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Early age at first breeding and high natal philopatry in the Red-necked Nightjar *Caprimulgus ruficollis*

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Recruitment rates, natal philopatry and the onset of breeding activity are documented for the first time in the order Caprimulgiformes. Out of 171 Red-necked Nightjars *Caprimulgus ruficollis* ringed as fledglings between 2008 and 2011, 31 (18%) were later recovered in south-western Spain. Females tended to disperse slightly further (680 m) than males (570 m), and no individuals from the study site or nearby locations were ever recovered outside the area where it hatched, suggesting high natal philopatry. Most males (94%) and females (73%) recruited into the breeding population in their first year of life, whereas only a few individuals were not recovered until their second (10%) or third (7%) year of life. In contrast to most long-lived birds, nearly all (95.5%) Red-necked Nightjars started to reproduce in their first potential breeding season.

Key words: age of reproduction, Caprimulgiformes, natal dispersal, philopatry, recruitment, Red-necked Nightjar

Juvenile recruitment into adult populations and the age at which long-lived species start to reproduce have a large influence on the evolution of life-history strategies (Ferrer *et al.* 2004, Krüger 2005). Reliable estimation of return rates, natal philopatry and age at first breeding is crucial to assess and ensure the viability of animal populations (Lindström 1999), but costly long-term studies involving marked animals are usually required to measure these parameters.

Nightjars, nighthawks, and relatives (Caprimulgiformes) are crepuscular and nocturnal insectivorous birds with highly cryptic plumage and behaviour, and are thus difficult to detect and monitor. As a result, many questions remain about their basic life-history strategies. Nonetheless, the family Caprimulgidae is one of the best studied avian taxa in terms of heterothermy (reviewed by Brigham *et al.* 2012), and there is a growing literature on several aspects of their breeding biology, including breeding success and productivity (e.g. Langston *et al.* 2007, Wilkinson 2009, Allen & Peters 2012). In contrast, little is known about life-history traits influencing population dynamics or viability (Forero *et al.* 2001, Silvano & Boano 2012).

In this study, I used a five-year dataset on Red-necked Nightjars *Caprimulgus ruficollis* in south-western Spain to provide the first data, to my knowledge, on recruitment, natal philopatry and age at first breeding in the order Caprimulgiformes. Average body mass of Red-necked Nightjars is approximately 100 g and maximum recorded longevity is 13 years (data from the Spanish Ringing Centre). In south-western Spain, the breeding season extends from mid May to late August (Camacho in press). The modal clutch size is two, and fledging success declines with the progress of the season (Cuadrado & Dominguez 1996). Recent data on Red-necked Nightjar population trends across its breeding range indicate a decline of over 20% in recent years

(SEO/BirdLife 2012), so there is an urgent need to carry out long-term research on basic life-history traits of this species.

METHODS

I used data from an intensive study of Red-necked Nightjars inhabiting Mediterranean shrublands in the north-western border of the Doñana National Park (SW Iberian Peninsula, 37°7' N, 6°33' W) during 2008−2012 (see Camacho 2012 for a description of the study area). Here, nightjar density is medium-high compared to other populations of caprimulgids (Doucette 2010), with 158 different adult individuals caught in the 2058 ha area in one year (author's unpublished data). Red-necked Nightjars were caught from 1–2 h after dusk until dawn along a 24-km road circuit using a LED torch and a hand-held net. Capture sessions were conducted weekly from spring arrival (April) to the end of the breeding season (October) in 2011 and 2012, starting in early August in the first three years of study. Success in finding Red-necked Nightjar nests is often low (Cuadrado & Domínguez 1996, Aragonés 2003), so hatch-year birds were captured as fledglings. All individuals were individually marked with numbered metal rings, and aged and sexed following criteria described by Forero *et al.* (1995). Capture locations were geo-referenced with a Garmin GPS 60 (2-4 m accuracy). Only locally born individuals (i.e. recruits) of known-age were considered in analyses. Reproductive activity of recruits (both males and females) was assessed by presence of brood patch (Camacho in press).

Recruitment rates were calculated as the proportion of fledglings hatched in the study area between 2008 and 2011 which returned to breed in the following years (i.e. 2009−2012). To reduce under-estimation of recruitment rates as a result of dispersal beyond the study area, I conducted additional capture sessions within a 20 km buffer of the study area between 2009 and 2012. At the study site, recently-fledged and breeding Red-necked Nightjars usually forage on the nearest roads to nests (mean distance: 123.3 m ± 69.6 se; author's unpublished data). Therefore, because nest-finding success is low, a crude estimate of natal dispersal distances (i.e. movements of individuals between near their birthplace and site of first breeding) were calculated with the ArcGIS10 software as the distance (to the nearest 5 m) between capture locations of individuals ringed as fledglings and later recovered as first time breeders.

RESULTS

Nocturnal surveys between 2008 and 2012 (176 trap nights) resulted in 898 captures in the study area and 263 additional captures in the buffer area, relating to 576 and 199 different individuals, respectively. Out of 171 fledglings ringed in years 2008 to 2011, 31 (18.1%) were later recovered in the study area (up to and including 2012). Overall recovery rates were 18% for males (n = 89) and 18.3% for females (n = 82; $\chi^2_1 = 0.002$, $P = 0.96$). The breeding activity of recruits could be determined for 27 individuals (87%) that were recovered during the laying period (the rest were only captured shortly after arrival of just before departure).

The majority of ringed fledglings (93.8% of males, 73.3% of females) that recruited to the study area did so in their first year of life, the sex difference being not significant ($\chi^2_1 = 0.03$, $P = 0.86$). First-year individuals seemed to be fully capable of breeding, as nearly all Red-necked Nightjars of this age (91.7% of males, 100% of females; $\chi^2_1 = 0.03$, $P = 0.87$) showed evidence of current or recent breeding activity. Just a few individuals were not recovered as breeders until their second (one male, two females) or third (two females) year of life (Fig 1). Not a single individual from the study site or buffer area was ever recovered outside the area where it hatched. Females tended to disperse slightly further than males (median (Q25–Q75): 680 m (180−910) *vs.* 570 m (270−835)), but median natal dispersal distances did not differ between the sexes (Mann-Whitney U test, $Z = 74.5$, $P = 0.91$).

DISCUSSION

Most Red-necked Nightjars recruited into the breeding population and attempted to breed in their first year of life. No individual was ever recovered outside the area where it hatched, suggesting high levels of natal philopatry.

Resident caprimulgids seem to exhibit high adult site fidelity (Jackson 1985, Doucette 2010) and these results suggest that the natal philopatry of nightjars is also very high. This is unusual given that natal philopatry is typically very low for migratory birds (Weatherhead & Forbes 1994). Both habitat familiarity (Greenwood & Harvey 1982) and the plentiful foraging and nest-site opportunities at the study site (Camacho in press) could have led to the high settlement success of young Red-necked Nightjars in their natal area. Alternatively, landscape structure around the study site may have been influential. Red-necked Nightjars have specialised habitat requirements and hence select structurally complex habitats for breeding, including roads, shrublands and pine woodlands (Camacho *et al.* unpublished data). Thus, dispersing individuals may fail to find new unoccupied sites of suitable quality n a mosaic landscape of intensive agriculture and semi-natural areas, with scattered human developments. Natal philopatry might also be promoted by conspecific attraction in densely populated areas (Forero *et al.* 2002). The lack of sexual differences in natal dispersal may be related to the absence of suitable habitat elsewhere, which may oblige Red-necked Nightjars to choose between breeding in their natal area or risk not breeding at all (Potti & Montalvo 1991).

Most Red-necked Nightjars initiated their breeding career within their first year of life. At the study site, the mean interval (years) between successive inter-annual captures of adults is 1.46 ± 0.07 se (author's unpublished data), so the few second and third-year breeders for the first time could well in fact have bred in their first year, passing unnoticed. The overall trend for early reproduction observed in Red-necked Nightjars differs from that reported for other long-lived birds, which commonly postpone the onset of breeding by at least two years from birth (Newton 1989). In long-lived species, physiological maturity probably occurs earlier than the actual age at first breeding (Newton 1989). However, in those species, individuals generally visit future breeding areas in one or more seasons before reproducing for the first time (Becker *et al.* 2008). In contrast, Red-necked Nightjars start breeding immediately after arrival in their first year. Several mutually non-exclusive hypotheses can be formulated to explain this pattern.

Theoretically, individuals are expected to start breeding as early as possible, but the onset of reproduction in nature is commonly determined by the availability of essential resources, such as food supply or nest sites (Newton 1989). After arrival, young often fail to become established as breeders, because preferred nest sites are already occupied by older birds (Ferrer 1993, Negro *et al.* 1997). Nonetheless, breeding opportunities for young would increase with food availability and as competition for nest sites is reduced, thus reducing the age of first breeding. At my study site, reduced competition for food and abundant nesting territories, together with a constant food supply throughout the season, increase breeding opportunities for Red-necked Nightjars (Camacho in press), thus enabling young birds to breed successfully. A second hypothesis is that the advance in the onset of reproduction could be a consequence of occasional declines in adult survival rates (Ferrer *et al.* 2003). In Doñana, specialist predators may seasonally increase predation pressure on Red-necked Nightjars, and especially incubating adults (Forero *et al.* 2001). If this occurs then the death rate of adults increases and more high-quality territories become vacant for younger birds to breed (Ferrer *et al.* 2003). A third plausible hypothesis is that the generally high rates of nest failure in caprimulgids due to nest predation (Langston *et al.* 2007) may have promoted early first breeding. Under severe predation pressure, Red-necked Nightjars could maximise their lifetime reproductive output either by increasing their annual reproductive investment or by starting to breed at an earlier age (Clutton-Brock 1990). Results from this Red-necked Nightjar population suggest that some caprimulgids might have the ability to extend their annual breeding season with replacement clutches and a protracted period of parental care (Camacho in press) or even to start reproducing unusually early (this study). Estimates of age at first breeding in other ground-nesting birds moderately threatened by nest predation, such as shorebirds (Thompson *et al.* 1994) or terns (Becker *et al.* 2008), are generally between two and four years. Nevertheless, the hypothesis that Red-necked Nightjars nest in their first year as a consequence of high predation pressure needs to be tested explicitly in further studies.

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Figure legends:

Figure 1. Distribution of ages at first breeding of Red-necked Nightjars fledged in 2008−2011 and later (≤ 2012) recovered in the study area. Numbers above bars denote sample sizes.