

## Timing of reproduction in a Darwin's finch: temporal opportunism under spatial constraints

Michaela Hau, Martin Wikelski, Helga Gwinner and Eberhard Gwinner

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In seasonally unpredictable habitats, organisms cannot anticipate and prepare for a regular yearly reproductive period. Therefore, they opportunistically breed at any time of year. Opportunistically breeding birds are thought to maintain an activated reproductive system all year around. However, always being prepared can be costly and we therefore examined whether an opportunistic breeding strategy is realized in birds that are confined to harsh, climatically unpredictable habitats from which they cannot escape. We studied temporal variations in reproductive activity in small ground finches (*Geospiza fuliginosa*) in the Galápagos archipelago, Ecuador, by determining gonad sizes and plasma luteinizing hormone (LH) concentrations. We compared populations from the arid coasts of St. Fé and St. Cruz islands with birds from the St. Cruz humid highlands. The population from the arid St. Fé island increased gonad sizes and LH concentrations at least four months earlier in a wet (El Niño) year compared to the following dry year, indicating high temporal flexibility and opportunistic breeding. However, birds had completely regressed gonads for about 10 months between breeding events during a period of drought. Long-term changes in environmental factors such as ambient temperature, daylength and light intensity did not appear to influence reproductive activity. Instead, environmental signals more directly connected to the occurrence of rains such as humidity, barometric pressure, or rainfall itself may stimulate reproduction. Our data demonstrate that small ground finches regulate the onset of reproductive activity flexibly like other opportunistic breeders. However, they differ from those by their unusual long-term quiescence of the reproductive system during dry periods, which might minimize costs. Our findings suggest that within the continuum from seasonal to opportunistic breeding strategies, organisms evolutionarily optimize reproductive strategies to match local ecological conditions.

*M. Hau and M. Wikelski, Dept. Ecology and Evolutionary Biology, Guyot Hall, Princeton Univ., Princeton, NJ 08544, USA (hau@princeton.edu). – H. Gwinner and E. Gwinner, Max-Planck Research Centre for Ornithology, Andechs, Germany.*

Most habitats worldwide exhibit temporal fluctuations in biotic and abiotic conditions. Since reproduction is energetically expensive, animals living in variable environments breed only when conditions are suitable for the production of viable offspring (Bronson 1989, Wingfield and Kenagy 1991, Wallen and Schneider 1999). In birds, reproduction is particularly closely tied to favorable environmental conditions, because most birds have small

body sizes, high metabolic rates and specialized dietary needs for raising their offspring (Dawson et al. 2001). During the non-breeding season, most birds completely shut down their reproductive system and are thereby able to allocate resources to other seasonal activities like molt, migration or overwintering.

While the complete inactivation of the reproductive system during the non-breeding season conveys energetic

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benefits, it also imposes a temporal constraint because the re-activation of the reproductive system can require weeks or even months (Murton and Westwood 1977, Dawson et al. 2001). To counteract this temporal constraint, animals living in seasonally predictable habitats prepare for the next reproductive season long in advance using photoperiod (daylength) as a reliable signal for the ensuing favorable conditions (Follett et al. 1985, Wingfield et al. 1992, Silverin 1994, Dawson et al. 2001). Increasing photoperiod in spring stimulates the hypothalamo-pituitary-gonad axis, leading to the secretion of reproductive hormones and the growth and maturation of reproductive organs. Photoperiod also controls the termination of reproduction, shutting down reproductive processes in summer or fall (Nicholls et al. 1988).

Such a strategy of advance preparation works only in seasonal environments where favorable conditions are highly predictable (Wingfield et al. 1992). If changes in environmental conditions occur unpredictably, other adaptations are required to adequately time reproduction. The reproductive strategy to cope with an unpredictable environment is to breed opportunistically, i.e. to reproduce whenever environmental conditions permit ('temporal opportunism', Bronson 1989, Hahn et al. 1995, 1997). To rapidly initiate breeding at any time of year, opportunistic breeders are thought to maintain their reproductive system at least partly activated all the time (Farner and Serventy 1960). This strategy has been inferred from early studies on the Australian zebra finch (*Taeniopygia guttata*), the prime example for an avian opportunistic breeder (Immelmann 1973, Zann 1996).

However, recent work on zebra finches and two temperate opportunists, red crossbills (*Loxia curvirostra*) and white-winged crossbills (*L. leucoptera*), has cast doubt on this simplistic picture (Hahn et al. 1997, Astheimer and Buttemer 2002). All three species of opportunistic breeders show conspicuous and regular seasonal lulls in breeding activity in the wild, and at that time have regressed gonads and low circulating levels of reproductive hormones (Berthold and Gwinner 1978, Zann et al. 1995, Hahn 1998, Deviche and Sharp 2001). Moreover, laboratory experiments have revealed that changes in photoperiod affect the reproductive system of zebra finches and red crossbills (Hahn 1995, Bentley et al. 2000). These findings imply that although opportunistic breeders may retain an active or semiactive reproductive system for most of the year, there is also an underlying – exogenously or endogenously controlled – annual rhythmicity susceptible to environmental changes.

Empirical work on natural populations of opportunistic breeders is still sparse and many problems remain unresolved. One question is: is the long-term maintenance of an active reproductive system characteristic for opportunistic breeders in general or only realized under

special ecological circumstances? Nomadic behavior is one classical adaptation of avian opportunists to cope with poor environmental conditions. Nomads leave their habitat when environmental conditions deteriorate, and this 'spatial opportunism' (Hahn et al. 1995) increases the likelihood of the birds encountering high food supply and suitable breeding conditions elsewhere. Nomadism might therefore allow zebra finches and crossbills to keep their reproductive axis in an activated state over extended periods of time. In contrast, animals that cannot escape their harsh environment (e.g. because they live on remote islands) may not be able to afford a long-term activated reproductive system. Instead they may have to reduce costs by completely deactivating their reproductive system. In this case, the question would arise how the birds cope with the need to reactivate their reproductive system quickly once conditions have become favorable for reproduction.

Spatially isolated habitats with unpredictable variations in environmental conditions can be found in diverse places, e.g. mountaintops, springs, crater lakes, islands in large rivers and oceanic islands, like the Galápagos islands. We investigated the breeding strategy of a species of Darwin's finch, the small ground finch (*Geospiza fuliginosa*), that breeds on most islands of the equatorial Galápagos archipelago, Ecuador. Ecological and behavioral data indicate that Darwin's ground finches (*Geospiza* spp.) breed opportunistically (Boag and Grant 1984, Schluter 1984, Millington and Grant 1984, Hahn et al. 1997). Darwin's ground finches can only reproduce during the rainy season when food abundance improves, but the timing and duration of the rainy season varies considerably among years (Grant and Boag 1980, Grant et al. 2000). During the dry season, food can become extremely sparse, and especially in drought years intense mortality selection can ensue (Schluter 1984).

We employed physiological techniques to directly monitor changes in reproductive state and responses to environmental fluctuations. Physiological measures provide a better insight into the temporal components of reproductive decisions than observational techniques, which only track the outcome of this process. We hypothesized that small ground finches inactivate their reproductive axis whenever environmental conditions deteriorate and re-activate it opportunistically during good environmental conditions. Alternatively, birds might activate and inactivate reproductive activity on a regular annual basis but breed only when conditions are suitable. This kind of strategy appears to be realized in stonechats from equatorial Africa (*Saxicola torquata axillaris*, Gwinner and Dittami 1990) and opportunistic crossbills (Hahn 1995, 1998). To distinguish between these possible strategies, we measured gonad sizes and plasma concentrations of luteinizing hormone (LH) in free-living males and females over the course of two

years. We correlated reproductive data with several climatic parameters measured continuously on-site to identify cues that might stimulate reproductive activity. Furthermore, we compared reproductive patterns of small ground finch populations from two different islands and elevations, utilizing a natural altitudinal increase in rainfall to further elucidate whether these birds show a direct response to local environmental patterns.

## Material and methods

### Background natural history

The small ground finch is the most common Darwin's finch, occurring on most islands in the Galápagos archipelago (Grant 1999). Small ground finches are predominantly granivorous, but typically require protein-rich insect food for raising their young (Schluter 1984). Insect abundance can increase as early as 10 days after rainfall (Boag and Grant 1984, Schluter 1984, Grant and Grant 1989). Darwin's ground finches (*Geospiza* spp.) have been suggested to be opportunistic breeders as they rapidly initiate reproduction in response to rainfall, breed at any time of year depending on rainfall, skip breeding in drought years, dramatically extend their breeding season under conditions of prolonged rainfall (e.g. El Niño events), and are able to reproduce at the precocious age of about 90 days (Boag and Grant 1984, Gibbs et al. 1984, Schluter 1984, Grant et al. 2000). During the breeding season, males establish and defend territories, and males and females form socially monogamous pairs (Grant 1999, Petren et al. 1999). Before and after the breeding season, adults and juveniles can form large mixed-species flocks, but adults also are often seen in the vicinity of their breeding territory (pers. obs., Schluter 1984). Spatial movements of ground finches are rather limited on most islands. Most adults stay in areas close to their breeding sites year-round, although limited altitudinal and horizontal migrations can occur on some islands (Schluter 1982, Gibbs and Grant 1987, Grant and Grant 1995).

### Study sites

Our main study site was at 'Bahía Paraiso' on St. Fé island, an arid coastal habitat (0°49'S, 90°01'W, altitude 10 m). The coast of St. Fé is characterized by open habitat with many grassy areas, 1–5 m high *Opuntia* cacti, and low (1–3 m high) trees and bushes. From March 1998 onwards we also studied finches at 'Los Gemelos' in the humid highlands on St. Cruz island (0°40'S, 90°21'W, altitude 630 m). The St. Cruz highlands harbor a cloud forest dominated by 3–5 m high endemic *Scalesia* trees, with a fairly open understory. In

November 1998, we began a parallel study on a third population, at the 'Barranco' on St. Cruz island (arid coast, 00°44'S, 90°21'W, at an altitude of about 6–20 m). The coastal habitat of St. Cruz is densely vegetated with 2–3 m high bushes and trees, and climatically similar to the St. Fé site. These three sites were chosen to test for possible inter- and intra-island differences in the seasonal timing of the birds.

### Physiological measurements

Small ground finches were captured between November 1997 and October 1999 by mistnetting. Nets were opened in the mornings at dawn (5:00–6:00 am) until about 11:00 am, and in the afternoons between about 3:00 pm and 5:00 pm. Birds were taken immediately out of the net and transferred into cloth bags for processing. Blood samples for hormone analysis were taken within 30 minutes after capture (mean  $\pm$  1 SE: 19.8  $\pm$  0.52 min,  $n = 353$ ). Birds were then banded with one numbered aluminum ring and a unique combination of up to three plastic color bands. Visible fat was scored at the furculum on a scale of 0 (no fat) to 5 (bulging and spilling over, Wingfield and Farner 1978). Plumage coloration was scored from 0 (completely brown) to 5 (completely black) according to Grant (1999). Birds were then laparotomized and subsequently released (Wikelski et al. 2000).

Blood samples were obtained by venipuncture of the alar vein with a 26-gauge needle. Up to 150  $\mu$ l of blood were collected into heparinized microcapillary tubes and immediately stored on ice. Within 4–6 hours samples were centrifuged at 500 g for 4 min. The hematocrit was determined from the ratio of red blood cells to plasma. The plasma was then aspirated off and frozen in a camp freezer powered by a car battery, or on dry ice. Samples were transported frozen to the USA and kept at  $-20^{\circ}\text{C}$  until analysis.

We used a different centrifuge in Nov 1997 and Oct 1998 than at all other times. Centrifuges can differ in their speed and thus in their effectiveness to separate plasma and red blood cells. Therefore, in February 1999 we took blood samples from six finches, divided each sample in two parts and spun one half of each sample in each centrifuge. Hematocrits calculated from the two centrifuges were closely correlated (Pearson's  $r = 0.95$ ,  $p < 0.0005$ ), with the centrifuge used in Nov 1997 and Oct 1998 yielding a hematocrit value on average 0.05 lower than the regular centrifuge. We therefore added 0.05 to all Nov 1997 and Oct 1998 hematocrit values.

Unilateral laparotomy was performed under a light isoflurane anesthesia as described previously (Hau et al. 1998, Wikelski et al. 2000). The length and width of the left testis in males, and the diameter of the largest follicle

in females was determined to the nearest 0.1 mm using forceps or modified digital calipers. In Nov 1997 only the width of the testis in males was measured, because measuring gonad length would have required a large incision in birds with enlarged gonads. In these cases the length of the gonads was calculated as 1.3-x width (in all other months, the ratio of gonad length to gonad width in small ground finches was mean  $\pm$  1 SE 1.3  $\pm$  0.18, n = 298). As males increased gonad sizes over more than one order of magnitude, the exact multiplication factor used only has a minor effect – multiplication of gonad width with either 1.2 or 1.4 yielded qualitatively similar general result). The incision was closed with Nexaband<sup>®</sup>, and antibiotic powder was applied to the wound. Birds were allowed to recover from anesthesia for 5–10 minutes in cloth bags, given a drop of water or fruit juice and then released at their capture site. Testis volume was calculated using a formula for ellipsoid cylinders ( $4/3\pi a^2 b$ , where a is half the testis width and b half the length).

### Environmental data

Climate sensors and data loggers for on-site data storage were placed in the habitat typical for each site, i.e. attached to a rock in the open on the less vegetated St. Fé, and to the base of a tree on the two more densely covered St. Cruz sites, not more than 500 m away from the farthest mistnetting site for each population. Photoperiod and light intensity were determined with a light sensor of a lower sensitivity threshold of about 0.001 lumen ft<sup>-2</sup>. Photoperiod was calculated as the daily interval between the first and the last positive reading of the light sensor (Hau et al. 1998, Wikelski et al. 2000). Temperature was measured by a sensor with a precision of  $\pm 0.2^\circ\text{C}$  and precipitation was determined by an automated rain gauge. Environmental loggers for light and temperature were set up in Apr 1998 at all three sites, and rain gauges were put up in Aug 1998. A significant correlation in rainfall between St. Fé and the arid St. Cruz site (Pearson's  $r = 0.66$ ,  $p < 0.024$ ; rainfall was generally lower on St. Fé) allowed us to estimate rainfall on St. Fé prior to Aug 1998, by multiplying with 0.66 rainfall data obtained by the Charles-Darwin-Research Station at the arid coast of St. Cruz (Snell and Rea 1999). These rainfall estimates for St. Fé matched our own qualitative observations of the vegetation and food abundance. To estimate rainfall patterns before Aug 1998 at the humid St. Cruz highland site, we multiplied the Charles-Darwin-Research Station rainfall data by 1.3 (rainfall was generally higher in the highlands; correlation between the coastal and highland St. Cruz sites, Pearson's  $r = 0.82$ ,  $p < 0.0005$ ).

### Hormone analysis

Plasma concentrations of LH were determined in a total of three radioimmunoassays, following Follett et al. (1972) and Sharp et al. (1987), with minor modifications by T. J. Van't Hof (Gwinner et al. 2002), at the Max-Planck Research Centre for Ornithology, Germany. Samples were transported to Germany on dry ice. The mean ( $\pm 1$  SE) lower detection limit of the assay was at  $0.15 \pm 0.003$  ng ml<sup>-1</sup>. Blanks included in each assay were below detection limit. The average intraassay coefficient of variation as determined from at least 6 (and up to 17, depending on size of assay) replicates of a chicken plasma pool at 2 ng ml<sup>-1</sup> was 6.42%, interassay variation was 8.1%. Samples below the detection limit were set at detection limit as a conservative estimate for statistical analysis.

### Statistics

Only data from males with at least partly black plumage (plumage scores B3–B5) were analyzed for this study. This excludes some young males that had significantly smaller gonads than B3–B5 males (Hau et al., unpubl.). No age or plumage distinction was made in females. All data were analyzed using SPSS (Version 10.0, Chicago). Data are given as means  $\pm 1$  SE in text and figures. Of a total of 87 adult St. Fé males that were caught, banded and measured during the study, eight individuals were measured twice and one bird three times. Out of 111 St. Fé females, 7 were captured and measured twice and 2 females measured three times. In the humid St. Cruz highlands two of 60 males, and three of 71 females were measured twice. At the arid St. Cruz coast, two of 59 males were caught twice and one individual three times, while none of the females was caught more than once. Hence, repeated measures in both sexes were spaced apart by many months and only very few birds (less than 5.2% of all birds) were measured more than once. We therefore considered the data points as independent for statistical purposes and used one-way analyses of variance (ANOVA) for the temporal comparison of physiological and morphometric parameters. Exclusion of repeated measures data did not change the outcomes of our analyses. Our 'null' hypothesis was a lack of temporal changes in physiological parameters. Seasons for which sample sizes were less than three were excluded from statistical analysis and are not displayed in the graphs. Some data, especially gonad and hormone data were log transformed before performing ANOVAs as indicated in the text. We then used Bonferroni pairwise comparison posthoc tests, in which significance levels are adjusted to multiple comparisons (posthoc results are shown in Figures). Fat levels were analyzed using Kruskal–Wallis (KW) tests, followed

by Mann–Whitney tests adjusted for multiple comparisons with the Bonferroni-method.

We were not able to take gonad or hormone measurements during the 1999 breeding season, but finches were observed breeding in March at all sites (Vargas et al., unpubl.). This was also confirmed by the observation that birds were still feeding young on St. Fé in April 1999, and at the two St. Cruz sites in April and May 1999. We can therefore safely assume that gonads of most birds were enlarged and active and plasma LH concentrations elevated around this time. We indicate this in the figures, assuming similar gonad size and LH concentration values as in the previous breeding season.

## Results

### Temporal variation in climatic parameters

In Nov 1997 an El Niño had already begun, which brought heavy and extended rainfall to the archipelago (Fig. 1). The next rainy season did not occur until Feb/Mar 1999 and lasted for only about one month at the two dry sites (Fig. 1). Ambient temperature varied by about 4–9°C and in a fairly regular annual pattern at all sites (Fig. 1). Fluctuations in photoperiod were minor and non-seasonal (Fig. 1). On St. Fé, maximal photo-periodic variation did not exceed 15 min. (Fig. 1a), which is consistent with field measurements from equatorial Africa (Dittami and Gwinner 1985). The

observed irregularity in photoperiodic fluctuations might be explained at least partly by changing cloud cover. Consistent with this interpretation, daylength on all sites was shortest during the long El Niño in 1997/1998 (Fig. 1) and then increased again after the rainy season had ended. The relatively large increase in photoperiod in Aug–Oct 1998 at the humid St. Cruz site is probably the result of structural changes in the habitat (e.g. leaf cover). At all sites, light intensity varied across the year and appeared to be lower during the long El Niño than during drier parts of the year (Fig. 1).

### Temporal variation in gonad sizes

Fluctuations in gonad sizes occurred fairly synchronously in males and females. On St. Fé, males and females had large gonads in Nov 1997 and Mar 1998 (only one adult male was caught in Mar 1998; it had large gonads) and presumably again in Mar 1999, but maintained regressed gonads throughout the rest of the year (temporal variation in gonad size, log-transformed data, males:  $F_{(8,78)} = 23.5$ ,  $p < 0.0005$ ; females:  $F_{(9,101)} = 11.99$ ,  $p < 0.0005$ ; Fig. 2) for posthoc tests. Gonadal growth and regression did not occur on a regular annual basis: In 1997 gonads of St. Fé birds were already fully developed in Nov. By May 1998, they were fully regressed and subsequently stayed small at least until mid Feb 1999 (Fig. 2). Assuming that it takes about 3–4 weeks to grow gonads from fully regressed to fully

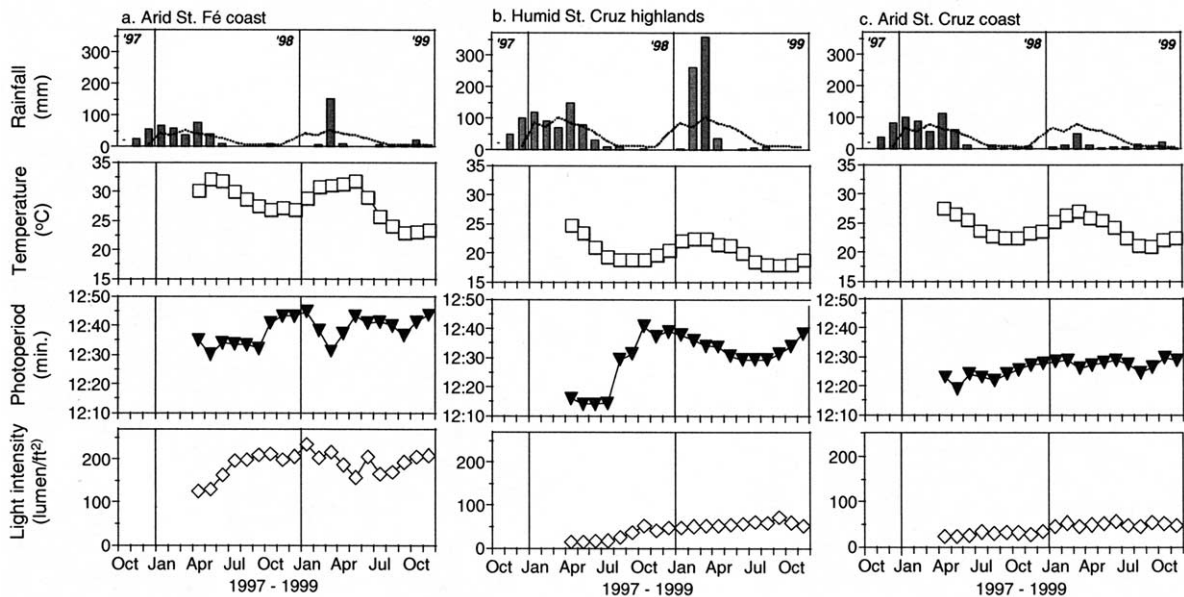


Fig. 1. Monthly rainfall (uppermost panels, columns), long term average rainfall (uppermost panels, broken line), average monthly temperatures (open squares, second panels), average monthly photoperiods (filled triangles, third panels) and average monthly light intensity (open diamonds lowest panels) at the arid coast of St. Fé (a), the humid highlands of St. Cruz (b) and the arid coast of St. Cruz (c). Vertical lines indicate beginning of each year. Rainfall data prior to Aug 1998 on St. Fé and the humid highlands of St. Cruz were extrapolated from rainfall records at the arid coast of St. Cruz.

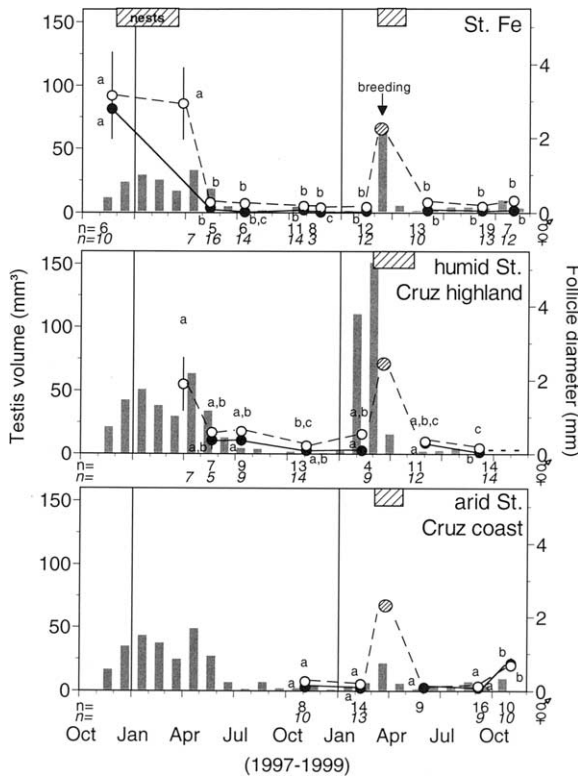


Fig. 2. Temporal variations in male testis volumes (filled circles) and female follicle diameters (open circles, mean  $\pm$  1 SE) of small ground finches from the arid St. Fé population (uppermost panel), the humid highlands on St. Cruz (middle panel) and the arid lowland on St. Cruz (lowest panel). Letters above symbols indicate differences among data as determined by post hoc tests, numbers below each panel indicate sample sizes for males (upper row) and females (lower row). Gray bars indicate monthly rainfall at each site, and hatched horizontal bars at the top of each panel indicate approximate nesting times. Hatched circles and dotted lines in each panel indicate likely gonad sizes of finches in March 1999; breeding was confirmed but physiological data were not collected. Nesting data are obtained from qualitative observations of breeding activity and the presence of active brood patches in females.

active sizes (Murton and Westwood 1977), there was at least a four-months difference in the onset of gonadal development between the two years of our study. In between, birds had regressed gonads for about 10 months. During the non-breeding season gonads of St. Fé males shrank to about 1.25% of their breeding volume (the lowest average within the non-breeding season sampling periods was 1 mm<sup>3</sup> compared to the average of 80 mm<sup>3</sup> in Nov 1997; Fig. 2). The regression of gonads after the breeding season on St. Fé occurred in May 1998 even though rainfall was still elevated. Rainfall in May 1998 on St. Fé was extrapolated from arid St. Cruz data, but since rainfall on the two sites was generally closely correlated and because the vegetation in May on St. Fé was lush, the assumption of continuing rainfall at least through May 1998 is realistic.

Birds from the humid highland site also showed temporal variations in gonad sizes (log-transformed data, males:  $F_{(5,52)} = 3.35$ ,  $p = 0.011$ ; females:  $F_{(6,63)} = 7.42$ ,  $p < 0.0005$ ; Fig. 2). Coincident with a generally earlier onset and a longer duration of the rainy season, highland females started to increase gonads in Feb 1999, a few weeks ahead of St. Fé and arid St. Cruz birds. In 1998, highland females also maintained slightly elevated gonad sizes longer than St. Fé birds (Fig. 2). Like St. Fé birds, highland birds had begun to regress gonads in May 1998 despite continuing rainfall.

Patterns of gonadal size of small ground finches from the two arid study sites were generally similar. Gonad sizes of males and females from the arid St. Cruz site showed significant temporal variation (log-transformed data, males:  $F_{(4,52)} = 23.37$ ,  $p < 0.0005$ ; females:  $F_{(3,29)} = 21.65$ ,  $p < 0.0005$ , Fig. 2). Birds had regressed testes in Oct 1998 through Feb 1999, bred in Mar/Apr 1999, and then had regressed gonads again until Sep 1999. Arid St. Cruz males and females showed a significant increase in gonad sizes in Oct 1999, coinciding with elevated rainfall (no data were taken from St. Cruz highland birds at this time).

#### Temporal variation in plasma LH concentrations

Plasma LH concentrations of St. Fé birds showed temporal variations (males: log-transformed data,  $F_{(8,65)} = 6.26$ ,  $p < 0.0005$ ; females: non-transformed data,  $F_{(7,66)} = 3.19$ ,  $p < 0.001$ , Fig. 3). In general and as expected, increases in plasma LH concentrations preceded gonad development. Male St. Fé birds had elevated LH concentrations in Feb 1999, about three weeks prior to the onset of the rainy season. The gonads of these birds were still fully regressed at this time (Fig. 2) and birds did not sing or display other reproductive behaviors (Hau et al., unpubl.). This increase in plasma LH concentrations came at a time when rainfall was still minimal. There was also a significant increase in plasma LH concentrations of both sexes in Oct 1999, coinciding with increased rainfall (Fig. 3).

We did not detect significant temporal changes in plasma LH concentrations of St. Cruz highland males (log-transformed data,  $F_{(5,41)} = 1.4$ ,  $p > 0.2$ , Fig. 3), although there was a trend for LH concentrations to be higher in Feb 1999 than during the rest of the year. Females had elevated LH titers in Apr 1998 and Feb 1999 (log-transformed data,  $F_{(4,37)} = 6.87$ ,  $p < 0.0005$ , Fig. 3) for posthoc results.

We did not detect temporal variations in plasma LH concentrations of arid St. Cruz birds (log-transformed data, males:  $F_{(3,46)} = 1.1$ ,  $p > 0.4$ ; females:  $F_{(2,22)} = 2.4$ ,  $p = 0.12$ , Fig. 3). This might be due to the fact that we

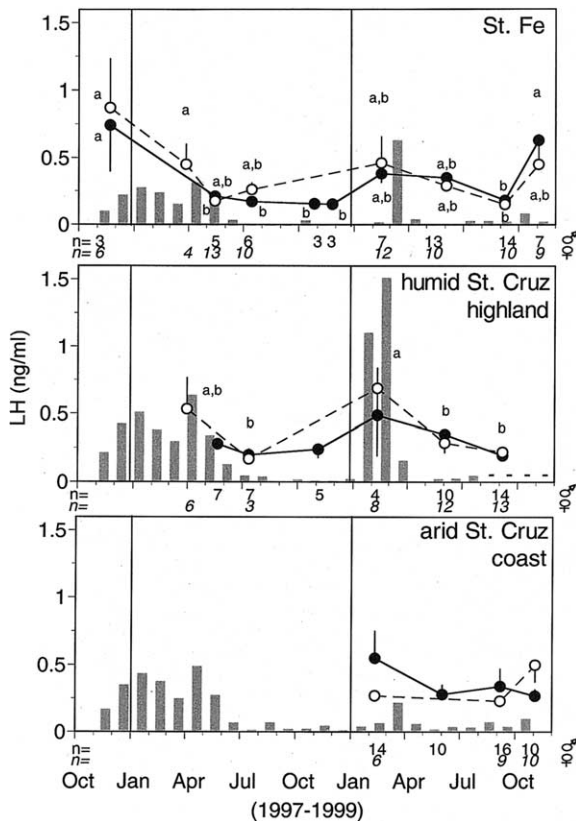


Fig. 3. Temporal variations in plasma LH concentrations of male (filled circles) and female (open circles, mean  $\pm$  1 SE) small ground finches from the arid St. Fé population (uppermost panel), the humid highland on St. Cruz (middle panel) and the arid lowland on St. Cruz (lowest panel). Differing letters above symbols indicate differences among data as determined by post hoc tests, numbers below each panel indicate sample sizes for males (upper row) and females (lower row). Gray bars indicate monthly rainfall at each site.

have only a limited data-set from this population and that hormone concentrations were variable between individuals.

### Variations in fat score and hematocrit

Fat score and hematocrit fluctuated roughly in a similar pattern in all populations. Therefore only data from our best-monitored study site, St. Fé, are presented in Fig. 4a and b and were used in correlational analyses.

#### Fat scores

Fat scores of St. Fé birds showed conspicuous changes (KW-tests, males:  $\chi^2 = 50.43$ ,  $df = 8$ ,  $p < 0.0005$ , females:  $\chi^2 = 66.7$ ,  $df = 9$ ,  $p < 0.0005$ ). The pattern was similar in males and females and showed no obvious relationship to either gonadal size or LH (Fig. 4). Birds

had hardly any fat from Nov 1997 through Jul 1998 (during and after the rainy season). Fat levels then increased during the course of the dry season in Oct and Nov 1998 and stayed high from about Feb 1999 through Sep 1999. Fat scores of St. Fé birds were negatively correlated with hematocrits (males: Spearman's  $\rho = -0.33$ ,  $p = 0.004$ ; females: Spearman's  $\rho = -0.25$ ,  $p = 0.024$ ).

St. Cruz highland birds showed a similar pattern as St. Fé birds, i.e. low fat scores during the first part of 1998, an increase during the second part of 1998, and high levels in 1999 (males:  $\chi^2 = 34.4$ ,  $df = 5$ ,  $p < 0.0005$ ; females:  $\chi^2 = 31.2$ ,  $df = 6$ ,  $p < 0.0005$ ; data not shown). In arid St. Cruz males, fat scores also varied in a similar pattern ( $\chi^2 = 17.7$ ,  $df = 4$ ,  $p = 0.001$ ; data not shown), except that they showed a decrease in May 1999. Females of this population did not show fat score fluctuations (data not shown).

#### Hematocrit

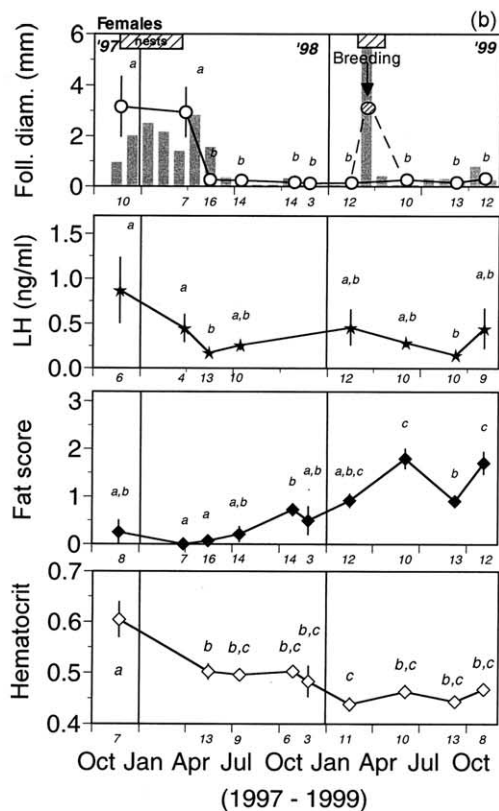
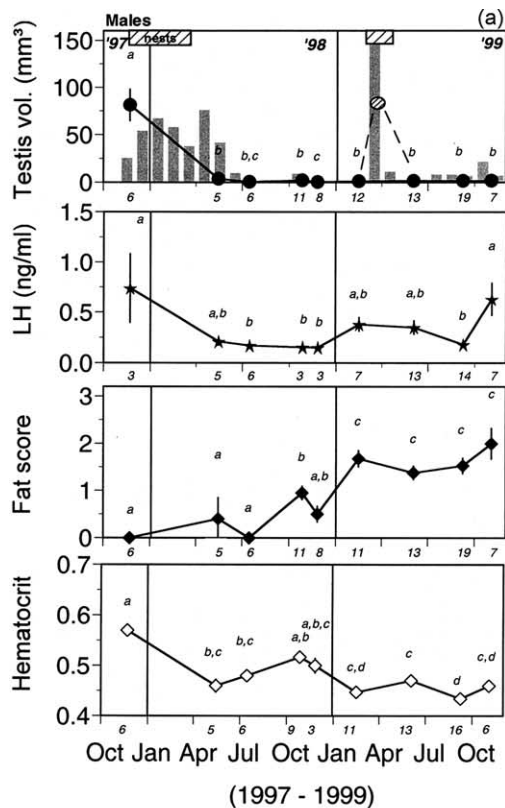
In St. Fé birds, hematocrit varied in an almost inverse pattern to fat score (males:  $F_{(8,66)} = 15.44$ ,  $p < 0.005$ ; females, log-transformed data:  $F_{(8,71)} = 9.11$ ,  $p < 0.0005$ ; Fig. 4). Hematocrit was highest in Nov 1997, declined after the breeding season and into the dry season in 1998, and reached lowest values in Feb and Sep 1999. Similarly, hematocrits of St. Cruz highland birds were higher in 1998 compared to 1999, with peaks after the breeding season in Apr 1998 (in females only) and in Oct 1998 (males:  $F_{(4,64)} = 10.75$ ,  $p < 0.0005$ ; females:  $F_{(5,46)} = 11.4$ ,  $p < 0.0005$ ; data not shown). Hematocrits of arid St. Cruz birds were also higher in Oct 1998 than in the following year (males:  $F_{(4,52)} = 14.6$ ,  $p < 0.005$ ; females:  $F_{(3,26)} = 5.33$ ,  $p = 0.005$ ; data not shown).

## Discussion

The present investigation documents the physiological characteristics of the unusual reproductive timing system of a Darwin's finch. We propose that the peculiar regulation of the small ground finch reproductive system represents an adaptation to the ecological situation of being confined to an unpredictable, harsh habitat.

### Flexible activation of reproductive capacity

The highly flexible initiation of reproduction in male and female small ground finches roughly matches the environmental variability to which these birds are exposed. Birds showed at least a four months difference in the activation of their reproductive system in the two years of our study, both on the arid St. Fé and the humid St. Cruz island. These findings strongly suggest that the regulation of their reproductive system is at least partly



opportunistic. In line with observational studies on other Darwin's finches (*Geospiza* spp.; Gibbs and Grant 1987, Grant and Grant 1987, Grant et al. 2000), factors associated with the rains appear to be important timing cues and responsible for the differences in activation of the reproductive system of birds on different islands (below). However, based on the available data we cannot at the present time entirely exclude the possibility that the opportunistic regulation of reproduction is seasonally modulated, either by annually recurring environmental cues or by an endogenous circannual rhythmicity. Such a possibility is suggested by the peculiar increase in LH in St. Fé birds in Feb 1999 prior to the onset of rains. Data on the response of small ground finches to rainfall between May and Feb are required for evaluating the possibility of an underlying seasonality.

### Complete inactivation of the reproductive system

Small ground finches of all three study populations shut down their reproductive system and showed fully regressed gonads and – most of the time – low concentrations of plasma LH concentrations. Especially in the arid St. Fé population, gonads were regressed over a period of about 10 months. Opportunistic crossbills also regress their gonads, but for a much shorter period of time (Berthold and Gwinner 1978, Hahn 1995, 1998, MacDougall-Shackleton et al. 2001).

The shut down of reproductive processes could be caused either by deteriorating environmental conditions such as a drought, a decrease in food abundance or quality, an exhaustion of body reserves after an extended breeding season, or by endogenous circannual timing mechanisms. Droughts are known to suppress reproduction in many vertebrates and indeed several species of Darwin's finch did not show any signs of reproductive activity for 2.5 years during a pronounced drought (Grant et al. 2000). However, water availability cannot fully account for changes in reproductive activity of small ground finches as birds on St. Fé regressed their gonads in May 1998 before the rainy season had ended. Food scarcity usually accompanies droughts and is

Fig. 4. Gonad sizes, hormone levels and several 'condition' measurements of (a) male and (b) female small ground finches from St. Fé island, from Nov 1997 to Oct 1999 (mean  $\pm$  1 SE). Sample sizes are given underneath each panel; periods for which sample sizes are less than three were omitted from statistical analysis and are not displayed in the figures (e.g. Apr 1998 value for males). Vertical lines indicate beginning of each year. Shaded gray bars indicate monthly rainfall (from Fig. 1). Hatched circle and dotted lines in first panel indicates likely gonad sizes of finches in March 1999; breeding was confirmed but physiological data were not collected. Hatched horizontal bars on top of first panel indicate approximate nesting times. Differing letters above symbols indicate differences among data as determined by post-hoc tests.

another potent inhibitor of reproductive activity in vertebrates (reviewed by Bronson 1989, Wingfield and Kenagy 1991). The most probable food-related factor that might suppress reproductive activity in small ground finches is a decrease in the abundance of high-protein food such as caterpillars, which can decrease precipitously even before the end of an El Niño (Grant and Grant 1987, 1989). During an El Niño, high population densities of finches resulting from extensive breeding can reduce food availability further (Grant et al. 2000). A decline in food abundance or quality may explain the regression of the reproductive axis in small ground finches in May 1998, at a time of continuing rainfall.

It is currently unresolved whether small ground finches undergo a period of refractoriness after the breeding season while regressing their gonads. Most temperate-zone seasonal breeders (Nicholls et al. 1988) and some equatorial birds (Lofts 1962, Gwinner and Scheuerlein 1999) enter a refractory period in which the reproductive system becomes spontaneously unresponsive to stimulatory environmental signals.

At the ultimate level, the regression of the reproductive system during the dry season may allow sedentary small ground finches to minimize costs associated with an active reproductive system. Such costs could arise at multiple levels, i.e. may be the result of elevated metabolic rates (King 1973, Ricklefs 1974, Walsberg 1983, Carey 1996), increased locomotor activity and display of conspicuous reproductive or aggressive behaviors, or suppressed immune function due to the actions of reproductive hormones (summarized in Ketterson and Nolan 1992, Wingfield et al. 2001).

### Which environmental cues stimulate reproduction?

In our study area, photoperiod, light intensity, and temperature showed seasonal variations, albeit of low amplitude. In 1999, when we collected environmental data throughout the prebreeding and breeding season, all three factors increased a few months prior the onset of the rainy season and their variations were thus potentially available as medium- or long-term cues. However, none of the small ground finch populations in our study activated their reproductive system in anticipation of the average long-term rainfall pattern (Fig. 1), which would be expected if these cues were used. Nevertheless, if not acting as a trigger changes in photoperiod, light intensity and temperature could at least function to prime the reproductive system for a fast response to short-term cues, i.e. act as a permissive factor (Gwinner 1989).

If long-term cues are not responsible for the activation of the reproductive system, which environmental cues do then trigger reproductive activity in small ground

finches? In all three populations gonad development was only initiated after substantial rainfall (Fig. 2). Increases in plasma LH concentrations of small ground finches usually preceded changes in gonad sizes and occurred at lower rainfall (Fig. 3). The latter is not surprising as hormones can change within hours or days in response to a stimulatory cue, while the development of gonadal tissue usually takes a few weeks (Wingfield and Farner 1993, Nelson 2000).

Rainfall itself or factors closely associated with the onset of the rainy season such as increased humidity, trade winds, or changes in barometric pressure could activate the reproductive system of small ground finches. Rainfall or rainfall-related noise stimulates singing of captive and free-living Darwin's ground finches (Orr 1945, Grant and Grant 1989, Grant 1999). Gonad growth and hormone production of captive zebra finches can be stimulated by an unlimited supply of water after a period of dehydration (Priedkalns et al. 1984, Vleck and Priedkalns 1985). Further, humidity can affect gonad growth and reproductive behavior in captive zebra finches (Vleck and Priedkalns 1985, Cynx 2001) and spotted munias (*Lonchura punctulata*, Sikdar et al. 1992). It has not yet been documented that birds can respond to changes in trade winds, but birds and bats can perceive changes in atmospheric pressure (Lehner and Dennis 1971, Kreithen and Keeton 1974, Paige 1995).

It is unlikely that small ground finch reproduction is stimulated by cues such as food abundance or quality (Ligon 1974, Hahn 1995, Hau et al. 2000, Scheuerlein and Gwinner 2002), which improve after rainfall. Insect abundance on Galápagos starts to increase about 10 days after the first rains (Grant and Grant 1989) and by relying predominantly on food cues, the finches would lose valuable time and potentially miss the main insect peak for breeding. However, *Opuntia* cacti on Galápagos typically start to flower in the late dry season with a peak in November–March (Grant and Grant 1981) and we observed a similar pattern on St. Fé (Vargas et al., unpubl.). Cactus finches (*G. scandens* and *G. conirostris*) with sufficient access to *Opuntia* flowers advanced breeding by 1–2 months and produced up to two clutches in years without rainfall (Grant 1996). Small ground finches utilize this food source as well (Grant and Grant 1981, Hau et al., unpubl.), and this might explain the interesting increase in LH concentrations of St. Fé males in Feb 1999 prior to the rainy season.

In general, opportunists have been suggested to respond to a variety of cues, which are often most effective when used in combination (Wingfield et al. 1992, Cockrem 1995, Hahn et al. 1997, Cynx 2001). The use of multiple cues can increase the precision with which the birds can evaluate environmental conditions, especially in unpredictable habitats.

## Body reserves and reproduction

Small ground finches had high fat levels for a tropical bird, and fat depots varied more strongly between years than within years. It is interesting to note that despite high fat scores in 1999 birds maintained regressed gonads (Fig. 4), supporting our interpretation that the finches do not use elevated fat stores as a trigger for reproduction as has been suggested for opportunistic zebra finches (Meijer et al. 1996).

Instead, both absolute levels and variability in fat depots of small ground finches might indicate that fat functions as an energy reserve to cope with increased energetic demands and environmental unpredictability (reviewed by Witter and Cuthill 1993). Temperate-zone birds typically have highest fat depots during periods of low ambient temperatures and food availability in winter (Lima 1986, Boswell et al. 1993, Bednekoff et al. 1994, Meijer et al. 1994, Bednekoff and Krebs 1995, Biebach 1996). Indeed, within-year fluctuations in fat scores of small ground finches paralleled seasonal changes in ambient temperature to some extent (Fig 1, 4). Although changes in ambient temperature on Galápagos are smaller than for most mid- or high-latitude birds, tropical birds might have a narrow range of temperature tolerance (Janzen 1967). However, considering the dramatic changes in food abundance on Galápagos (Grant 1999), a more likely explanation is that between-year variations in fat depots of the finches are inversely related to food availability, like in afrotropical red-billed queleas (*Quelea quelea*, Ward 1965). Metabolizing fat depots is also a source of metabolic water and could provide an important internal water resource during the dry season (Serventy 1971).

Hematocrits were generally higher during periods of rainfall and lower during the drought, changing inversely to fat stores (Fig. 4). High hematocrit during wet periods suggests that birds were in better health compared to dry periods. Hematocrit also decreased throughout the long breeding season from Nov 1997 to May 1998 in both males and females. This decline might be related to reproduction like in temperate zone bird species: Hematocrit decreases in laying females, perhaps caused by the reproductive hormone estradiol, which can suppress hemopoiesis (Kern et al. 1972, DeGraw et al. 1979, Keys et al. 1986, Morton 1994).

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