafless during the dry season, but rapidly comes into leaf during the onset of rain. Budworm numbers rise rapidly to a peak and then decline rapidly (Fig. 1). Coincident with this decline is an equally rapid rise in the number of flowers from the later-formed buds. In the absence of further rain all larvae and nearly all flowers have disappeared by two months after initial rainfall. In four out of five bouts of rainfall the peak flowering occurred approximately five weeks after the rainfall. It does not take this long for the flowers to develop because the buds are formed in only a few days, and a few of these develop into flowers within a week. There is a graded response by both plants and larvae to rainfall, varying apparently in parallel (Fig. 1). This explains the association between budworm numbers and flower numbers. In May 1980, the low larval infestation meant

Table 2. Pattern of *Portulaca* flowering inside and outside two 2 m × 1 m finch-proof exclosures, 1982

	17 Mar	21 Mar	26 Mar	31 Mar	5 Apr	11 Apr
No. flowers in exclosures	5	10	13	20	2	20
No. flowers in the same area outside exclosures	1	11	4	15	2	23

that many of the early-flowering buds escaped predation, resulting in the earlier flowering peak, coincident with the budworm peak (Fig. 1).

To determine if the decline in budworm numbers is brought about by the foraging pressure of finches, flowering periods were compared between plants inside and outside two 2 m × 1 m finch-proof exclosures in 1982. The patterns were very similar (Table 2), suggesting a negligible role for finch predation (data kindly supplied by L. Gibbs).

d) Herbs. Several annual species are important to finches as food sources as indexed by the relative amount of time spent feeding on them. The principal ones, in decreasing order of importance are, *Boerhaavia erecta, Amarananthus sclerantoides, Cenchrus platyacanthus, Acalypha parvula,* and *Sida salviifolia.* Buds, pollen, fruits, and various invertebrates are all occasionally taken from the living plants, and seeds of several species are important in the dry season when all plants are dead. There is a characteristic sequence of appearance of some of these plants. For example in 1981, *Amaranthus* appeared within 3 to 4 days of the rain, *Boerhaavia* in about two weeks and *Cenchrus* in about a month. Plant production, and production of seeds, varied among years in relation to rainfall.

Feeding ecology

With the onset of *Opuntia* flowering in September, adult finches feed almost exclusively on this plant, predominantly on the flowers from which they gain nectar and pollen (Grant and Grant 1981), but also on the fallen fruits. They continue to feed on *Opuntia* flowers (if present) and, to a lesser extent the fruits, during periods of rainfall from January onwards. However, rain results in the production of a wide array of food items not present in the dry season. *Amaranthus* shoots appear first and are readily eaten by the finches which then increasingly exploit the rising caterpillar populations on *Bursera* and *Portulaca*. When these decline the birds switch to *Boerhaavia* buds and fruits, and Portulaca flowers, the latter now abundant with the decline of the budworms. Later the unripe seeds of *Cenchrus,* if present, are exploited and the small seeds of other annuals are taken off the plants and from the ground (e.g. *Amaranthus, Acalypha, Sida*). As the number and variety of potential food items declines at the end of the wet season, the finches become more dependent on *Opuntia* fruits. Juvenile finches up to several months old cannot crack *Opuntia* seeds however, and rely almost exclusively on small seeds or *Opuntia* flowers and/or *Portulaca* flowers, if present. Thus in September 1979 birds of the year were noted feeding almost entirely on the small seeds of annuals.

This pattern of resource switching appears to be a consistent pattern, since it was observed in all three years. Tracking of the available resources is indicated by the high correlation between first the proportion of feeding observations on budworms and the estimated number of budworms
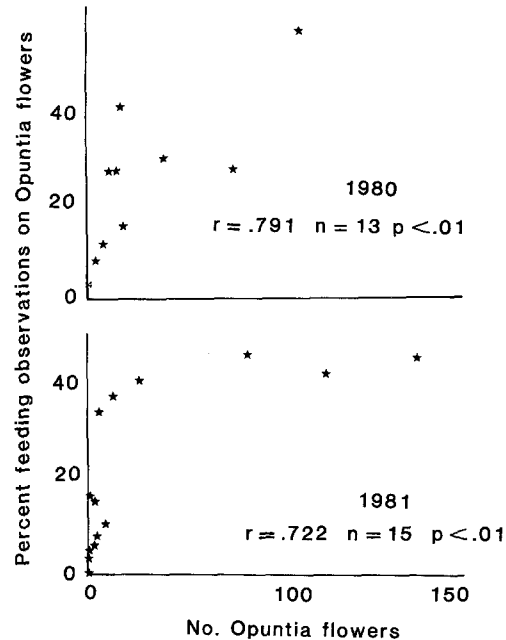
Fig. 3. Exploitation patterns of *Opuntia* flowers by *G. scandens* in 1980 and 1981

available (all years combined; $r = 0.62$, $N = 27$, $P = <0.01$), and second the proportion of feeding on *Opuntia* flowers and their abundance (1979 too few data; 1980 $r = 0.79$, $N = 13$, $P = <0.01$; 1981 $r = 0.72$, $N = 15$, $P < 0.01$).

Different patterns of *Opuntia* exploitation were observed in the two years as shown in Fig. 3. This figure should be interpreted from right to left to indicate the decline in abundance of *Opuntia* flowers as the season progresses. Thus in 1980 there was a regular decline in flower feeding with a decrease in flower abundance (Fig. 3). In 1981 there was a typical Type II feeding response (Holling 1966). In the latter year birds fed disproportionately on flowers at high densities (with an apparent asymptote at about 50% of feeding observations) and then suddenly switched at low flower densities to other food types. The difference in exploitation between years results from a difference in the timing of rainfall. In 1981 birds fed on *Opuntia* flowers, even when flowers were scarce, until the rain fell in late March when they all switched to caterpillars and annuals. In 1980 the rain fell while *Opuntia* flowers were still relatively abundant and so birds fed both on these flowers and other items available as a result of the rain, and consequently the switch was not so abrupt.

In contrast to these results, the proportion of feeding on *Opuntia* fruits was negatively correlated with the abundance of budworms (all years combined $r = -0.41$, $N = 28$, $P < 0.05$) and of *Opuntia* flowers (1980–1981 $r = -0.50$, $N = 22$, $P < 0.05$). The fact that these are significant despite the potentially confounding effects of the difference in timing of the rains and of the *Opuntia* flowering season indicates
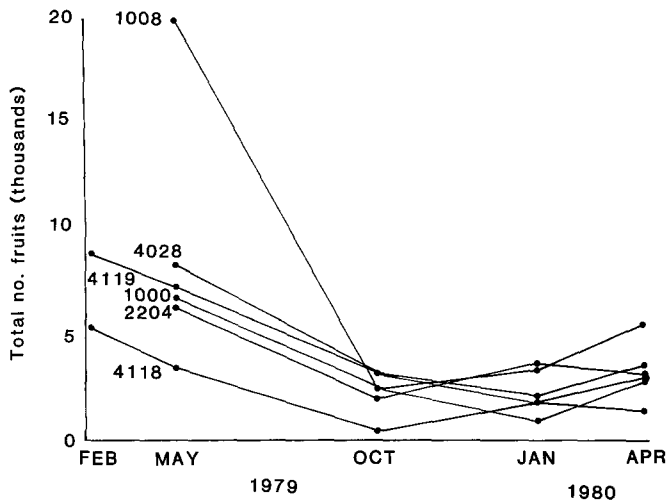
Fig. 4. Total numbers of *Opuntia* fruits on the bush in six territories, 1979–1980
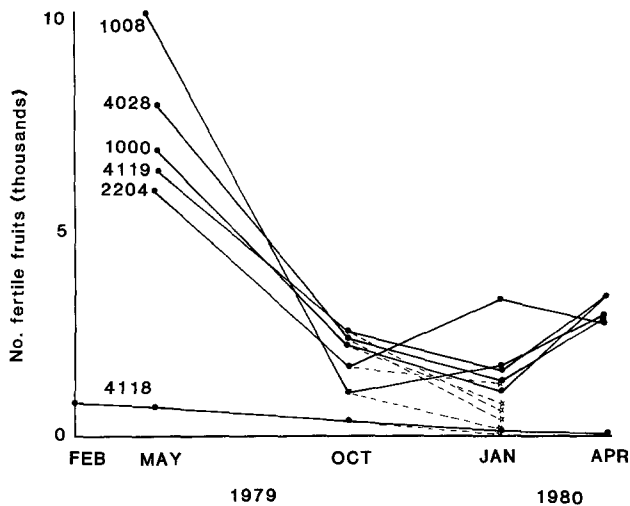

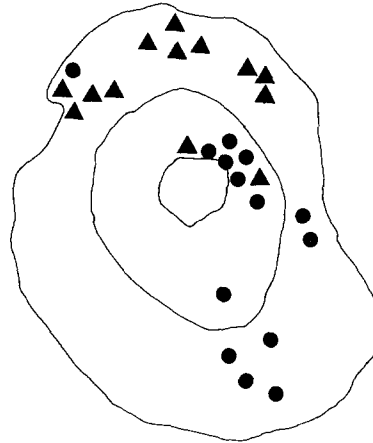Fig. 5. Number of fertile fruits on the bush in six territories, 1979–1980

Fig. 6. Distribution of early-flowering and late-flowering territories on Daphne in 1980. Territories marked as early or late if >10% decrease or increase in total flower number between 21 January and 2 February 1980. ● = early; ▲ = late

that the proportion of feeding on *Opuntia* fruits decreases with increasing availability of alternative food types. Thus cactus finches rely almost exclusively on *Opuntia* fruits only when other food types are unavailable.

Variation in Opuntia phenology

a) Between territories. *Opuntia* fruit numbers peaked at the end of the flowering season and then declined through the dry season in the six monitored territories (Fig. 4) and on the ten sample bushes. In both sets of data the lowest number was reached sometime during the next flowering season, before the majority of flowers had formed new fruits (Fig. 5). In 1980 the low point was reached before January in three territories and between January and April in the other three. The former were on the northern outer slope and the latter were on the eastern slope and crater and form part of a clear geographical division between 'early' and 'late' flowering territories (see Fig. 6 and legend). The division accounts for the observation that in late September

1979, at the very beginning of the flowering season, the only bushes in flower were situated on the southern inner slope and plateau. Furthermore, the ten sample bushes on the plateau had apparently produced maximum flower numbers before S.J.M.'s arrival in early January 1980.

A large number of fruits were of no value to *G. scandens* because they were infertile and hence contained no, or few, seeds. Cactus finches feed to a large extent on *Opuntia* seeds but only occasionally on the aril and then probably to obtain moisture. Figure 5 shows the number of fertile fruits per territory for the six territories. The pattern is generally consistent among territories except that in territory 4118 fertile fruit numbers started at a low number and continued to decrease throughout the study period. Figure 5 also shows the production of new fruits between September and January. The old fruits at this time are distinguishable from the new fruits by being much larger and yellower. The "earlier-flowering" territories (1000, 4028 and 4199) show a greater fruit production by January than the late-flowering ones.

Comparison of Figs. 4 and 5 indicates considerable variation among territories in the proportion of fruits that are fertile. There are at least two reasons for this. Some of the cactus clumps are rather large as a result of bushes or individual pads falling and propagating vegetatively. Often these clumps are at the bottom of slopes and may consist of very few individual plants. *Opuntia* on Daphne has been shown to be an obligate outcrosser (Grant and Grant 1981). Many of these flowers may not receive pollen from a genetically different plant, and so produce infertile fruits. This is especially likely to be true if a bird's territory consists of one or two of these clumps. It was noticed that many of the large clumps contained a high proportion of infertile fruits (e.g. territory 1008).

A second reason is the practice of stigma snipping. In late September 1979 all but one of 25 *Opuntia* flowers in several territories had their stigmas snipped. However, in another territory 14 out of a further 15 flowers had stigmas intact, indicating substantial individual variation among birds in this behavior, assuming that the territory owners are responsible for the amount of snipping within their terri-

tory. Table 3 provides further evidence that there is considerable variation among territories in the amount of stigma-snipping. The consequence of the effects of reduced outcrossing and stigma-snipping can be examined by a comparison of two territories. The proportion of stigma-snipping in territory 1008 was extremely low, yet it contained a high proportion of infertile fruits. The territory had two large clumps at the bottom of the crater and there was probably little outcrossing by the cactus. Moreover, large clumps on the crater floor typically contain a high percentage of infertile fruits (*pers obs*). The area of cactus contained in crater-floor territories is much greater than the mean area of territories on the inner and outer slopes (206.5 ± 23.7 m^2 *SE* versus 113.0 ± 8.6 m^2 *SE*, $t_{24} = 3.48$, $P < 0.01$). This suggests that birds in these territories need to compensate for high cactus fruit infertility by defending larger territories. Territory 4118 had a consistently high incidence of stigma-snipping. This territory had by far the lowest proportion of fertile fruits, yet the temporal pattern of total fruit production between September 1979 and January 1980 was similar to the other territories (Fig. 4). Furthermore it did not contain a single large cactus clump but rather dispersed bushes. Thus stigma-snipping is likely to be responsible for the high level of infertile fruits since fruit inviability is unlikely in this territory.

b) Between years

There was considerable variation between years in both the amount and pattern of flower production. For seven monitored territories the average maximum flower number in 1980 was twice that of 1981 (169.9 ± 19.5 *SE* versus 82.7 ± 7.7 *SE;* Wilcoxon matched pairs sign rank test $P < 0.05$). The 1980 figure is likely to be conservative since only occasional counts were made in that year whereas flowers were counted regularly in 1981.

There was also variation in the length of the flowering period. In 1979 there were virtually no flowers after mid-February; in 1980 flowers were present through to April and in 1981 flowering was almost at an end in mid-March. To give a quantitative example, there were significantly more flowers in the six territories on 4 April, 1980 than on 7 April, 1981, when flower numbers were declining (32.6 ± 7.3 *SE* versus 21.5 ± 7.6 *SE;* Wilcoxon matched pairs sign rank test $P < 0.05$) despite the fact that the cactus showed a response to heavy rainfall in late March 1981.

Both the amount and pattern of stigma snipping differed between years. Table 3 shows a higher proportion of stigmas snipped in 1981 than in 1980. The difference is significant between mid-January each year (Wilcoxon matched pairs sign rank test $N = 5$, $P < 0.05$) and between mid-January 1980 and late January 1981, the peak of flowering in that year (Wilcoxon matched pairs sign rank test $N = 6$, $P < 0.05$). Moreover there were different patterns of stigma-snipping in 1980 and 1981 in relation to flower abundance. In 1980 there was a highly significant negative correlation between the proportion of stigmas snipped and the number of flowers present ($r = -0.75$, $N = 20$, $P < 0.01$) although the relationship resembles a Type II pattern of curvilinearity (Holling 1966). In 1981 there was no correlation ($r = -0.01$, $N = 6$, $P > 0.01$). The difference can be explained in terms of a difference in the pattern of exploitation of *Opuntia* flowers (see Fig. 3). In 1980 the number of flowers exploited declined with a decrease in absolute flower

Table 3. Percentage flowers with damaged stigmas, with total number of flowers shown in parentheses

Territory	17 Jan 80	17 Jan 81	26 Jan 81
4,119	25 (120)	46 (68)	62 (77)
1,000	18 (123)	41 (44)	27 (79)
4,028	7 (152)	28 (58)	40 (78)
4,113	92 (123)	92 (88)	94 (99)
2,204	22 (165)	26 (34)	44 (63)
1,008	2 (272)	n.c.	41 (120)
	$X_5^2 = 425.96$	$X_4^2 = 82.61$	$X_5^2 = 43.56$
	$p < 0.001$	$p < 0.001$	$p < 0.001$

X^2 values are comparisons of the number of snipped and unsnipped flowers among specified territories on each date
n.c. = not counted

abundance. As flowers became scarcer, more were attacked at the bud stage. Stigmas are more likely to be damaged if the bud is attacked rather than the flower (Grant and Grant 1981). In 1981, by contrast, there was a sharp decrease in flower exploitation late in the season as birds switched to other foods (Fig. 3) and so late buds were probably not opened.

Total fruit numbers and fertile fruit numbers each showed a 61% decline from early May 1979 to early April 1980. Presumably 1979 was a year of high fruit production (and flower production), perhaps as a consequence of the high 1978 rainfall. 1980 and 1981 were poor years in terms of flower and fruit production possibly because of the low rainfall in the preceding years. There is further indirect evidence for an effect of the previous year's rainfall on the magnitude of the flowering response. In January 1982 the *Opuntia* flowering was the highest since early 1979 (T.D. Price *pers comm*), and rainfall in the preceding wet season (1981) was the highest since 1978.

c) Effects of territory size

Territories are based on cactus. Territorial boundaries are defined by cactus bushes and areas of open ground. *Portulaca* and *Bursera* are not defended unless they are between cactus bushes. Territories vary greatly in size but vary much less in area of cactus (Boag 1981 and *pers obs*). The mean area of cactus in 26 territories of adult male *G. scandens* on the island was 141.8 ± 12.6 m^2 *SE* (ranging from 49 m^2 to 292 m^2). All adult birds maintained the same territories from year to year with minor adjustments following the disappearance of neighbors. Only 10 out of 102 males (9.8%) holding territory disappeared between 1979 and 1981.

Territories occupied by males in immature plumage were much smaller (54.0 ± 7.9 *SE*) than those occupied by the generally older adult-plumaged (black) males referred to above ($t_{27} = 5.47$, $P < 0.001$).

A sex ratio bias in favor of males occurred after the 1977 drought. This resulted in many males being unmated in early 1979 (Millington MS). Those males that remained mated through 1979 (some females changed mates) had significantly larger territories than those who did not, including the unmated birds ($t_{18} = 4.03$ $P < 0.001$). Furthermore, those males that obtained one-year old females as mates in 1979 had larger territories than those remaining unmated

(Mann-Whitney $U_{2,5}=0$ $P=0.05$, one-tailed). These comparisons exclude the crater floor territories, which as previously noted, were larger but tended to contain a high proportion of infertile fruits because of reduced outcrossing. The differences provide evidence that territory quality may be important in the choice of mates by females (see Price MS). But within a breeding bout reproductive success has been shown to be very similar among breeding pairs, irrespective of territory size (Millington MS).

Discussion

The results show that the pattern of exploitation of most food types is very closely tied to the phenology of those food types, which in turn is governed by the timing and amount of rainfall. Thus within any one year the feeding behavior of the finches may be largely predicted from a knowledge of the available food supply. However, between years these phenologies are very different. For example, 1973, 1976 and 1978 were years of high *Bursera* fruit production and finches fed extensively on these berries in these years (Grant et al. 1976; Boag 1981). But during the study period, production was low and birds rarely fed on the fruits.

Close linking of exploitation patterns with a seasonally varying food supply has also been shown in hummingbirds and other species of birds dependent on nectar as a food source. In these species territoriality has been shown to be based on short-term (daily) food requirements (Stiles 1973; Gill and Wolf 1975). However, these are migrating or nomadic species that move elsewhere when the food supply declines or fails. Thus they differ from the non-migratory Cactus Finch which is dependent on local food sources year-round.

In the wet season there is low variance in breeding performance in any one breeding bout and variations in territory quality appear to be relatively unimportant contributors to this variance (Millington MS). There is evidence, e.g. from *Portulaca*, that in the wet season food supplies may not be limiting. Instead, whether or not an individual has a mate is the critical factor in determining breeding success. Approximately half of the total variance in fledging success is due to variance in mating success (Price MS). The present study shows mating success to be strongly correlated with territory size (cf. Zimmerman 1971; O'Donald 1977).

Food supply may be limiting in the dry season (e.g. Smith et al. 1978). Cactus finches feed almost exclusively on *Opuntia* fruits in the dry season, before the flowering season begins in September to October, especially if there are few small seeds produced in the previous wet season. Thus another advantage to having a large territory is enhancement of the probability of survival through access to a sufficient food supply during periods of food scarcity.

This last point can be illustrated with an example. The mean number of fertile fruits for the six territories was approximately 1800 in September 1979. If we assume an annual 61% decline in fruit number, such as occurred between May 1979 and April 1980, 700 fruits would have been left in September 1980. Given the 50% lower flower production in 1981 compared to 1980 and translating this into fruit production, about 350 fruits would have been present in the dry season of 1981, all other things being equal. If more stigmas were snipped because more buds were attacked before they flowered, then even fewer fruits

would have been fertile. Thus the food situation could have been precarious for those territory owners had 1981 been a drought year, especially for those individuals with smaller territories.

But 1981 was not a drought year. Small seeds provided an abundant alternative to *Opuntia* fruits and the subsequent cactus flowering was high. Even so, for birds such as 4118, the number of fertile fruits in their territories could have fallen dangerously low. It may not be a coincidence that this bird was involved in intense territorial disputes on several occasions in 1980 (although this was not quantified).

Territory size presumably decreases as finch density increases. When this is combined with low alternative food availability, as in 1977, the effects may be drastic. In that year, all first-year birds and 55% of adult *G. scandens* died over the dry season (Boag 1981; Grant and Price 1981).

Clearly the mating advantage and the postulated survival advantage of high territory quality are related. A female, once mated, remains on that territory most of the time, although a small minority change mates (Millington MS). Females do wander occasionally, especially when accompanied by dependent juveniles, but in September 1979 females were rarely seen off territory. A female choosing among males will clearly do better if that male has a territory likely to get them both through adverse conditions, e.g. food shortage.

The relative importance of reproductive and survival advantages vary in time. We suggest the mating advantage is generally more important at low densities when the food to finch ratio is high, such as during the study period, and the survival advantage is generally more important at high densities when the food to finch ratio is low. A comparison of the territory quality of survivors and non-survivors after a drought year is needed to test this.

Thus sampling the population in a year of high rainfall and even sex-ratio could well lead to the conclusions that (1) territory quality is unimportant if reproductive success remains relatively uniform, and (2) the owner may be defending a larger territory than it needs (cf., Verner 1977). This point was made by MacLean and Seastedt (1979) and, like those authors, we emphasize the need for longterm studies of variations in territory quality in relation to the survival and reproductive success of their owners.

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