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ORIGINAL ARTICLE

Temperature but not rainfall influences timing of breeding in a desert bird, the trumpeter finch (*Bucanetes githagineus*)

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Abstract Reproductive performance in birds depends on several factors, one of the most important being the time of breeding. Birds try to fit offspring birth and growth to peak vegetative production in order to assure fledgling survival. In arid environments, where weather conditions are often extreme, birds must face unpredictable abiotic conditions. This study uses a border population of the trumpeter finch (*Bucanetes githagineus*) as a model to test whether climate variables (rainfall and temperature) influence breeding parameters by comparing 2 years with very different weather. The study was carried out in the Tabernas desert (southeastern Spain) in 2004 and 2005. A comparison of laying dates in the 2 years shows a 40-day delay in the date of the first clutch in the coldest year (mean minimum temperature 3°C lower in 2005 than in 2004). However, once the breeding season started, the number of clutches, clutch size, duration of the incubation period, nestling phase, fledgling rates and productivity were similar. One likely explanation for this delay is that low temperatures did not allow the germination of *Diplotaxis* sp., a plant forming the bulk of the trumpeter finch diet during spring. Its absence could prevent onset of breeding, although other temperature-related factors could also be involved. Although rainfall has frequently been reported as a limiting factor for arid bird species, our 2-year study shows that temperature can also influence the breeding biology of arid bird species, by affecting its timing.

Keywords Arid lands · Breeding season · *Bucanetes githagineus* · Laying date · Low temperatures

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Introduction

Among breeding parameters, the decision on when to start breeding, or timing, is one of the most important factors influencing reproductive performance in most northern temperate birds (Lack 1968; Dunn 2004), and, therefore, crucial to understanding variation in fitness among individuals and populations (Daan et al. 1990). To assure breeding success, birds must breed only when conditions are suitable for the production of viable offspring (Wallen and Schneider 1999). The main factor determining onset of breeding is the photoperiod (Wingfield and Farner 1980; Dawson et al. 2001), but climate variables such as rainfall and temperature also play an important role (Immelmann 1971). These environmental variables can also affect breeding factors such as cost of incubation (Reid et al. 2000) or food provisioning (Hoset et al. 2005) among others.

Specifically, for birds from arid regions, rainfall is the climate parameter most frequently analyzed with regard to breeding parameters (e.g., Zann et al. 1995; Li and Brown 1999; Lloyd 1999; Morrison and Bolger 2002), mainly because of its importance in primary productivity and consequent food availability. However, other climate variables, such as temperature, have not been studied with regard to breeding parameters (but see Lloyd 1999; Illera and Díaz 2006), although its influence on food availability is also obvious. In general, higher temperatures directly favor egg formation and laying adjustment aimed at fitting hatching to peak food availability (Lack 1950, 1968). In fact, warm temperatures in early spring advance breeding in some birds (Schmidt 1984; Brown et al. 1999). Moreover, during cold springs in temperate climates, delayed breeding has been recorded under both natural (Dhondt and Eyckerman 1979) and controlled (Meijer et al. 1999) conditions. Climate variables can be even more important in granivorous species due to their effect on the reproductive cycle of plants (Lloyd 1999). In this paper, we use the trumpeter finch (*Bucanetes githagineus*), a strictly granivorous species distributed across the warm arid regions of the Middle East and the Iberian Peninsula (Cramp and Perrins 1994), as a model to test the influence of both temperature and rainfall on the breeding of a desert bird in semiarid areas. As the test period, we took 2005, a year in which temperatures were unusually low in February and March but precipitation was high compared to 2004.

In addition, most passerine reproduction studies have focused on species subject to low predation rates, whereas the breeding biology of species with high nest predation rates, like the trumpeter finch, is not well known (Suárez et al. 2005). Moreover, European arid regions have been studied little even though they are one of the most original landscapes in the Western Palaearctic. A large number of endemic or rare species of birds dwell in these ecosystems, and conservation of most of them is of concern (Suárez et al. 1993). Recently, the distribution ranges and abundance of many of them have been undergoing changes (BirdLife International 2004). In most cases, their habitat ranges are decreasing due to changes in land use (Serrano and Astraín 2005; Tella et al. 2005) while, in a very few cases, their habitat ranges have spread as a result of recent climate changes (BirdLife International 2004; Carrillo et al. 2007).

Therefore, this article reports on (1) the relative importance of two climate variables, temperature and rainfall, in 2 years with very different weather for the breeding of a desert bird, and (2) presents, for the first time, comprehensive data on the breeding biology of the trumpeter finch from a recently established population resulting from this species' expansion (Carrillo et al. 2007).

Methods

The study area was located in the Tabernas Desert, in Almería province (37°02′N, 02°30′W), southeastern Spain. It is an area of 12 km^2 lying 260 m a.s.l. and 10 km from the nearest urban population. The area is characterized by badlands crisscrossed by ravines with abrupt slopes at mid-hillside. Sandy cliffs face in several directions, and dry riverbeds have substrates with a high percentage of bare ground. Vegetation, concentrated at the bottom of dry riverbeds, is dominated by perennial grasses like *Stipa tenacissima* and *Lygeum spartum* and xerophytic shrubs like *Salsola genistoides*, *Artemisia barrelieri*, *Launaea arborescens, Limonium tabernense* and *Anabasis articulata*. Annual *Cruciferae* species, such as *Diplotaxis* spp. and *Moricandia* spp., are also common. The study area has a Mediterranean-semiarid climate, with a mean annual precipitation of less than 250 mm. This kind of habitat is characteristic of many other localities in the arid south-eastern Iberian Peninsula (Peinado et al. 1995).

We monitored a population of trumpeter finches during their breeding seasons from February to August in 2004 and 2005. The study area was the same in both years. Nest searching (5–6 days per week) was conducted with the same effort (i.e., identical number of researchers and time expended in nest searching) throughout the breeding period and in both years. Nests were found following parents with a telescope from exposed observation points that enabled wide areas to be scanned. Nests, for which either the incubation phase or the nestling periods were not completely monitored, were not included in the corresponding analyses. During incubation, parental activity in the nests was observed by telescope every 3–5 days and the number of visits (2–5) was limited to minimize both disturbance to breeding pairs and possible increase in predation risk due to human visits. When no parental activity was recorded during incubation, the nest was approached to verify its status. After no increase in clutch size between consecutive visits, the clutch was considered complete. The incubation period was calculated only in those nests observed from laying to hatching. Although partial incubation occurs before the clutch is complete (authors, unpublished), we considered the number of days from the last egg laid to hatching of the first egg the incubation period. Nests were visited daily after 7 days of incubation to ascertain the exact hatching date. The nestling period was calculated from hatching to fledging. Nests were observed daily by telescope after 7 days of incubation to record the fledging date and number of fledglings. A nest was considered successful if at least one chick fledged or if the chicks were out of the nest and developed well enough to fly. The fledgling rate was calculated as the mean number of fledglings per nest in those nests in which at least one chick fledged. Productivity was calculated as the number of fledglings per pair controlled, including pairs with nest failure.

Trumpeter finches spend 4–6 days courting and 2–6 building their nests (Cramp and Perrins 1994; authors, unpublished). Thus, every pair makes the decision to start breeding roughly 2 weeks before the first egg is laid. Therefore, to study how climate variables influence timing of breeding, we compared daily minimum temperatures and daily precipitation before the first known clutch in 2004 and 2005. Minimum temperatures were employed because, at the beginning of the breeding season, they are the strongest constraint (Sanz 1998; Brown et al. 1999; Dunn 2004). We considered the following periods to analyse the variation of weather parameters: (1) 14 days before the first recorded clutch in 2004 (PB04); (2) the same calendar days in 2005 (PB0405); (3) 14 days before the first recorded clutch in 2005 (PB05), and (4) the delay in start of breeding in 2005 compared to 2004 (D05) defined as the days between PB04 and PB05 (see Fig. 1 for details). Climate data (daily minimum temperatures and daily precipitation) were from the Tabernas meteorological station (37°05′N, 02°18′W) located 18 km from the breeding area (Andalusian government database). For inter-annual comparison of the distribution of active nests during the season, they were grouped by weeks (Fig. 1).

Statistics were analysed using Mann–Whitney U-tests and Wilcoxon matched pairs to test for inter-annual differences in breeding parameters. Differences in temperature and rainfall were analyzed by the Student t-tests.

Results

Daily minimum temperatures in the Tabernas desert, which were markedly different in the periods defined for the two years studied (Fig. 1), were (mean °C ± standard error) for PB04 (4.09 ± 0.59), PB05 (8.80 ± 0.57), PB0405 (1.11 ± 0.79) and D05 (2.16 ± 0.65). Daily precipitation in the different periods was (mean mm ± standard error) for PB04 (0.02 ± 0.02), PB05 (0.00 ± 0.00), PB0405 (2.07 ± 1.44) and D05 (1.73 ± 0.68). The temperatures were lower in 2005 on the same dates when breeding started in 2004 (PB04 vs PB0405, $t = 4.02$, $n = 14$, $P < 0.01$) and until

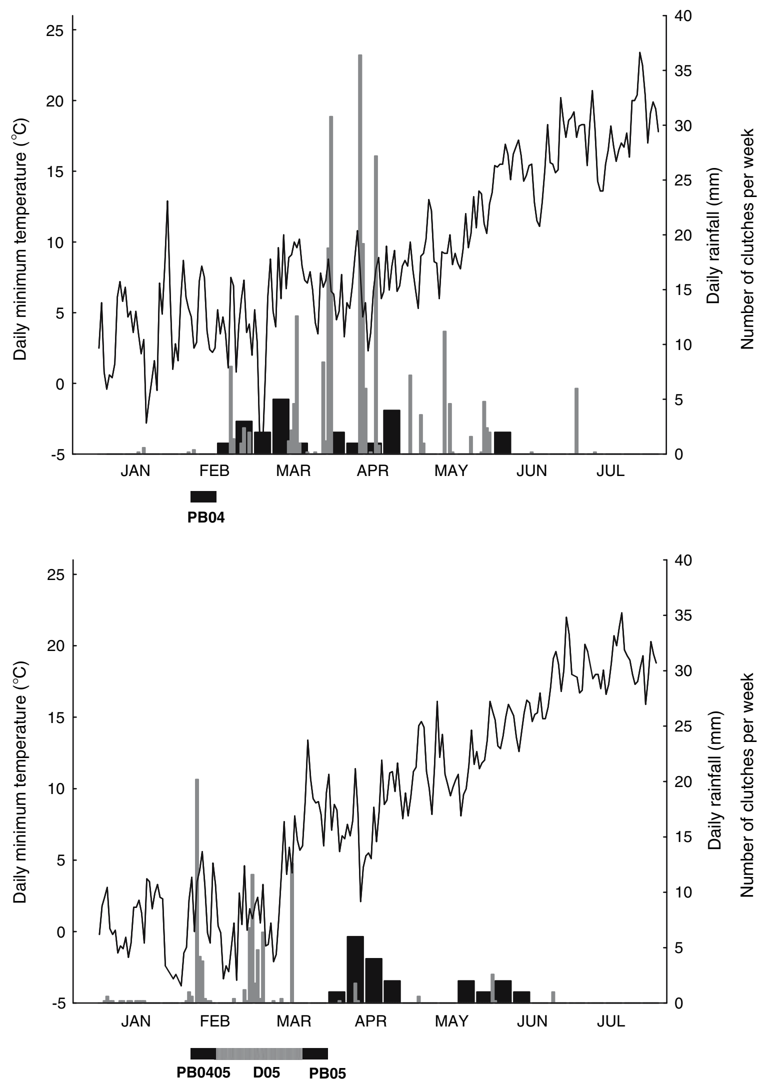

Fig. 1 Daily minimum temperature (°C, *black line*), daily rainfall (mm, *grey bars*) and number of trumpeter finch (*Bucanetes githagineus*) clutches per week (*black bars*) in the Tabernas desert in 2004 (*upper*) and 2005 (*lower*). *Bars* at the bottom mark the periods for which climate variables were compared, included for weather analysis in every figure

breeding started in 2005 (PB04 vs D05, $n_{2004} = 14$, $n_{2005} = 27$, $t = 2.32$, $P = 0.03$). However, no differences in rainfall were found during these same periods ($t = 1.40$, $n = 14$, $P = 0.18$; $t = 0.24$, $n_{2004} = 14$, $n_{2005} = 27$, $P = 0.81$, respectively). On the contrary, during the period before breeding started in 2005 (PB05), minimum temperatures increased sharply over the previous days (D05), $t = 7.51$, $n_{PB05} = 14$, $n_{D05} = 27$, $P < 0.001$). Although rainfall increased in the same period, the differences were not statistically significant ($t = 1.74$, $n_{PB05} = 14$, $n_{D05} = 27$, $P = 0.08$).

Totals of 25 nests in 2004 and 24 in 2005 were monitored, although for some nests not all breeding parameters could be recorded, either because breeding had already started when the nests were found, or because nests were predated before the eggs or fledglings had completely developed (Table 1). Timing of breeding was different in the 2 years because in 2005 the first clutch was recorded 40 days later (1 April) than in 2004 (20 February) (Fig. 1). However, we did not find any correlation between the number of clutches in the same periods in 2004 and 2005 ($r_s = 0.20$, $n = 20$, $P = 0.38$). There were no significant inter-annual differences in the following breeding parameters (Table 1): number of clutches per week ($z = 0.39$, $n = 20$, $P = 0.69$), clutch size ($z = 0.65$, $n_{2004} = 12$, $n_{2005} = 3$, $P = 0.48$), duration of incubation period ($z = 0.16$, $n_{2004} = 11$, $n_{2005} = 3$, $P = 0.85$), duration of nestling phase ($z = 0.73$, $n_{2004} = 5$, $n_{2005} = 5$, $P = 0.44$), fledgling rates ($z = 0.09$, $n_{2004} = 6$, $n_{2005} = 5$, $P = 0.93$) or productivity ($z = 0.30$, $n_{2004} = 22$, $n_{2005} = 17$, $P = 0.77$).

Discussion

Our results show that temperature, not rainfall, affects timing of breeding in a desert bird such as the trumpeter finch. Low temperatures caused a 40-day delay in the first clutch in 2005, a cold year, compared to a warmer 2004. Once breeding started, all the parameters analyzed were similar in both years. Several studies have pointed out how low temperatures in early spring can cause a delay on breeding starting, but most of them were in bird species from cold regions (Lack 1968; Dunn 2004). To our knowledge, this is the first time that such an effect has been reported in a bird species in an arid environment.

One of the most likely explanations for the effects of temperature on timing of breeding is its relationship with abundance of food (Lack 1968; Dunn 2004). *Diplotaxis* spp. is one of the main sources of food during the breeding season in southeastern Spain, both for adults and offspring of fringillid species (Valera et al. 2005), including the trumpeter finch (Carrillo et al., unpublished data). This annual *Cruciferae* has low germination rates below mean temperatures of 15°C (PerezGarcia et al. 1995). Therefore, low temperatures during early spring can reduce the availability of seeds until new *Diplotaxis* plants germinate, grow and produce fruits. As a result, birds are forced to delay breeding to assure enough food for chick development (Murphy 1986; Meijer et al. 1999). Other explanations for the relationship between temperature and timing of breeding include low temperatures not allowing females to allocate the energy necessary for egg production because it is needed for thermoregulation, and an effect on gonad growth/maturation (Dunn 2004), although the exact mechanisms are unclear (Jacobs and Wingfield 2000), and their importance remains to be tested.

Some authors have found an inverse relationship between temperature and timing of breeding in desert birds. Van Heezik et al. (2002) found that low winter temperatures produced earlier laying in houbara bustards (*Clamydotis macqueenii*). Nevertheless, as the study was conducted in captive birds with food and water ad libitum, such a relationship could be due to internal physiological factors such as luteinizing hormone plasma levels (van Heezik et al. 2002).

Our study population is at the northernmost edge of the trumpeter finch's breeding range, which has been expanding since the 1970s (Carrillo et al. 2007). The influence of abiotic factors on demographic rates may be higher in border populations than in the centre (García and Arroyo 2001), and may therefore determine range limits (Root 1988). In this trumpeter finch population, abiotic factors such as temperature seem to influence some basic breeding decisions. However, our results suggest that there are no inter-annual differences in the number of clutches, clutch size, duration of incubation period, duration of nestling

Table 1 Breeding parameters of the trumpeter finch (*Bucanetes githagineus*) in the Tabernas desert (Almería, southeastern Spain) in the 2004 and 2005 seasons

Year	Clutch size	Incubation period	Nestling period	Fledgling rate	Productivity
2004	5.1 ± 0.3 ($n = 12$)	12.5 ± 0.2 ($n = 11$)	13.4 ± 1.0 ($n = 5$)	3.5 ± 0.7 ($n = 6$)	1.0 ± 0.4 ($n = 22$)
2005	4.7 ± 0.3 ($n = 3$)	12.7 ± 0.9 ($n = 3$)	12.2 ± 0.4 ($n = 5$)	3.4 ± 0.7 ($n = 5$)	1.1 ± 0.4 ($n = 17$)

Data are expressed as the mean number of eggs ± SE (clutch size), mean number of days ± SE (incubation and nestling period) and mean number of chicks ± SE per successful nest (fledgling rate) and per nest (productivity). Samples sizes are shown in brackets phase, fledgling rates nor productivity. These results can be explained by lower temperatures in 2005 only at the very beginning of spring, whereas later on, temperatures were similar to 2004, probably allowing the breeding season to proceed under similar conditions. However, as sample sizes were small for some parameters, they should be treated with some precaution.

Rainfall has frequently been reported as the most important meteorological event for birds in arid land areas (Li and Brown 1999; Lloyd 1999; Morrison and Bolger 2002; Illera and Díaz 2006) due to its importance to life in these scarce-water habitats. In fact, Zann et al. (1995) found that rainfall, rather than low winter temperatures, determines the first clutches of the zebra finch (*Taeniopygia guttata*), an Australian desert bird. The importance of water in arid lands is commonly linked to its integral effect with temperature on the plant reproductive cycle (Lloyd 1999; Dunn 2004). We did not find any statistical difference in rainfall between the 2 years and, therefore, in our study, this variable was not directly related to either start of breeding or variation in the other breeding parameters (number of clutches, clutch size, duration of incubation period, duration of nestling phase, fledgling rates or productivity). Although some authors have found increases in clutch size during wet years in some arid land birds, these are not consistent in all the species studied, suggesting species-specific patterns (e.g., Lloyd 1999).

On the other hand, it has been suggested that in favorable years in unpredictable environments, like arid lands, the productivity of birds increases due to an extended breeding season (i.e., more breeding attempts) (e.g., Zann et al. 1995) rather than modified breeding parameters. However, we did not find any change in the length of the breeding season. Moreover, the breeding season ended in June in both years, in spite of having begun 6 weeks later in 2005. Some non-mutually-exclusive explanations may account for this: (1) a decline in abundance of food due to withering of annual plants, like *Diplotaxis* sp., in summer (Hegazy 2001); (2) high day-time temperatures and intense solar radiation on chicks in the nest could compromise chick survival (Yanes et al. 1996); (3) high temperatures cause water scarcity in the study area, and consequently prevent later breeding because chicks need water for their development (Coe and Rotenberry 2003); and (4) energy allocation trade-offs between breeding and moulting (Sanz 1999; Hemborg et al. 2001) can also impose limitations on reproduction during summer.

Finally, it has been suggested that changes in timing of breeding in birds is related to increases in the minimum temperature due to global climate change (e.g., Brown et al. 1999). The Mediterranean region is one of the areas most sensitive to climate change, showing important inter-annual variability in precipitation and temperature (Sánchez et al. 2004). Extreme events, such as the unusual temperatures recorded in 2005 in southern Spain, can produce phenological changes in wild animals (Easterling et al. 2000) as reported here for the trumpeter finch.

In conclusion, this article reports on the first thorough study on the breeding biology of the trumpeter finch. Rainfall has frequently been reported as a limiting factor for arid bird species, but our 2-year study shows that temperature can also influence the breeding biology of arid bird species, by affecting its timing.

Zusammenfassung

Die Temperatur und nicht der Niederschlag beeinflusst den Zeitpunkt der Brut bei einem Wüstenvogel, dem Wüstengimpel (*Bucanetes githagineus*)

Der Reproduktionserfolg von Vögeln hängt von mehreren Faktoren ab, wobei die Zeitigung der Brut einer der wichtigsten ist. Vögel versuchen die Zeit der Geburt und Aufzucht ihrer Jungen an Produktivitätsmaxima der Vegetation anzugleichen, um deren Überlebenswahrscheinlichkeit beim Ausfliegen zu verbessern. In Wüstenlebensräumen, wo die Wetterbedingungen häufig extrem ausfallen, müssen Vögel mit unvorhersagbaren abiotischen Faktoren zurechtkommen. Die vorliegende Arbeit verwendet eine Randpopulation des Wüstengimpels als Modell um herauszufinden, ob Klimavariablen (Niederschlag und Temperatur) Brutparameter beeinflussen, indem zwei Jahre mit stark unterschiedlicher Witterung verglichen werden. Die Studie wurde in der Wüste von Tabernas (Südost-Spanien) in den Jahren 2004 und 2005 durchgeführt. Ein Vergleich der Legedaten der beiden Jahre zeigt eine Verspätung von 40 Tagen beim ersten Gelege für das kälteste Jahr (die mittlere Minimal-Temperatur lag 2005 um 3°C niedriger als 2004). Sobald jedoch die Brutzeit begonnen hatte, waren die Anzahl an Gelegen, Gelegegröße, Dauer der Inkubationszeit, Nestlingszeit, sowie die Ausfliegeraten und die Produktivität gleich. Eine wahrscheinliche Erklärung für die Verspätung liegt darin, dass niedrige Temperaturen verhinderten, dass *Diplotaxis* sp., die Hauptnahrung des Wüstengimpels im Frühjahr, keimen konnte. Das Fehlen dieser Pflanze könnte den Start des Brutgeschäfts unterbinden, aber auch andere temperaturabhängige Faktoren könnten eine Rolle spielen. Wenngleich Niederschlag häufig als limitierender Faktor für Wüsten bewohnende Vogelarten angeführt wurde, zeigt unsere Arbeit über zwei Jahre, dass die Temperatur die Brutbiologie von Wüstenbewohnern ebenso beeinflussen kann, indem sie den Brutzeitpunkt steuert.

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