Reproduction in an endemic bird of a semiarid island: a food-mediated process

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We analyse the effects of rainfall, temperature, food availability and nest predation on the between-year variation in reproduction of the Canary Islands stonechat *Saxicola dacotiae*, a bird species endemic of the semiarid island of Fuerteventura (Canary Islands, Spain). We monitored the reproductive performance and output of the species across its whole distribution area during three consecutive breeding periods, also measuring rainfall, temperature and food (arthropod) availability on the ground monthly. Rainfall varied from 27.3 mm in 2000–2001 (dry year) to 124.5 mm and 125.1 mm (average years), respectively, in the 2001–2002 and 2002–2003 breeding seasons. The onset of breeding closely matched variation in the onset of the autumn-winter rains among years. Arthropod availability was strongly and positively related to rainfall one month before. Reproductive investment (number of clutches and clutch size) was correlated to arthropod availability both among years and among sites within years. Stonechat pairs bred once or did not breed at all in the dry year whereas they bred twice in the other two years. Clutch size was smaller in the dry year and larger in the second as compared with the first in the other two years. Reproductive investment largely determined reproductive output (number of fledglings) as there were no significant spatial or temporal variation in hatching success (90% on average) or nest predation (29% on average, mostly due to feral cats *Felis catus*). Within- and among years variability in temperature or predation did not match variability in the onset, length or reproductive investment and output recorded throughout the study years. These results suggest that variability in annual fecundity in the Canary Islands Stonechat was mainly driven by rainfall through a food-mediated process.

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In arid ecosystems there is a considerable year-to-year variation in both the amount and the duration of productivity due to the limiting role of the scarce and unpredictable rains on biological processes (Noy-Meir 1973, Whitford 2002). For example, reproduction in birds living in arid habitats tends to be related to yearly variation in rainfall (Immelmann 1970, MacLean 1970, Wiens 1991, Ostfeld and Keesing 2000). The correlation between rainfall and reproductive performance is thought to be caused by the positive effect of rainfall on food availability for adults and/or chicks (Boag and Grant 1984, Gibbs and Grant 1987, Rotenberry and Wiens 1991, Zann et al. 1996), although long-term studies demonstrating these associations are only available for some Darwin's finch populations inhabiting the Galápagos Islands (Grant et al. 2000). Moreover, rainfall-mediated factors other than food availability such as water availability (Coe and Rotenberry 2003), direct predator effects (Rotenberry and Wiens 1989, Suárez and Manrique 1992, Mezquida and Marone 2001, Morrison and Bolger 2002) and temperature (Grant et al. 2000) have also been suggested to affect the

reproductive success of birds in arid environments. Nevertheless, studies that measure all these factors and relate them to breeding success in contrasting rainfall conditions are certainly absent.

Rainfall-mediated factors affecting breeding success would act at different stages of the reproductive cycle, a fact that provides a way for analysing their role for determining rainfall-mediated variation of reproductive success. Rainfall, rather than photoperiod or endogenous circannual rhythms, could act as a proximate factor triggering the beginning of specific physiological processes such as sex hormone production or gonad growth (Hau 2001, Leitner et al. 2003, Hau et al. 2004), thus determining the onset of the breeding season in arid ecosystems. This mechanism would be maintained by natural selection if rainfall is a good predictor of the availability of food at the times of egg laying and/or chick raising periods. The length of the breeding season and the reproductive investment (clutch size and number of clutches) could be determined indirectly by the duration of rains if food availability depends closely on rainfall (Immelmann 1970, Lloyd 1999, Patten and Rotenberry 1999), or directly, if water availability influences egg laying (Coe and Rotenberry 2003). An apparently more straightforward method for analysing the relative contribution of each factor to reproductive success is the analysis of long-term data sets including all rainfall-related factors and proper measures of breeding success (Grant et al. 2000). Nevertheless, the number of years needed for proper analyses of multiple factors could be prohibitively large, the fact that each factor is measured at different spatial scales (from predation at nest sites to regions monitored by weather stations) implies difficulties for proper comparisons and, finally, results from cross-correlational analyses may be either due to direct causality or to the effect of uncontrolled secondary variables. For these reasons, most recent studies on the effects of rainfall-related factors on bird breeding performance have been based on testing specific hypotheses rather than on looking for correlations (Morrison and Bolger 2002, Coe and Rotenberry 2003, Bolger et al. 2005).

The goal of this paper is to analyse the effects of rainfall, temperature, food availability and predation on reproduction of the Canary Islands stonechat *Saxicola dacotiae*, a bird species endemic to the semiarid island of Fuerteventura (Canary Islands, Spain), during a three-year period. Our general prediction is that Canary Islands stonechats should adjust their breeding period to the onset and duration of the scarce and unpredictable rains that characterise the climate of the island, i.e., that the onset and duration of the bird's breeding period will match the period of rains both within a given year and among years of contrasting rainfall. To test what rainfall-mediated factors could account for the observed patterns, we also analysed: (1) whether food availability matched rainfall patterns within- and among-years, (2) whether food availability was related to the duration of breeding seasons and to the overall reproductive investment (clutch size and number of clutches), and (3) whether between-year differences in reproductive success were related to differences in food availability, temperature and/or nest predation.

Materials and methods

Species

The Canary Islands stonechat is a narrow range endemic of the Fuerteventura Island (Illera 2004a). It is a small passerine (length: 11 cm; body mass: 12.2 g; n = 125; J.C. Illera, unpubl. data) which breeds across the whole island in places with specific habitat characteristics (Illera 2001). The species is thought to be monogamous, sedentary and territorial after initial settlement that seems to occur in the first year of life (Illera 2004b). Females build the nests under boulders and bushes and, to a lesser extent, in wall fissures (Collins 1984, J.C. Illera unpubl. data). Only females incubate. Adults are primarily insectivorous (Martín and Lorenzo 2001, Illera 2004b). Nestlings are fed by both sexes with arthropods mainly (Martín and Lorenzo 2001, Illera 2004b). Fruits of *Lycium intricatum* and, exceptionally, lizard tails were also given to chicks (Illera 2004b). Fledglings remain in the natal territory until the pair starts a new breeding attempt, and are fed by the parents with the same food as nestlings during their first month of life (Illera 2004b).

Study area

The Canary Islands archipelago is composed of seven main volcanic islands (Fig. 1) located in the Northeastern Atlantic Ocean, 100 km west of mainland Africa. The climate of the islands is determined by their proximity to the high atmospheric pressures of Azores and to the Sahara desert, the Canaries cold current, and the different topography of each island. Fuerteventura (28°46′N, 14°31′W) is the second largest island (1659.71 km^2) and the closest to the African mainland. Being the oldest island (c. 22 million years old; Carracedo and Day 2002), its topography is mostly low and flat (c. 200 m a.s.l.), with a maximum elevation of 807 m. Past and present-day climatic conditions of Fuerteventura reflect the scarcity of water due to its low relief and eastern situation (García-Herrera et al. 2001). These predominant arid or semiarid conditions have been present in the island at least from the late Pleistocene (Alonso-Zarza and Silva 2002, Genise and Edwards 2003). Rainfall is scarce (143 mm/year on average) and concentrated during the autumn/winter months, whereas mean monthly temperatures vary between 19°C in January
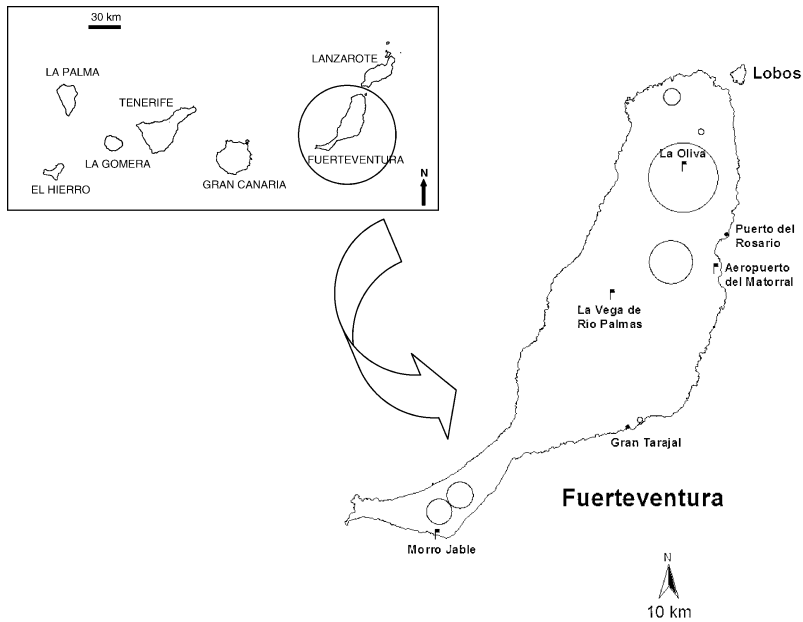
Fig. 1. Map of the study area, showing the location and relative size of Fuerteventura island within the Canary Islands and the distribution of study sites (circles) and weather stations (flags). We monitored the Canary Islands stonechat's reproduction in 12 study sites: five in the larger circle, two in the central and one in each of the remaining. Circle sizes indicate the number of pairs monitored during 2000–2003. Arthropod availability was measured inside the four larger circles located in the northern, central and southern parts of the island.

and 21°C in August (Marzol-Jaén 1984). The vegetation is xerophytic and is dominated by sparse grassland and scrubland (Rodríguez et al. 2000). We obtained monthly rainfall records from four weather stations located close to the study sites (Fig. 1). Mean monthly and daily temperature records were obtained from the weather station C249I (Aeropuerto del Matorral), which is the only station in the island providing this kind of data and is located close to the main study site (Fig. 1).

Food availability

Canary Islands stonechats are sit-and-wait predators that detect prey from perches and hunt for them on the ground (Illera 2001). Food availability was evaluated by counting all arthropods ≥1 mm found during careful examinations lasting 2 min of the ground and low vegetation within 0.5 m × 0.5 m wooden frames. Low herb and scrub cover facilitated this type of estimation. A millimetre is the minimum length of prey of the common stonechat Saxicola torquata (Martínez-Cabello et al. 1991), a sister species of the Canary Islands stonechat. Frames were located at 100-m intervals along fixed 1000-m line transects, that were monitored monthly. Line transects were randomly established in 10 sites within three study areas (northern, central and southern) of Fuerteventura (for locations see Fig. 1). The northern study area was monitored from December 2000 till June 2003 (no data were obtained in July,

August and October 2002) by means of 12 transects (120 samples) located at four sites. The central study area included two transects monitored from February 2001 until June 2002 in one site and two transects per site in three sites from September 2001 until June 2002. The southern study area included two transects per site in three sites monitored from September 2001 until June 2002.

Reproductive traits

We monitored the full breeding cycle of Canary Islands stonechats during three consecutive years (2001–2003). We selected 12 study sites within the whole distribution area of the species in which 1–10 pairs bred at least one year out of the three (Fig. 1). Four sites were monitored during all study years, three in two and five in only one year. The numbers of sites and pairs included in different years were 9 and 32 in 2001, 8 and 27 in 2002 and 6 and 28 in 2003. Most birds (80%, n =139) were marked with a unique combination of coloured leg bands and ringed within the Spanish scheme. A few birds (20%, n =35) that could not be caught were identified by means of plumage traits (short tail, small white supercilium, etc.) during a given breeding season. Only seven out of the 87 pairs studied could be monitored in successive breeding seasons, so that we considered data for each pair as statistically independent.

Visits to territories started in late October-early November (prebreeding period) and were carried out at least weekly throughout the breeding period. We finished territory monitoring a month after the last fledgling left the nest (postbreeding period). We found nests during the building, incubation and nestling stages. Nests found during the building stage were checked at 1–2 day intervals to determine laying date (the day when the first egg was laid) and clutch size (the number of eggs in the nest at the start of incubation). We assumed that each nest contained a complete clutch. This procedure could underestimate clutch size if some clutches suffered partial losses, but this was not the case: none out of the 26 nests monitored from the building stage until chicks fledged suffered partial predation of either eggs or chicks, and most of the few eggs that did not hatch (5 out of 89; 5%) stayed in the nest (4 out of 5; 80%). Nests were checked 11–12 days after the start of incubation at 1–2 day intervals until hatching to determine hatching date, brood size (number of chicks hatched) and hatching success (proportion of eggs that resulted in fledged young), and then visited at 2–4 day intervals to determine fledging success (brood size at fledging divided by brood size at hatching in nests that survived until fledging), fledging production (number of chicks leaving the nest) and fledging date (the day when the last chick left the nest). Nests found during the incubation or nestling stages were checked at 2–4 day intervals to determine brood size and/or fledgling production. Laying, hatching and/or leaving dates for these nests were determined by back dating using mean incubation (number of days between laying of the last egg and hatching) and nesting periods (number of days from hatching to fledging) taken from nests where the exact laying, hatching or fledging dates were known. We classified breeding attempts as first, repeat of first (after predation or desertion), second (after a successful first attempt) and repeat of second (new attempt after predation or desertion of the second).

Results

Rainfall and temperature

Rainfall patterns during the study period showed strong between-year variation ($F_{2,6} = 11.39$, $P < 0.01$), but this variation was consistent across the whole island ($F_{3,6} = 0.94$, $P = 0.48$ for the effect of locality and $F_{6,133} = 0.38$, $P = 0.89$ for the year by locality interaction; two-way ANOVA with log-transformed monthly rainfall as the dependent variable and year and locality as random factors). The first study year (2000–2001) was a dry year (27.3 mm between August 2000 and July 2001, as compared with the 13-year average of 132.24 mm), whereas the other two were average years (124.5 mm and 125.1 mm, respectively; Fig. 2).
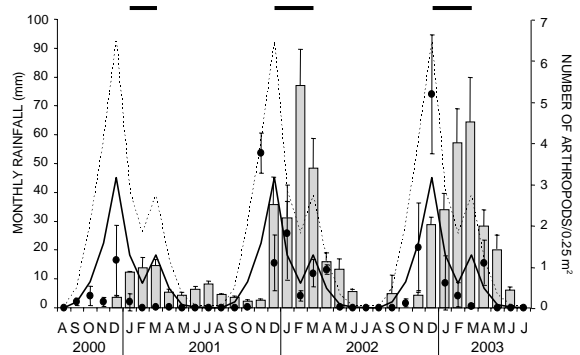

Fig. 2. Patterns of rainfall and food availability. Solid line: 13-year average rainfall (1989–2003) measured in the four weather stations close to the study sites; dotted line: upper 90% confidence interval for average rainfall (the lower interval is zero); dots: average ± SD monthly rainfall values for the study period (n = 4 stations); bars: average + SE number of arthropods (n = 4–6 depending on month; see text for details). Horizontal lines indicate the extent of the breeding period of Canary Islands stonechats for each study year (see Table 1 for details).

Temperature, on the other hand, did not vary significantly among study years. Mean monthly temperatures differed seasonally ($F_{11,22} = 36.22$, $P < 0.001$) but not among years ($F_{2,22} = 2.57$, $P = 0.1$; two-way ANOVA without replication with mean monthly temperature as the dependent variable, month as a fixed factor and year as a random factor). The highest mean monthly temperature was reached on August 2001 (24°C) and the lowest on February 2001 (17.3°C). The observed variability along the study years was within the 95% confidence intervals of the 31-year series available. The mean daily temperature of the month previous to the main laying period differed among years ($F_{2,88} = 29.25$, $P < 0.001$; one-way ANOVA with square-root transformed temperatures; Scheffé's test: $P < 0.001$ for all pairwise comparisons between December 2000, November 2001 and November 2002, and $P = 0.047$ for the comparison between November 2001 and November 2002). Mean daily temperatures for the fortnights just after and just before the end of the breeding periods did not show a consistent pattern, as significant differences were found in 2001 ($t_{29} = 2.73$, $P = 0.011$), but not in 2002 ($t_{29} = 1.72$, $P = 0.090$) and 2003 ($t_{29} = -1.01$, $P = 0.320$). Finally, mean daily temperature during the breeding season differed significantly among years (ANOVA; $F_{2,329} = 6.32$, $P = 0.002$), but this result was due to differences between 2001 and 2002 only (Scheffé's test, $P = 0.002$).

Food availability

Consistency of the pattern of arthropod availability across the island was tested using the data taken in 2002 only, when northern, central and southern sites

were sampled throughout the whole year. Due to missing data from some months in some central and southern sites, we used the pooled average of all central and the pooled average of all southern sites. Pooling reduced the number of sites to six, the four of the northern study area, one pooled estimate for the central study area and one pooled estimate for the southern study areas. No significant site effects were found ($F_{5,49} = 0.48$, $P = 0.79$; one-way ANOVA with square-root transformed mean monthly numbers of arthropods per sample as the dependent variable and site as a random factor). Temporal changes in arthropod availability were analysed using the three-year time series of the four northern localities. Arthropod availability was highly variable both seasonally ($F_{11,14} = 3.74$, $P = 0.01$) and among the three study years ($F_{2,14} = 11.93$, $P < 0.01$). Month by year interaction was also significant ($F_{14,80} = 4.35$, $P < 0.001$; two-way ANOVA with square-root transformed mean monthly numbers of arthropods per sample in the four northern localities as dependent variable, year as a random factor and month as a fixed factor). Density of arthropods on the ground was below one per square meter from June to November, then reaching the peak between December and March depending on the study year (Fig. 2). Low values of food availability after the winter peak were reached more quickly during the 2001 than during 2002 and 2003 (Fig. 2). Overall arthropod availability during breeding months was three times lower in 2000–2001 (0.96 ± 0.09 arthopods/0.25 m^2 (mean$\pm$SE); n = 3 breeding months; see below) than in the other two years (3.37 ± 0.41, n = 4 and 3.31 ± 0.44, n = 4, for 2001–2002 and 2002–2003, respectively). Monthly arthropod availability depended strongly on the amount of rainfall in the previous month ($Y = 1.19(0.09) + 0.62(0.13) \times X$; regression parameters and their standard errors; $R^2 = 45.80\%$; $P < 0.001$; Y: mean number of arthopods/0.25 m^2, square-root transformed; X: rainfall (mm), log-transformed; n = 27).

Reproductive traits

Onset and length of the breeding period

The onset of the breeding period differed significantly among years (ANOVA, $F_{2,73} = 68.02$, $P < 0.001$). This difference was due to the later laying date in 2000–2001 (Scheffé's tests, $P < 0.001$ for the comparisons between the first and each of the last two years; Table 1), as there were no significant differences between 2001–2002 and 2002–2003 (Scheffé's test). No second clutches were found in 2000–2001, whereas the laying dates for second clutches in 2001–2002 and 2002–2003 were not significantly different ($t = -0.62$, $P = 0.537$; Table 1).

The duration of the breeding season varied among years as well (Table 1). It was shorter in 2000–2001 than in 2001–2002 (Mann-Whitney U test, $U = 40.0$, $P < 0.001$) and 2002–2003 ($U = 52.5$, $P < 0.001$), but differences between 2001–2002 and 2002–2003 were not significant ($t = -1.07$, $P = 0.290$; Table 1). Incubation usually began when the penultimate egg was laid. The length of the incubation period did not differ among years (Kruskal-Wallis test, $\chi^2_2 = 0.06$, $P = 0.97$; 16.4 ± 0.3 days (mean$\pm$SE), range: 13–18, n = 17 nests). Nestlings remained in the nest for 17.7 ± 0.3 days on average (range: 14–20, n = 42 nests), and the duration of this period did not vary significantly among years (Kruskal-Wallis test, $\chi^2_2 = 5.71$, $P = 0.06$) even though most data on this breeding parameter (74%) was gathered in 2002–2003. The number of breeding attempts varied among years and determined the length of the breeding period. Excluding replacement clutches, females laid one or no clutch in 2000–2001 whereas in 2001–2002 and 2002–2003 they laid always two clutches. In 2000–2001, the females of 11 out of 32 pairs (34%) did not lay eggs at all despite the fact that their males were observed singing after the late fall rains and that at least two of those 11 females built a nest. No nesting attempt was recorded after a successful first one in this year, and only two pairs out of the 10 that suffered nest predation (22%) attempted a replacement clutch. In contrast, in 2001–2002 and 2002–2003 all breeding females studied (n = 27 and n = 28, respectively) laid two clutches, and all pairs that suffered nest predation carried out replacement clutches. Four females even started a second replacement clutch when the first one was predated. Therefore, the number of laying attempts per pair in each breeding season varied between 0 and 3, although the third attempts were always replacement clutches.

Table 1. Laying (the day when the first egg was laid) and fledging (the day when the last fledgling left the nest) dates ($\pm$SE) for first and second clutches in the three study years (1: December 1st). For pairs that suffered nest predation only data previous to the predation event were considered.

	2000–2001	2001–2002		2002–2003	
	First	First	Second	First	Second
Laying date $\pm$ SE	55.22 ± 2.69	29.72 ± 1.16	75.21 ± 1.34	30.93 ± 1.08	76.62 ± 1.60
Sample size	23	25	14	28	21
Range	32–83	18–42	64–82	22–43	64–91
Fledging date $\pm$ SE	90.82 ± 3.03	64.0 ± 1.11	108.69 ± 1.39	64.18 ± 1.17	111.19 ± 1.61
Sample size	22	13	13	22	21
Range	67–118	58–72	99–117	57–73	97–125

Reproductive investment and success

Reproductive investment was lower in 2000–2001 than in the other two years. In addition to the lower number of clutches, clutch size was smaller in 2000–2001 than in 2001–2002 and 2002–2003 (ANOVA, $F_{2,68} = 5.64$, $P = 0.005$), although significant differences were found between 2000–2001 and 2002–2003 only (Scheffé's test, $P = 0.006$; Table 2). Clutch size was significantly larger for second than for first clutches (excluding replacement clutches) laid by the same females both in 2001–2002 (2.92 ± 0.67 vs 3.58 ± 0.67 eggs (mean $\pm$ SE), $n = 12$, $t = -2.96$, $P = 0.013$; t-test for matched pairs) and in 2002–2003 (3.35 ± 0.49 vs 3.74 ± 0.62, $n = 23$, $t = -2.32$, $P = 0.03$). Mean clutch size (excluding replacement clutches) increased with mean arthropod availability both among years ($r_s = 0.5$, $P = 0.667$) and among localities ($r = 0.879$, $P < 0.001$; Fig. 3). The lack of significance of the among-years relationship was most likely due to low sample size ($n = 3$).

Between-year variation in reproductive output was mainly determined by reproductive effort, as components of reproductive success did not vary significantly among years or clutches. Hence, mean number of fledglings also increased with mean arthropod availability both among years ($r_s = 0.5$, $P = 0.667$) and among localities ($r = 0.868$, $P < 0.001$; Fig. 3). Hatching success was very high (Table 2) and did not vary significantly among the first clutches of the three years studied (Kruskal-Wallis test, $\chi_2^2 = 2.27$, $P = 0.320$), between the second clutches of 2001–2002 and 2002–2003 (Mann-Whitney U test, $U = 8.0$, $P = 0.220$; Table 2), or between the first and second clutches laid by the same females in 2001–2002 and 2002–2003 (Wilcoxon test, $Z = -0.68$, $P = 0.490$ and $Z = -1.11$, $P = 0.260$). Thus, more eggs laid generally produced more fledglings. The number of offspring successfully raised per pair differed significantly among years (ANOVA, $F_{2,64} = 23.52$, $P < 0.001$). This difference was due to the lower productivity of pairs during 2000–2001 (1.55 ± 0.31, $n = 20$, mean $\pm$ SE fledged young per pair that laid eggs) than during the following two years (4.30 ± 0.53, $n = 20$ and 5.78 ± 0.39, $n = 27$ for 2001–2002 and 2002–2003, respectively; Scheffé's tests, $P < 0.001$ for the comparisons between the first and each of the last two years). These differences were also due to differences in reproductive investment, as nest losses did not vary significantly among years. Out of 128 nests monitored (first, second and replacement clutches), 37 (29%) were predated and only one (0.8%) was deserted because it was flooded during a strong storm. Only two nests (5%) were predated during incubation and the remaining during the nestling stage. Most predated nests were found almost destroyed (67%), suggesting that feral cats *Felis catus* or other introduced mammals such as domestic dogs *Canis familiaris*, rats *Rattus* spp. or Algerian hedgehogs *Atelerix algirus* were the predators (Illera,

Table 2. Components of the breeding success of the Canary Islands stonechat (means±SE and sample sizes in brackets) for first, second and replacement clutches during the three study years.

| | 2000–2001 | | 2001–2002 | | | 2002–2003 | | |
	First	Replac.	First	Second	Replac.	First	Second	Replac.
Clutch size	2.70±0.15 (n=20)	2.50±0.50 (n=2)	3.12±0.14 (n=24)	3.64±0.17 (n=14)	3.75±0.25 (n=4)	3.29±0.10 (n=27)	3.74±0.13 (n=23)	3.50±0.34 (n=6)
Hatching success	0.95±0.04 (n=20)	1.00±0.00 (n=2)	0.86±0.06 (n=24)	0.93±0.07 (n=14)	1.00±0.00 (n=4)	0.90±0.05 (n=27)	0.89±0.05 (n=24)	0.67±0.21 (n=6)
Fledging success	1.00±0.00 (n=12)	0.33±0.00 (n=1)	1.00±0.00 (n=14)	1.00±0.00 (n=11)	1.00±0.00 (n=3)	1.00±0.00 (n=22)	1.00±0.00 (n=20)	1.00±0.00 (n=4)
Productivity	1.55±0.31 (n=20)	1.00±0.00 (n=2)	1.44±0.28 (n=25)	2.78±0.42 (n=14)	2.75±0.95 (n=4)	2.61±0.28 (n=28)	2.87±0.31 (n=24)	2.33±0.80 (n=6)
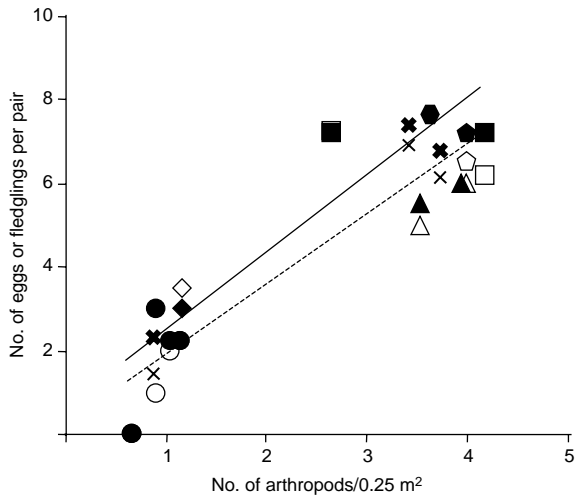
Fig. 3. Relationships between local and between-year arthropod availability and the mean number of eggs laid by each pair (excluding replacement clutches) and reproductive success (mean number of young fledged) of Canary Islands stonechats. Lines are back-transformed linear regression models (all variables were square-root transformed for analyses) based on average values of study sites (number of eggs: $Y = -0.01 + 1.37X$; number of fledglings: $Y = -0.22 + 1.37X$). Solid line, filled symbols: eggs; dotted line, empty symbols: fledglings. Circles: northern sites in 2000−2001; diamonds: central sites in 2000−2001; triangles: northern sites in 2001−2002; hexagons: central sites in 2001−2002; pentagons: southern sites in 2001−2002; squares: northern sites in 2002−2003. Annual averages are indicated by crosses (thick: number of eggs, thin: number of fledglings).

2004b). The few nests that were found undisturbed but empty could have been predated by native birds (*Lanius meridionalis*, *Corvus corax* or *Larus cachinnans*). Overall nest predation rates did not differ significantly among years ($G_2^2 = 2.94$, $P = 0.23$) or between first and second clutches in 2001−2002 and 2002−2003 ($G_1^2 = 1.14$, $P = 0.28$ and $G_1^2 = 0.39$, $P = 0.53$, respectively; Williams' correction).

Discussion

Between-year variation in the onset, end and thus length of the breeding period closely matched between-year differences in rainfall patterns (Fig. 2). Canary Islands stonechats started breeding significantly later and finished breeding significantly earlier in 2000−2001, the dry year, than in 2001−2002 and 2002−2003, two years with rainfall close to the long-term average. Between-year variability in temperature, on the other hand, did not match variability in breeding parameters. Canary Islands stonechats could have used seasonal changes in rainfall as a reliable cue (the proximate factor) to start preparing for breeding, as rainfall was a good predictor of future food availability. Hau et al. (2004) have demonstrated that small ground finches

(*Geospiza* spp.) in the Galápagos Islands respond to rainfall directly by starting gonad development and increasing production of sexual hormones such as LH. We had no direct measures of such physiological changes, although evident behavioural changes of birds in Fuerteventura just after the first autumn rains would support this hypothesis. All songbirds living in Fuerteventura, including stonechats, started to sing after rains, and male chats increased their territorial behaviour after rains being more aggressive to intruders than outside the breeding season (J.C. Illera pers. obs.). Rainfall, rather than photoperiod, light intensity or ambient temperature, has been proposed as the main stimulus triggering the onset of reproduction in arid and semiarid ecosystems (Leitner et al. 2003, Hau et al. 2004). Our results support this proposal as between-year variation in the breeding phenology of Canary Island stonechats matched variation in rainfall but not variation in temperature. However, because the main rainfall period occurs at similar times each year in Fuerteventura (Marzol-Jaén 1984; Fig. 2), photoperiod can not be excluded properly as a proximate factor triggering breeding, albeit in a way opposite to the most usual (decreasing rather than increasing daylenght would have been the triggering signal). Further studies relating rainfall, photoperiod, levels of sexual hormones and gonad development, either observational or manipulative, would be needed to test these alternative hypotheses.

Rainfall effects on reproduction can be direct, if water availability limits egg production (Tieleman et al. 2004), or indirect, if rainfall influences food availability. Direct effects of water shortage have been demonstrated for birds eating dry food items (i.e. seed-eating birds; Coe and Rotenberry 2003), but are hardly expected for insectivores due to the high levels of water provided by insect prey (Bartolomew and Cade 1963, Díaz 1996). Arthropod abundance was strongly and consistently predicted by rainfall, so that rainfall was a reliable cue for birds to estimate future food availability, which would constitute the ultimate factor determining the onset of the laying period. Apart from accounting for between-year differences in the onset of laying, this hypothesis could explain why some pairs did not lay any eggs during the breeding period of 2000−2001. Rains were scarce and of low duration in that period, and consequently food availability was also low. At least in one locality (Fimbapaire valley, in the northern area), food availability was also ephemeral, as it decreased dramatically as soon as in February (0.4 ± 0.10 arthropods/0.25 m^2 as compared to 0.87 ± 0.33 in January, just after rains, and 0.32 ± 0.10 in December, just before rains). The seven pairs monitored in this valley did not lay any eggs, despite some of them built a nest. No indication of breeding behaviours was observed during visits to other territories in the valley along February

and March (22–24 pairs were estimated that year). Low food availability at the time of laying was probably able to produce important physiological changes in females, shutting down secretions of sexual hormones that in turn produce the collapse of gonads thereby precluding oogenesis (Rotenberry and Wiens 1991, Kitaysky et al. 1999, Hau et al. 2004). Suppression of reproduction in years of scarce rainfall and low food supply is characteristic of birds in arid ecosystems (Boag and Grant 1984, Wiens 1991, Lloyd 1999, Tieleman 2002, Bolger et al. 2005).

Food availability could also have determined the reproductive investment (clutch size, number of clutches and length of the breeding period) of birds. Between-year differences in all these breeding parameters matched the variability in rainfall and arthropod abundance. Only one (or none) clutch per pair of smaller size was laid in the dry year as compared with the two other years, when all pairs bred twice, laid larger clutches and continued breeding for one month more on average. Food abundance was also related to annual reproductive investment at the local scale (Fig. 3). The same pattern was found for productivity (number of young fledged; Fig. 3), as expected by the lack of spatial and temporal variation in bird density, hatching success and predation rates. In contrast, the lack of temporal changes in food abundance within the breeding seasons of 2001–2002 and 2002–2003 apparently did not account for the observed increase in clutch size between first and second clutches laid by the same pairs. A possible explanation for this mismatch could be the difference in daylight hours available for females to forage during the laying period (Sanz 1999). The main laying period of the first clutches both in 2002 and 2003 occurred in late December-early January, the dates of longer nights in the Northern Hemisphere, whereas laying of second clutches occurred in mid February. Smaller first than second clutches are general in the Northern Hemisphere birds that usually lay two clutches, apparently because first clutches are usually laid early in the breeding season, when food availability is still increasing, whereas second clutches usually coincide with the seasonal peak of arthropod abundance (Crick et al. 1993, Soler et al. 1995). Between-year variation in the onset of the breeding period of Canary Islands stonechats and other arid land birds, that produce natural variation in the photoperiod experienced by birds, combined with food addition experiments, would be the best way for testing these alternative hypotheses.

Among-years variation in reproductive output was mainly determined by reproductive investment, since components of reproductive success (hatching and fledgling success) did not vary significantly among years or clutches. Lack of variation in hatching success, together with low variability of ambient temperature, implies that the influence of temperature on the repro-

ductive output proposed by Grant et al. (2000) for other arid islands was not at work in our study system. Nest predation, an important factor determining avian reproductive success in arid ecosystems (Rotenberry and Wiens 1989, Suárez and Manrique 1992, Mezquida and Marone 2001), has been recently proposed as an alternative mechanism to explain the observed associations between rainfall and reproductive output (Morrison and Bolger 2002). As rainfall is associated to lower temperatures that impose thermoregulatory constraints for ectothermic predators such as snakes and lizards, dry years could be not only poorer in food but also riskier for eggs and chicks. If this is the case, annual variation in fecundity could be due to primarily food-mediated processes in wet-cool years and by predator-mediated processes in dry years (Morrison and Bolger 2002). In our study system, however, this mechanism could not explain between-year variability in reproductive success. Most predation events were likely due to endotherms, especially feral cats, an opportunistic alien predator whose strong effects on the native species of the Canary Islands are well known (Nogales et al. 2004 and references therein). Nest predation reduced the number of young fledged each breeding season, but this negative effect was similar among years and, therefore, it could not account for the observed annual variation in breeding success (Mezquida and Marone 2003).

Summarising, rainfall itself, or perhaps other factors associated with the onset of rains such as changes in barometric pressures or increased humidity (Hau et al. 2004), seems to be the proximate factor triggering the onset of reproduction of the Canary Islands stonechat, whereas food (arthropod) abundance, which was strongly dependent on the rainfall of the previous month, seems to be the ultimate factor determining the onset of laying (Scheuerlein and Gwinner 2002), the length of the reproductive period and the reproductive investment of individual pairs (Grant et al. 2000, Bolger et al. 2005). Therefore, the annual variation in reproductive output was due to among-years variability in reproductive investment (number of broods and clutch sizes), which in turn was based on food-mediated processes rather than on temperature- or predation-mediated processes. Overall, results suggest that the Canary Islands Stonechat can be considered as a seasonal opportunistic breeder responding to favourable conditions by producing larger clutches and prolonging the breeding season (Grant et al. 2000).

Close dependence of annual reproductive output on rainfall, together with narrow range and short lifespan, makes Canary Islands stonechats highly vulnerable to future changes in the Islands' climate. Rainfall in the Canary Islands is influenced by the North Atlantic oscillation (NAO) and by the development of convective cells during autumn and spring (García-Herrera et al. 2001, 2003). Although climatic fluctuations produced by

the NAO are much less intense than those produced by the well-known El Niño Southern Oscillation (ENSO), recent papers have demonstrated significant effects on the breeding biology of mainland western Palaearctic birds (Sanz 2002, 2003). Unfortunately, knowledge on expected climate changes in the Canary Islands area is still too scarce to anticipate whether climate change could threaten Canary Islands stonechats. No detailed predictive models have been developed to date for this area (M. Castro, M.A. Gaertner and C. Gallardo, pers. com.), and the most recent study on precipitation trends during the second half of the 20th century (García-Herrera et al. 2003) reached mixed conclusions. It seems that overall rainfall on the archipelago has decreased strongly, but this trend was highly variable among islands. In fact, the only station available for Fuerteventura did not show any significant trend (García-Herrera et al. 2003). More detailed models of climate change developed at a high spatial resolution are thus needed to ascertain whether rainfall changes would interact with other better known threats for the species such as tourism or overgrazing (Illera 2001).

References

Alonso-Zarza, A. M. and Silva, P. G. 2002. Quaternary laminar calcretes with bee nests: evidences of small-scale climatic fluctuations, Eastern Canary Islands, Spain. – Palaeogeogr. Palaeoclimatol. Palaeoecol. 178: 119–135.

Bartolomew, G. A. and Cade, T. J. 1963. The water economy of land birds. – Auk 80: 504–539.

Boag, P. T. and Grant, P. R. 1984. Darwin's finches (*Geospiza*) on Isla Daphne Major, Galápagos: breeding and feeding ecology in a climatically variable environment. – Ecol. Monogr. 54: 463–489.

Bolger, D. T., Patten, M. A. and Bostock, D. C. 2005. Avian reproductive failure in response to an extreme climatic event. – Oecologia 142: 398–406.

Carracedo, J. C. and Day, S. 2002. Canary Islands. Classic geology in Europe series. – Terra Publishing, Hertfordshire.

Coe, S. J. and Rotenberry, J. T. 2003. Water availability affects clutch size in a desert sparrow. – Ecology 84: 3240–3249.

Collins, D. R. 1984. Studies of West Palearctic birds. 187. Canary Islands stonechat. – Brit. Birds 74: 467–474.

Crick, H. Q. P., Gibbons, D. W. and Magrath, R. D. 1993. Seasonal changes in clutch size in British birds. – J. Anim. Ecol. 62: 263–273.

Díaz, M. 1996. Food choices by seed-eating birds in relation to seed chemistry. – Comp. Biochem. Physiol. 113A: 239–246.

García-Herrera, R., Gallego, D., Hernández, E., Gimeno, L. and Ribera, P. 2001. Influence of the North Atlantic Oscillation on the Canary Islands precipitation. – J. Climate 14: 3889–3903.

García-Herrera, R., Gallego, D., Hernández, E, . Gimeno, L., Ribera, P. and Calvo, N. 2003. Precipitation trends in the Canary Islands. – Int. J. Climatol. 23: 235–241.

Genise, J. F. and Edwards, N. 2003. Ichnotaxonomy, origin, and paleoenvironment of Quaternary insect cells from Fuerteventura, Canary Islands, Spain. – J. Kansas Entomol. Soc. 76: 320–327.

Gibbs, H. L. and Grant, P. R. 1987. Ecological consequences of an exceptionally strong El Niño event on Darwin´s Finches. – Ecology 68: 1735–1746.

Grant, P. R., Grant, B. R., Keller, L. F. and Petren, K. 2000. Effects of El Niño events on Darwin's finch productivity. – Ecology 81: 2442–2457.

Hau, M. 2001. Timing of breeding in variable environments: tropical birds as model systems. – Horm. Behav. 40: 281–290.

Hau, M., Wikelski, M., Gwinner, H. and Gwinner, E. 2004. Timing of reproduction in a Darwin's finch: temporal opportunism under spatial constraints. – Oikos 106: 489–500.

Illera, J. C. 2001. Habitat selection by the Canary Islands stonechat (*Saxicola dacotiae*) (Meade-Waldo, 1889) in Fuerteventura Island: a two-tier habitat approach with implications for its conservation. – Biol. Conserv. 97: 339–345.

Illera, J. C. 2004a. Tarabilla Canaria (*Saxicola dacotiae*). – In: Madroño, A., González, C. and Atienza, J. C. (eds). Libro Rojo de las Aves de España. SEO/BirdLife-Dirección General de Biodiversidad/Ministerio de Medio Ambiente, Madrid, pp. 327–328.

Illera, J. C. 2004b. Biogeografía y ecología de la Tarabilla Canaria (*Saxicola dacotiae*) con implicaciones para su conservación. – PhD Thesis, University of La Laguna, Spain.

Immelmann, K. 1970. Environmental factors controlling reproduction in African and Australian birds-a comparison. – Ostrich. Supl. 8: 193–204.

Kitaysky, A. S., Wingfield, J. C. and Piatt, J. F. 1999. Dynamics of food availability, body condition and physiological stress response in breeding black-legged kittiwakes. – Funct. Ecol. 13: 577–584.

Leitner, S., Van't Hof, T. J. and Gahr, M. 2003. Flexible reproduction in wild canaries is independent of photoperiod. – Gen. Compar. Endocrinol. 130: 102–108.

Lloyd, P. 1999. Rainfall as a breeding stimulus and clutch size determinant in South African arid-zone birds. – Ibis 141: 637–643.

MacLean, G. L. 1970. The breeding seasons of birds in the south-western Kalahari. – Ostrich. Supl. 8: 179–192.

Martín, A. and Lorenzo, J. A. 2001. Aves del Archipiélago Canario. – Francisco Lemus Editor, La Laguna, Spain.

Martínez-Cabello, A., Soler, M. and Soler, J. J. 1991. Alimentación de la Tarabilla Común (*Saxicola torquata*) en el sureste de la península Ibérica durante el período otoño-invierno. – Ardeola 38: 317–326.

Marzol-Jaén, M. V. 1984. El Clima. – In: Afonso, L. (dir) Geografía de Canarias. Editorial Interinsular Canaria, Santa Cruz de Tenerife, Spain, pp. 157–202.

Mezquida, E. T. and Marone, L. 2001. Factors affecting nesting success of a bird assembly in the central Monte Desert, Argentina. – J. Avian Biol. 32: 287–296.

Mezquida, E. T. and Marone, L. 2003. Comparison of the reproductive biology of two Poospiza warbling-finches of Argentina in wet and dry years. – Ardea 91: 251–262.

Morrison, S. A. and Bolger, D. T. 2002. Variation in a sparrow's reproductive success with rainfall: food and predator-mediated processes. – Oecologia 133: 315–324.

Nogales, M., Martín, A., Tershy, B. R., Donlan, C. J., Veitch, D., Puerta, N., Wood, B. and Alonso, J. 2004. A review of feral cat eradication on islands. – Conserv. Biol. 18: 310–319.

Noy-Meir, I. 1973. Desert ecosystems: environment and producers. – Annu. Rev. Ecol. Syst. 4: 25–51.

Ostfeld, R. S. and Keesing, F. 2000. Pulsed resources and community dynamics of consumers in terrestrial ecosystems. – Trends Ecol. Evol. 15: 232–237.

Patten, M. A. and Rotenberry, J. T. 1999. The proximate effects of rainfall on clutch size of the California Gnatcatcher. – Condor 101: 876–880.

Rodríguez, O., García, A. and Reyes, J. A. 2000. Estudio fitosociológico de la vegetación actual de Fuerteventura (islas Canarias). – Vieraea 28: 61–104.

Rotenberry, J. T. and Wiens, J. A. 1989. Reproductive biology of shrubsteppe passerine birds: geographical and temporal variation in clutch size, brood size, and fledging success. – Condor 91: 1–14.

Rotenberry, J. T. and Wiens, J. A. 1991. Weather and reproductive variation in shrubsteppe sparrows: a hierarchical analysis. – Ecology 72: 1325–1335.

Sanz, J. J. 1999. Does daylength explain the latitudinal variation in clutch size of pied flycatchers Ficedula hypoleuca? – Ibis 141: 100–108.

Sanz, J. J. 2002. Climate change and breeding parameters of great and blue tits throughout the western Palaearctic. – Global Change Biol. 8: 409–422.

Sanz, J. J. 2003. Large-scale effect of climate change on breeding parameters of pied flycatchers in Western Europe. – Ecography 26: 45–50.

Soler, M., Moreno, J., Møller, A. P., Lindén, M. and Soler, J. J. 1995. Determinants of reproductive success in a Mediterranean multi-brooded passerine: the black wheatear Oenanthe leucura. – J. Orn. 136: 17–27.

Scheuerlein, A. and Gwinner, E. 2002. Is food availability a circannual zeitgeber in tropical birds? A field experiment on stonechats in tropical Africa. – J. Biol. Rhythms 17: 171–180.

Suárez, F. and Manrique, J. 1992. Low breeding success in Mediterranean shrubsteppe passerines: Thekla lark Galerida theklae, lesser short-toed lark Calandrella rufescens, and black-eared wheatear Oenanthe hispanica. – Ornis Scand. 23: 24–28.

Tieleman, B. I. 2002. Avian adaptation along an aridity gradient: physiology, behavior and life history. – PhD Thesis, University of Groningen, Groningen.

Tieleman, B. I., Williams, J. B. and Visser, G. F. 2004. Energy and water budgets of larks in a life history perspective: parental effort varies with aridity. – Ecology 85: 1399–1410.

Whitford, W.G. 2002. Ecology of desert systems. – Academic Press, San Diego.

Wiens, J. A. 1991. The ecology of desert birds. – In: Polis, G. A. (ed.). The ecology of desert communities. University of Arizona Press, Tuscon, pp. 278–310.

Zann, R. A., Morton, S. R., Jones, K. R. and Burley, N. T. 1996. The timing of breeding by zebra finches in relation to rainfall in central Australia. – Emu 95: 208–222.