

TROPICAL PHENOLOGY IN TEMPERATE REGIONS: EXTENDED BREEDING SEASON IN A LONG-DISTANCE MIGRANT

CARLOS CAMACHO¹

Department of Evolutionary Ecology, Estación Biológica de Doñana (EBD-CSIC), Américo Vespucio s/n, 41092, Seville, Spain

Abstract. The chronology of birds' breeding has traditionally been thought to depend strongly on latitude, although it can be rather uneven among populations in close proximity. I estimated the extent of the breeding season in a population of the Red-necked Nightjar (*Caprimulgus ruficollis*) over three years in southwestern Spain. Data from brood patch development and appearance of recently fledged young provided evidence for a breeding season unusually extended (110 days) for a long-distance migrant. Flexible timing in reproduction appeared to affect individual's departure in migration. Although most adult nightjars gradually left the study area beginning in mid August, some late breeders left the area about a month later than the earliest migrants. Decreasing competition for food and free nesting territories, together with a food supply and predation pressure constant through the season, resemble conditions in the tropics and enable the nightjars to breed over an extended period despite inhabiting a temperate region. The nightjars' phenology was further expanded by a protracted period (≥ 35 days) of parental care, which also led to later molt prior to autumn migration. However, birds partially compensated for time costs to adjust to the annual cycle by initiating a simultaneous shedding of flight feathers immediately after hatching. In accordance with current studies showing how breeding events carry over into the annual routines of birds, results from this nightjar population come on top of recent hypotheses regarding new ways in which breeding, molt and migration could interact and condition each other.

Key words: annual cycle, breeding season, *Caprimulgus ruficollis*, migration, molt, Red-necked Nightjar.

Fenología Tropical en una Zona Templada: Período Reproductor Prolongado en un Migrante de Larga Distancia

Resumen. La latitud es considerada habitualmente como un factor determinante de la cronología reproductiva de las aves, aunque ésta puede resultar dispar entre poblaciones cercanas. Durante tres años, estimé la duración del período reproductor en una población de *Caprimulgus ruficollis* del suroeste de España. Los datos sobre el desarrollo de la placa incubatriz y la aparición de pollos recién volados mostraron la existencia de un período reproductor inusualmente prolongado (110 días) para un migrador de larga distancia. La flexibilidad temporal en la reproducción aparentemente afectó a la partida migratoria de los individuos. Aunque la mayoría de los chotacabras abandonaron el área de estudio de forma gradual desde mediados de agosto, algunos reproductores tardíos partieron con una diferencia de un mes respecto a los primeros. La disminución en la competencia por el alimento y los territorios de cría, junto con el constante aporte de alimento y presión de depredadores, parecen emular condiciones típicamente tropicales, permitiendo a los chotacabras criar durante un largo periodo de tiempo a pesar de habitar regiones templadas. La fenología de los chotacabras se vio además extendida por un cuidado parental prolongado (≥ 35 días), lo que también generó retrasos en la muda previa a la migración otoñal. Sin embargo, las aves compensaron parcialmente estos costes temporales para ajustarse al ciclo anual, iniciando una muda simultánea de plumas de vuelo inmediatamente después de la eclosión. De acuerdo con los estudios actuales que ilustran la incidencia de los eventos de reproducción sobre las rutinas anuales de las aves, los resultados de esta población de chotacabras se suman a las recientes hipótesis que contemplan nuevas formas en las que la reproducción, la muda y la migración pueden interactuar y condicionarse entre sí.

INTRODUCTION

Accurately timing reproduction is especially favored by natural selection in temperate latitudes (Murton and Westwood 1977), where seasonally changing cues drive birds to schedule breeding to coincide with appropriate conditions to maximize success and survival (Lack 1968, Perrins 1970, Stearns 1992). In relatively stable tropical regions, however, birds' breeding seasons are not only longer but also far more variable in duration than in

temperate areas (Stutchbury and Morton 2001). Even though latitude has long been recognized to be an accurate predictor of birds' breeding phenology (Baker 1939), recent studies challenge conventional assumptions (see Stutchbury and Morton 2001) by showing how seasonal reproduction can be widely asynchronous both within a population and among populations inhabiting nearby areas, as a result of different habitat features (Aragonés et al. 2001), genetic and cultural differentiation (Moore et al. 2005), or migratory behavior (Tökölyi and Barta 2011).

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¹E-mail: ccamacho@ebd.csic.es

The Red-necked Nightjar (*Caprimulgus ruficollis*) is a long-distance migrant widespread across dry warm regions of the Iberian Peninsula (Cleere 1999). In southern Spain, its numbers increase notably from early April to mid May, as migrants pass through and breeders arrive (Camacho 2013). Previous studies of the phenology of the species' breeding have revealed the chronology of populations in close proximity to be rather uneven. At two sites about 110 km apart, though the first nightjars initiate laying around mid May at both, there is a difference of nearly two months (53 days) in the date of laying of the last clutches (Cuadrado and Domínguez 1996, Aragonés 2003).

In comparison to insectivores resident in the Mediterranean region and those migrating across the Sahara, some populations of the Red-necked Nightjar arrive and lay relatively late, and their breeding season is notably extended (e.g., Lessells and Avery 1989, Bechet et al. 1998, Aparicio and Bonal 2002). Yet typically long-distance migrants often have breeding seasons shorter than those of their sedentary counterparts and of short-distance migrants breeding at the same latitude. For example, a comparative study of shorebirds revealed an interaction between migration distance, latitude, and the length of the breeding season: the distance shorebirds from high latitudes migrate tends to decrease more rapidly as the egg-laying season lengthens than does the distance shorebirds from lower latitudes migrate (García-Peña et al. 2009). More recently, Tökölyi and Barta (2011) found support for the correlated evolution of migratory behavior and breeding phenology and showed that both the onset of breeding and the length of the breeding season in small and medium-sized passerines is significantly correlated with migration distance. With its asynchronous breeding and migratory habits, the Red-necked Nightjar seems to be an appropriate model that may provide insight into the plasticity of breeding of species within narrow areas and to explore possible carry-over effects on the annual routines of migratory birds (see McNamara and Houston 1996).

The synchrony of birds' breeding is usually determined by the availability of food resources (likely influenced by ambient temperature), breeding habitat, the intensity of competitive interactions, and predation pressure (Monteiro and Furness 1998). In contrast to those in the tropics (Stutchbury and Morton 2001), birds from temperate regions usually synchronize their breeding activities to conditions declining seasonally from the optimum (Stearns 1992). Therefore, it could be predicted that locally stable conditions should promote a prolonged breeding season even within temperate regions. In this study, I used data on brood-patch development and appearance of recently fledged young to ascertain the overall length of the breeding season in the Red-necked Nightjar. At the same time, I assessed seasonal changes in food abundance, predation pressure, and numbers of neighboring conspecifics to determine whether temporally increasing or stable favorable conditions (food supply and breeding habitat) and steady or declining adverse

factors (competitive interactions and predation pressure) allow birds to extend their breeding phenology locally within a temperate scenario. In addition, migrants are generally constrained by time to complete breeding and molt from arrival to departure (Hemborg et al. 2001, Flinks et al. 2008, Conklin and Battley 2012). Therefore, asynchronous reproduction of a long-distance migrant should lead to differing molt strategies and staggered departure dates to the winter range. Here, I explore and discuss possible consequences that the wide interval in which the Red-necked Nightjar breeds could have on its annual life cycle.

METHODS

I studied the seasonal reproductive output of the Red-necked Nightjar in a flat sandy area within the highly protected core of Doñana Biological Reserve and in a nearby property where resources are exploited (e.g., agriculture, cattle raising, and hunting). The sites are in southwestern Spain (37° 1–7' N, 6° 32–33' W; Fig. 1). The vegetation consisted mainly of a mixture of Mediterranean shrublands with cattle-grazed grasslands and plantations of pine trees. Preliminary observations from August to October 2009 and 2010 preceded the core field season from March to November 2011.

GENERAL FIELD PROCEDURES

Every other night, driving a vehicle at a constant speed of 30 km hr⁻¹, I counted nightjars along a 35-km transect following roads crossing the protected and the managed area. During these transects, I captured nightjars by using a LED flashlight and a hand-held net (Jackson 1984). All individuals were marked with numbered metal bands, sexed according to the size of the pale spots on the wing and tail feathers (Forero et al. 1995), and aged as either hatch year or after hatch year according to the criteria of Gargallo (1994) and Forero et al. (1995). I gently checked adult females for presence of eggs in their abdomen and scored their brood patches as active (females carrying an egg or showing a completely bare patch with obvious blood vessels) or inactive (forming feathered patch, regressing wrinkled patch, or completely absent). Recently fledged nightjars are easily distinguishable from juveniles because their body mass is significantly lower (~15%) than that of juveniles and growth of their flight feathers is incomplete; development of the tail is always slightly delayed behind that of primaries and secondaries (unpubl. data). Hence I categorized hatch-year birds into two age classes on the basis of feather development: recently fledged young (new feathers not fully grown, feathers still emerging from sheaths or retaining waxy sheath at base) and juveniles (new feathers fully grown). For adults growing flight feathers, I noted the number of molting primaries and rectrices (from new feathers just emerging to almost fully grown) and assessed their state of molt on this basis. I used the proportion of birds in active molt (one or more growing flight feathers) to assess temporal variation in the timing of molt.

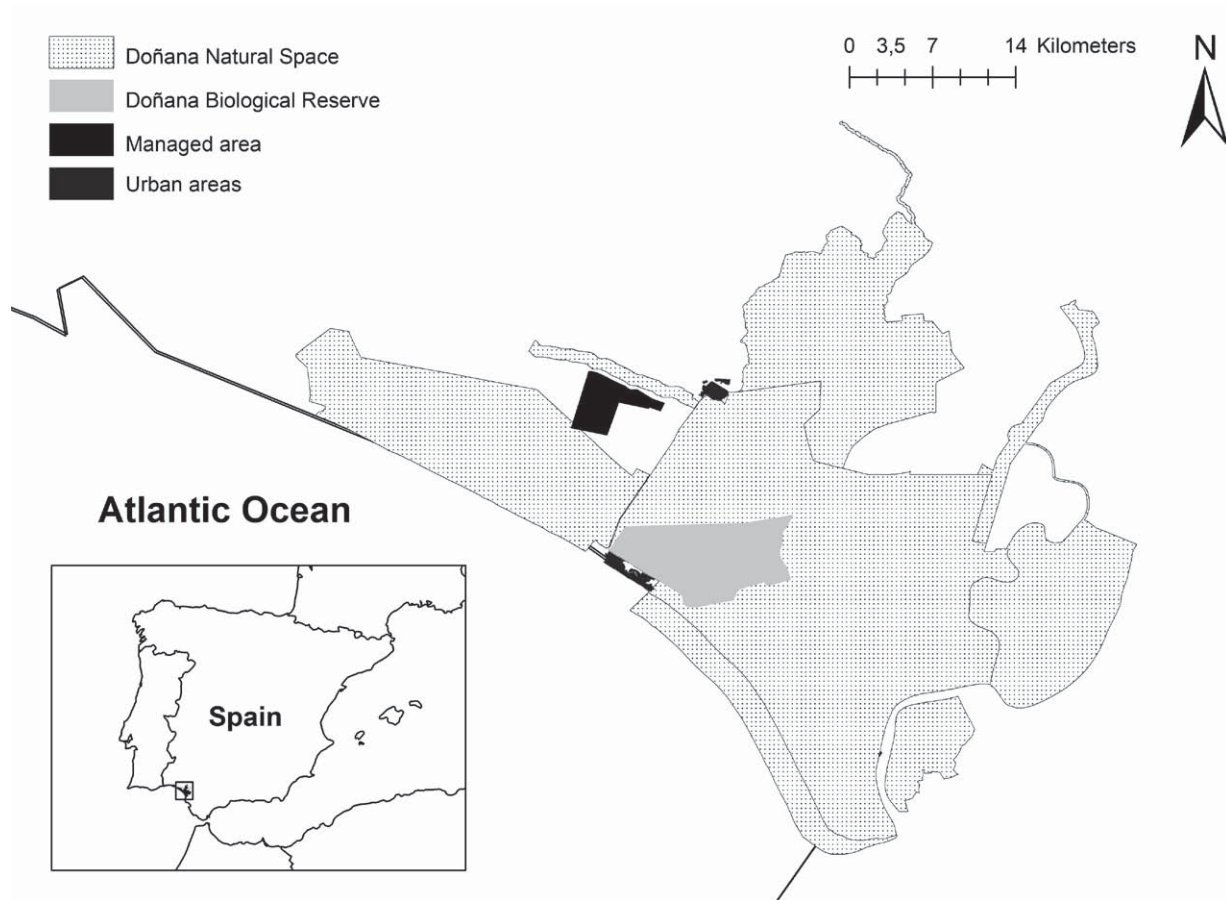


FIGURE 1. Geographical situation of the two sites (Doñana Biological Reserve and managed area, southwestern Spain) of study of the breeding of the Red-necked Nightjar.

BREEDING PHENOLOGY

The highly cryptic habits and color patterns of nightjars make finding their nests difficult, so I used alternative indirect measures to assess the phenology of breeding. As a proxy for breeding activity, I used a kilometric index of abundance (Tellería 1986) from systematic transect counts of recently fledged young. Additionally, the proportion of females carrying an egg or showing an active brood patch served as supporting evidence of the timing of breeding.

I used the laying period, defined as the number of days between completion of the first and the last clutch and estimated by backdating young (Jackson 1985, Vilella 1995), to estimate the overall length of the breeding season. Applying the age at fledging (18–22 days after hatching) and the incubation period (16–19 days) reported for the Red-necked Nightjar in southwestern Spain (Cuadrado and Domínguez 1996, Aragonés 2003), I projected the duration of the laying period from the dates on which I trapped recently fledged young. Finally, I conservatively estimated the total length of the laying period from the earliest date of laying and the latest date of detection of fledglings with the minimum and the

maximum “laying-to-fledging” intervals, respectively (i.e., 18 + 16 and 22 + 19 days).

CONSTRAINTS ON PLASTICITY IN TIME OF BREEDING

Following Monteiro and Furness (1998), I assessed temporal variation in potential constraints on plasticity in the nightjar’s time of breeding: availability of food resources and breeding habitat, intensity of competition for food, and predation pressure. I used the mean number of neighboring conspecifics, quantified by the systematic transect counts of adult nightjars, as a measure of momentary competition at the population level (Löhmus and Väli 2004) and as a coarse proxy for the availability of potential breeding territories (Forsman et al. 2008). I used temporal changes in the nightjars’ occurrence on roads to assess adults’ migration phenology (Camacho 2013). Only the maximum values for a week served as a basis for my assessment of the seasonal variation in potential competition and breeding habitat.

I quantified the availability of food from June to October 2011 by means of 20 transects of 4000 m along which I drove

at a constant speed of 40 km hr⁻¹ a car on the roof of which a tow net (50 × 50 cm entrance, 2-m length and 0.5-mm mesh size; see Jetz et al. 2003) was mounted. All aerial insects from each sample were stored at -20 °C then sorted to the level of order, counted, and weighted together to the nearest 0.01 mg. Diptera (mainly mosquitoes) predominated in terms of abundance, although their contribution to the overall aerial biomass was negligible, so I excluded them from subsequent analyses. Following previous studies of the diet of afrotropical nightjars (Jackson 2000a, b) as well as my own data from regurgitates, I considered only the orders Lepidoptera, Homoptera, and Neuroptera as potential aerial prey of the Red-necked Nightjar.

From June to August 2011 I assessed predation pressure through nest-predation experiments. For this purpose, I baited 72 experimental nests with two quail (*Coturnix coturnix*) eggs across several patches in which real nightjar nests had been previously discovered. To avoid attracting predators by human odor, I used latex gloves while handling eggs. I considered a nest depredated when one or both eggs were damaged or missing in the three following days. The total proportion of depredated nests per two-week period yielded a time-point index of the predation rate. When possible, I identified predators to species by their tracks in the sand. To assess possible temporal changes in predation pressure and food availability, I grouped data from nest predation and insect sampling into two well-separated periods defined by the temporal distribution of gravid and incubating females: the main breeding season (1–30 June), when ~80% females showed an active brood patch, and the late breeding season (17 July–15 August), when only ~20% females showed an active brood patch (see Fig. 2).

STATISTICAL ANALYSES

For all analyses I used a generalized linear model (with Poisson distribution and log-link function) unless otherwise stated. I used chi-squared (χ^2) tests to compare rates of predation of experimental nests in the main and the late breeding seasons and to assess the temporal differences in molt

patterns. For statistical analyses I used R (version 2.15; R Core Team 2012) and set the significance level for each test at $P < 0.05$. All values are reported as mean ± SD.

RESULTS

BREEDING PHENOLOGY

Between 2009 and 2011, I marked 605 individuals (222 adult males, 203 adult females and 180 hatch-year birds), of which 31% of males, 43% of females, and 22% of hatch-year birds were recaptured (1–7 times) at some point during the study.

The proportion of females with an active brood patch and the appearance of recently fledged young were complementary (Fig. 2). Between 16 and 30 June 2011, 90% of females were already carrying an egg or showing fully developed brood patches, coinciding with the earliest recently fledged young from early clutches. In accordance with the incubation and nestling periods (16–19 and 18–22 days, respectively), the highest rate of occurrence of recently fledged young was not observed until the period between 17 and 31 July 2011. Brood-patch development also showed that 20% of pairs initiated clutches late (i.e., beyond the main breeding season).

Backdating from recently fledged young (first and last detected on 16 June and 11 October 2011, respectively) revealed that laying must have been spread over at least 110 days, from 13 May to 31 August (see Fig. 2). In both 2009 and 2010, recently fledged young were also observed until late September (last record on 29 September), indicating temporal consistency in dates of delayed laying. Recapture of two gravid females that had been radiotagged in June 2011 to test other hypotheses provided the first evidence in the Red-necked Nightjar for the laying of replacement clutches after failure of a first nest.

In three focal nests monitored from hatching to fledging, chicks fledged at 20 to 22 days old and, though they were already capable of catching insects, seemed to be still heavily dependent on adults. Recaptures of recently fledged birds

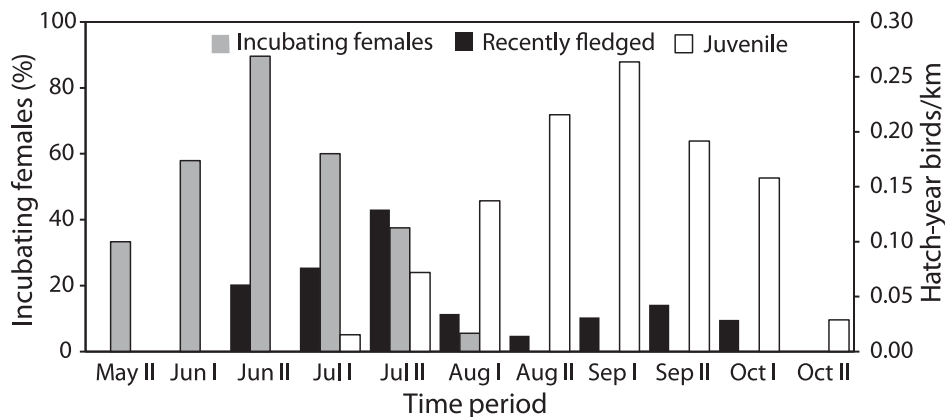


FIGURE 2. Seasonal variation in the breeding of the Red-necked Nightjar in Doñana by half month (I, first half; II, second half). Shaded bars show the proportion of females already incubating (active brood patch) or about to lay (carrying an egg). Solid and open bars represent the relative abundance of fledglings and juvenile, respectively. Two-week periods in which values for all three variables were zero are omitted (i.e., April I–II, May I, and November I–II).

($n = 41$; 2009–2011) showed that they moved daily to bare open areas (usually gravel roads), where they were visited by their parents in close succession from dusk to dawn. Association of fledglings with their parents and nest site extended well beyond fledging, as parents brooded even 35-day-old chicks at night.

TEMPORAL MOLT PATTERNS

Most adult nightjars (75%, $n = 325$) initiated molt after the main breeding season ($\chi^2_1 = 119.85$, $P < 0.001$). Timing of breeding seemed to have a major effect on molt-initiation dates, although nightjars modulated molt processes to advance the completion of postnuptial partial molt. In both males and females, more than half (55%) of actively molting birds ($n = 259$) showed ≥ 5 feathers growing simultaneously, up to a maximum of 10–15 being shed at the same time ($n = 27$). Point estimates of molt investment were significantly higher in males (5.5 ± 3.5 feathers) than in females (4.6 ± 2.9 feathers; $F_{1,258} \approx 10.53$, $P = 0.001$), probably because of the overlap of molt and breeding in females. Growing flight feathers rarely (5.5%) occurred with an active brood patch ($n = 182$ females). However, the number of females still showing regressing patches and already molting at the time of capture (59 of 81) was significantly higher than the number that had not yet initiated molt (22 of 81; $\chi^2_1 = 21.16$, $P < 0.001$), indicating that females started to shed flight feathers immediately after their chicks hatched, well before they fledged.

CONSTRAINTS ON PLASTICITY IN TIME OF BREEDING

Intraspecific competition should be greatest and availability of breeding habitat should be lowest between 16 May and 30 June,

coinciding with the main breeding season (Fig. 3). From mid August, adult nightjars gradually left the study area (Fig. 3), although capture–recapture data showed that some local birds (defined as those captured before 20 August) remained on their breeding ground beyond mid September ($n = 24$ males, 15 females). Females that laid their first clutch in the main breeding season (i.e., showing an active brood patch between 20 May and 30 June) and were recaptured later confirmed that some local breeders remained in the study area for almost three months after their first attempt at breeding (81 ± 21.9 days, $n = 9$).

The transects for prey sampling yielded 461.16 mg of arthropods of the orders Lepidoptera, Homoptera, Neuroptera, and Diptera. The availability of suitable prey remained constant through the season and accounted for 88% and 92% of the overall biomass filtered during the main and the late breeding season, respectively (main breeding season: 52.5 ± 99.8 mg dm⁻³, late breeding season: 52.6 ± 50.6 mg dm⁻³; $F_{1,7} \approx 0$, $P = 0.98$). Predators, mainly Eurasian Magpies (*Pica pica*), damaged or stole 35 of 144 eggs (19 out of 72 experimental clutches), and the rate of predation suffered by experimental nests during the main breeding season (33.3%) did not differ statistically from that during the late breeding season (19.3%; $\chi^2_1 = 0.58$, $P = 0.45$).

DISCUSSION

The extension of the breeding season in this population of the Red-necked Nightjar is, to my knowledge, the longest recorded not only for this species but for any long-distance migrant so far studied. The only two previous studies of the breeding biology of nightjars in southwestern Spain have

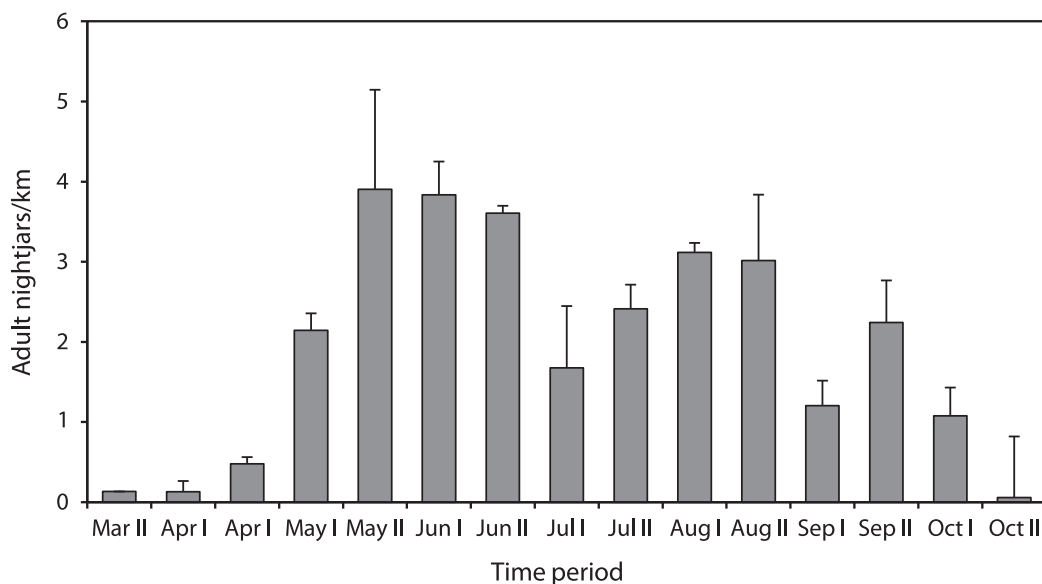


FIGURE 3. Seasonal variation in the relative abundance (mean \pm SD) of adult Red-necked Nightjars in the study area through the breeding season of 2011 by half month (I, first half; II, second half). Two-week periods in which values for all three variables were zero are omitted (i.e., November I–II).

TABLE 1. Length of the breeding season (duration of the laying period) in migrant and sedentary nightjars of the genera *Caprimulgus*, *Anrostomus*, and *Eleothreptus*. Reproductive phenology may strongly vary across range, so only species for which accurate (to the nearest 24 h) population data on breeding events are available are presented.

| Species | Migratory behavior | Location | Laying period (days) | Reference |
|--------------------------|--------------------|-------------------------|---------------------------------|----------------------------------|
| <i>C. ruficollis</i> | Migratory | Doñana, SW Spain | 13 May–31 Aug (110) | Present study |
| <i>C. ruficollis</i> | Migratory | Doñana, SW Spain | ≥17 Aug (??) | Hidalgo (1974) |
| <i>C. ruficollis</i> | Migratory | Guadalcázar, SW Spain | 14 May–10 Jun (26) | Aragonés (2003) |
| <i>C. ruficollis</i> | Migratory | Los Palacios, SW Spain | 21 May–2 Aug (73) | Cuadrado and Domínguez (1996) |
| <i>C. ruficollis</i> | Migratory | E Morocco–W Tunisia | 12 May–11 Aug (91) | Heim de Balsac and Mayaud (1962) |
| <i>C. aegyptius</i> | Migratory | Haouf, C Morocco | 16 Mar–10 Aug ^a (??) | Robin (1969) |
| <i>C. europaeus</i> | Migratory | Several, C and S UK | Not reported (41) | Perrins and Crick (1996) |
| <i>A. carolinensis</i> | Migratory | C Florida, SE USA | 17 Mar–17 Jul (122) | Rohwer (1971) |
| <i>A. noctitherus</i> | Sedentary | Guanica, SW Puerto Rico | 24 Feb–1 Jul (127) | Vilella (1995) |
| <i>A. sericocaudatus</i> | Sedentary | Manu, SE Peru | 20 Aug–25 Oct (66) | Wilkinson (2009) |
| <i>E. candicans</i> | Sedentary | Mbaracayú, E Paraguay | 14 Sep–21 Nov (68) | Pople (2003) |
| <i>C. pectoralis</i> | Sedentary | Ranelia, E Zimbabwe | 14 Sep–17 Nov ^b (64) | Jackson 1985 |
| <i>C. tristigma</i> | Sedentary | Ranelia, E Zimbabwe | 24 Aug–20 Oct ^b (57) | Jackson 1985 |
| <i>C. fossii</i> | Sedentary | Ranelia, E Zimbabwe | 14 Sep–8 Dec ^b (85) | Jackson 1985 |

^aOnset and duration of the laying period may fluctuate annually (≤4 months long) according to the rainfall regime.

^bEgg-laying dates may vary annually because of synchrony with the lunar cycle.

shown the phenology of laying within a population to vary little within periods of 2–4 consecutive years (Cuadrado and Domínguez 1996, Aragonés 2003). Conversely, laying dates of geographically close populations seem to diverge substantially. In the northernmost population studied (37° 45' N, 4° 56' W; 158 km NE of Doñana), Aragonés (2003) found a laying period of only 23–26 days, whereas only slightly farther south (37° 09' N, 5° 55' W; 57 km NE of Doñana), Cuadrado and Domínguez (1996) found fertilized eggs over 73 days. In Doñana, the southernmost studied population to date, the laying period is spread over at least 110 days (minimum range: 13 May–31 August). Remarkably, even though dates of initiation of laying in these three Iberian populations are quite similar, last clutches are laid significantly later in Doñana, where the breeding season is therefore extended. Some afrotropical nightjars time their breeding phenology to coincide with the peak in prey abundance (Jetz et al. 2003), suggesting that food availability rather than latitude might act as a constraint at the seasonal level and explain the wide differences among populations (Perrins and Birkhead 1983). Unfortunately, no data on food supply at the other two sites are available to test this hypothesis.

The late appearance of recently fledged young in all three years of my study, together with anecdotal evidence of late laying 25 km NE of my study site (Hidalgo 1974), suggests that delayed laying by the Red-necked Nightjar in Doñana is not a mere isolated or opportunistic phenomenon but annually repeatable. Even though some chicks at the other sites could have fledged without being noticed, it is unlikely

that differences in bird detection alone account for the differences among populations in the extent of the breeding season. Furthermore, if fledging of the first and the last fledglings was detected accurately, the breeding season would be estimated as even longer.

With double brooding of the Red-necked Nightjar now confirmed, such extremely delayed laying is likely attributable to birds laying replacement clutches after failure of a first attempt (Cuadrado and Domínguez 1996). Regardless, the overall laying period in this population is not only the largest recorded for the Red-necked Nightjars and the sibling migratory species *C. europaeus*, but it is similar to or even longer than those of other tropical nightjars, migratory and sedentary (Table 1). The length of breeding season of the Red-necked Nightjar at Doñana also exceeds the longest reported so far in the literature for any species of migrant with an annual breeding cycle (e.g., Perrins and Birkhead 1983, Lessells and Avery 1989, Bechet et al. 1998, Aparicio and Bonal 2002).

Several features could be underlying the asynchronous breeding of the nightjars in Doñana. Monteiro and Furness (1998) proposed four main factors as constraining plasticity in time of breeding in birds: (1) availability of food resources, (2) intensity of competition for those resources, (3) availability of breeding habitat, and (4) predation pressure. At temperate high latitudes the food supply usually declines through the season, which usually restricts birds' breeding to periods of high food availability (Perrins 1970). At Doñana, however, the constant food supply available may constrain nightjars' time for breeding less. In addition, the density of breeding

nightjars can increase considerably in structurally complex habitats, where loosely aggregated pairs breed earlier than those isolated in areas with less vegetative cover (Aragonés et al. 2001). The high density of nightjars (up to 3.5 birds km⁻¹) and high fraction of females (pre)laying during the main breeding season (90%) emphasize the study site's attractiveness for breeding, which may lead to spatial segregation of nightjars. However, the stable food supply and predator pressure may enable some birds to avoid the negative effects of intraspecific competition through temporal segregation. Thus initially overcrowded patches may be accessible to late pairs after early breeders leave the study area beginning in mid-August. The decreased competition for food and increased availability of free nesting territories, together with the steady food supply and predation pressure, make conditions at Doñana more like those in the tropics and allow nightjars to breed over a strikingly extended periods despite the temperate latitude.

CARRY-OVER EFFECTS WITHIN A SEASON

An already delayed phenology could be extended further by extended parental investment. Stutchbury and Morton (2001) suggested asynchronous breeding as an important selective force behind strong fledgling–parent bonds in the tropics. This factor might promote such extended breeding seasons in temperate areas. Prolonged fledgling–parent bonds following delayed laying should constrain the time available for molting prior to autumn migration (see Flinks et al. 2008). This constraint might explain both the occasional suspension of molt of the Red-necked Nightjar (Gargallo 1994) and the overlap of flight feather molt and fledgling care as strategies by which the species adjusts to the annual cycle. At this point, the question may arise why females with successful first nests withhold reproductive effort under such optimal and stable conditions. According to Ogden and Stutchbury (1996), constraints on double brooding in migratory birds seem to be unrelated to the parents' experience, body condition, or reproductive output at their first nest. In the long-distance migrant *Setophaga citrina*, Ogden and Stutchbury (1996) noted that double-brooded individuals were usually feeding fledglings while undergoing their molt. They concluded that the main cost of double brooding was a three-week delay in the annual cycle beyond that of single-brooded birds. Time and energetic costs due to the overlap of molt and fledgling care might also explain why Red-necked Nightjars rarely attempt a second brood to enhance their annual reproductive output. Delayed reproduction followed by completion of partial molt apparently affected the nightjar's migration by imposing a delay of over 30 days on individuals laying late first or replacement clutches beyond the schedule of the earliest migrants (considered to be those leaving Doñana beginning 20 August, probably after successfully raising early broods). High reproductive effort late in the season might be responsible for some local birds remaining in the study area long after the early migrants have departed.

Current findings suggest that such delayed breeding need not disrupt the nightjar's annual life cycle. Birds that increase the time spent on breeding could reduce the time invested in molt and migration by overlapping breeding and molt (Flinks et al. 2008), increasing the rate of molt (Conklin and Battley 2012), reducing distance of migration (Tökölyi and Barta 2011), reducing the length of stopovers (Stutchbury et al. 2011) or winter residence or even increasing speed of travel between staging sites (Tøttrup et al. 2012). The distance to the winter range and conditions birds experience there (e.g., food and competitors) might also influence the timing of the nightjar's breeding and molt in its breeding range (Tökölyi and Barta 2011, Conklin and Battley 2012). On the other hand, over the last two decades climate change has led to an advancing spring phenology in some temperate regions. Some species have responded to this change by advancing the timing of migration or the onset of breeding (Marra et al. 2005, Potti 2009). With a relatively stable food supply at Doñana, the Red-necked Nightjars there might benefit from earlier springs by advancing their seasonal schedule, increasing opportunities for breeding. The long period spent on the breeding ground might indicate that this nightjar population is in the process of switching from migratory to sedentary life style. The seasonal plasticity of breeding, molt, and migration schedules in this population of the Red-necked Nightjar adds to the recently advanced understanding of temporal plasticity in long-distance migrants (see Helm et al. 2005, Flinks et al. 2008, Conklin and Battley 2012), although further field data are needed to provide insight into the adjustments of the birds' current annual routines in response to the continuing environmental changes.

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