Annual survival rates of adult Red-necked Nightjars *Caprimulgus ruficollis*

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Nothing is known about the survival rates of Nightjars. Here we estimate annual survival rates of adult Red-necked Nightjars *Caprimulgus ruficollis* in and around the Doñana National Park, southwest Spain. During the period 1989–95, 557 adults were marked and 19.7% of them were recaptured at least once in subsequent years. Capture–recapture models were built to estimate separately survival and recapture probabilities. The final selected model showed that probabilities of recapture differed between years (0.06–0.30) but not between sexes, and were independent of recapture effort. Survival was dependent on the interaction between sex and rainfall, this effect being negative for females and positive for males. However, it is not clear why rainfall influences the survival of males and females differentially due to the lack of accurate information on other life history traits. Average adult survival for the whole period was 0.74 for males (95% CI: 0.63–0.82) and 0.64 for females (95% CI: 0.56–0.72).

The estimation of survival rates is of primary importance for the study of life-history strategies and population dynamics of birds, as well as for modelling their population trends for conservation and management (Lebreton *et al.* 1992, 1993). Thus, survival has been studied in many groups of birds (Weimerskirch *et al.* 1987, Spindelov *et al.* 1995, Arnold & Clark 1996, Hiraldo *et al.* 1996, Siriwardena *et al.* 1998, Oro *et al.* 1999) using methods of capture–mark–recapture, which account for missed individuals due to low probabilities of recapture (Lebreton *et al.* 1992). However, to our knowledge this life-history parameter is unknown for any species of Caprimulgiformes (120 species, del Hoyo *et al.* 1999), probably because their nocturnal habits, secretive behaviour and cryptic plumage make difficult their detection and capture, and thus long-term studies based on marked birds. In the present study, we provide the first estimates of survival rates for adult Red-necked Nightjars *Caprimulgus ruficollis*, using seven years of capture–recapture data.

The Red-necked Nightjar is a migratory Mediterranean species which feeds on aerial insects in dry

warm regions of the Iberian peninsula and northwest Africa (Cramp 1985). For this species, very little is known about any aspect of its biology or life-history traits (Cramp 1985, Gargallo 1994, Forero *et al.* 1995, Cuadrado & Domínguez 1996, Forero *et al.* 1997, Forero & Tella 1997) and no information is available about its population trends (SEO/BirdLife 1997). In southern Spain the breeding season lasts from April to August, females probably laying two clutches, each of two eggs. Incubation lasts 18–19 days, females probably taking the larger share, and an average of 1.2 fledglings are raised per clutch (Cuadrado & Domínguez 1996).

METHODS

Data were collected from 1989 to 1995 in and around the Doñana National Park, southwest Spain (Forero *et al.* 1995). This is mainly a marsh area, temporarily flooded, combined with Mediterranean scrubland and cultivated land surrounding the park. Primary productivity of this ecosystem is positively related to rainfall, which varies greatly between years (Valverde 1967). During our study period, rainfall during the breeding season ranged between 38 and 133 mm.

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Red-necked Nightjars were captured from June to October and marked with metal leg rings. We caught the birds using a torch and a hand-net in the course of systematic nocturnal car transects along gravel roads (Forero *et al.* 1995). Capture effort varied annually between three and 12 nights of fieldwork (18–44 hours for year, mean = 27). Sex of individuals was determined according to the size of the pale spots on wing and tail (Cramp 1985, Forero *et al.* 1995). We grouped birds on the basis of moult stages into two age-classes: juveniles (born during the year of capture) and adults (Gargallo 1994, Forero *et al.* 1995). Due to the low number of recaptures of birds marked as juveniles during the study, only adult survival was estimated.

Estimates of adult survival were calculated using separate data sets for each sex and following Jolly–Seber mark–recapture models for open populations (Lebreton *et al.* 1992, 1993). We used the program RELEASE (Burnham *et al.* 1987) to assess the goodness-of-fit of the initial models ($\phi_{t,s}$, $p_{t,s}$), where survival (ϕ) and resighting (p) probabilities are both time (t) and sex (s) dependent. Tests showed homogeneity between and within groups for adult data sets ($P > 0.05$ for all tests). Therefore, our data were appropriate for a Jolly–Seber modelling approach, and subsequent models were fitted by the maximum likelihood method using program SURGE v5.0. We used Akaike's Information Criterion (AIC) to select the most parsimonious model, i.e. the model with the lowest AIC value (Lebreton *et al.* 1992). The models were considered to be statistically equivalent if the difference in AIC between models was less than 2 (see for instance Anderson *et al.* 1994). Models were constrained by ecological hypotheses based on factors that might affect survival or capture probabilities. The possibility that rainfall during the breeding season in year t may have influenced survival until year $t + 1$ was considered in the models using a logit-linear constraint (Lebreton *et al.* 1992): the hypothesis was that food availability

(i.e. flying insect populations) was positively associated with rainfall, and in turn with adult survival, this being lower in years with lower rainfall. Several studies have recorded changes in survival of adult birds related to environmental features such as rainfall, flooding or temperature in winter (Clobert *et al.* 1987, Lebreton *et al.* 1992, Senar & Copete 1995). Rainfall in the winter quarters has also been proved to influence survival in some migratory bird species (Kanyamibwa *et al.* 1990, Peach *et al.* 1991). Unfortunately, no accurate information is available about the location of wintering areas for Red-necked Nightjars (no recaptures were obtained in winter from 1538 birds ringed in Spain in 1973–97, Cantos & Gómez-Manzanque 1998), thus making it difficult to test this hypothesis properly at present. To estimate capture probability, models were also constructed which included all combinations of time and sex and the different recapture effort (e) made each year, measured as the number of hours spent catching birds. A model testing for trap-dependence (m) after capture was also considered (Pradel 1993).

RESULTS

During the study period, 557 adults were marked and 19.7% of them were recaptured at least once in subsequent years (Table 1). Recapture probability was not related to the number of hours spent catching birds each year (Table 2). Recapture differed between years, but not between the sexes either as an interaction or an additive effect (Table 2). Probabilities of recapture ranged between 0.06 and 0.30 (Table 3). Survival was dependent on the interaction between rainfall and sex (Table 2). The model showed that rainfall positively influenced survival for males, whereas female survival decreased when rainfall increased (Table 3, Fig. 1). The correlation of survival with rainfall was significant for both males and females (95% confidence interval for the slope: 0.014 to 0.026 and –0.029 to –0.227 respec-

Table 1. Number of adult Red-necked Nightjars ringed and subsequently recaptured each year.

Year	Number ringed	Year of recapture					
		1990	1991	1992	1993	1994	1995
1989	94	4	13	6	3	1	2
1990	138	–	28	12	6	3	0
1991	150	–	–	21	5	2	2
1992	93	–	–	–	6	2	2
1993	53	–	–	–	–	3	2
1994	40	–	–	–	–	–	3

Table 2. Survival models and associated biological hypotheses for Red-necked Nightjars in southern Spain. Best-fitting model is in bold. Dev, deviance of the model as given by program SURGE; np, number of identifiable parameters; AIC, Akaike information criterion computed as Dev + 2np. Factors considered potentially to affect survival (ϕ) or capture (p) probabilities were: time (t), sex (s), rainfall (r), effort of capture (e) and trap-dependence (m).

Model	Dev	np	AIC	Biological hypothesis
$\phi_{t's'}, p_{t's}$	830.77	20	870.77	Interaction of sex with time for survival and recapture
$\phi_{t's'}, p_t$	835.27	16	867.27	Interaction of sex with time for survival; recapture varied with time
$\phi_s, p_{t's}$	840.14	14	868.14	Survival depended on sex; interaction of sex with time for recapture
$\phi_{t's'}, p_s$	847.33	14	875.33	Interaction of sex with time for survival; recapture depended on sex
$\phi_{t'}, p$	847.62	12	871.62	Interaction of sex with time for survival; constant recapture
ϕ_t, p_t	844.83	10	864.83	Survival and recapture depended on time
ϕ_s, p_t	844.56	8	860.56	Survival depended on sex; recapture varied with time
ϕ_t, p	854.83	7	868.83	Survival depended on time; constant recapture
ϕ, p_t	846.34	7	860.34	Constant survival; recapture depended on time
ϕ_s, p_s	882.32	4	890.32	Both survival and recapture depended on sex
ϕ_s, p	884.29	3	890.29	Survival depended on sex; constant recapture
ϕ, p_s	886.51	3	892.51	Constant survival; recapture depended on sex
ϕ, p	886.58	2	890.58	Constant both survival and recapture
$\phi_{t+s'}, p_{t+s}$	838.60	14	866.60	Additive effect of time and sex for both survival and recapture
ϕ_{t+s}, p_t	835.28	13	861.28	Additive effect of time and sex for survival; recapture varied with time
ϕ, p_{t+s}	846.18	8	862.18	Constant survival; additive effect of time and sex for recapture
ϕ_s, p_{s+e}	882.32	5	892.32	Survival depended on sex; recapture varied with the interaction of sex and effort of capture
ϕ_s, p_e	878.83	4	886.83	Survival depended on sex; recapture varied with effort of capture
ϕ, p_e	880.92	3	886.92	Constant survival; recapture varied with effort of capture
$\phi, p_{m \cdot t}$	843.45	12	867.45	Constant survival; recapture was trap-dependent
ϕ_s, p_{s+e}	876.63	5	886.63	Survival depended on sex; additive effect of sex and effort for recapture
ϕ, p_{s+e}	880.87	4	888.87	Constant survival; additive effect of sex and effort for recapture
$\phi_{r's'}, p_t$	837.88	10	857.88	Survival depended on the interaction of sex and rainfall; recapture varied with time
$\phi_{t's'}, p_{t+s}$	837.09	11	859.09	Survival depended on the interaction of sex and rainfall; additive effect of time and sex for recapture
ϕ_r, p_t	846.33	8	862.33	Survival depended on rainfall; recapture varied with time
ϕ, p_r	882.94	3	888.94	Constant survival; recapture depended on rainfall during breeding
$\phi_{r's'}, p_r$	863.63	5	873.63	Survival depended on the interaction of sex and rainfall; recapture varied with rainfall

tively). Average survival for the whole period (ϕ_{av}), calculated following the equation:

$$\phi_{av} = e^{\text{mean}(\ln \phi_i)}$$

(Cormack 1964), was 0.74 for males (95% CI: 0.63–0.82) and 0.64 for females (95% CI: 0.56–0.72).

DISCUSSION

The absence of information on survival rates of other Caprimulgiformes prevents us from comparing our results with other species or with other populations of the same species. Adult survival depended on the interaction between the birds' sex and rainfall during the breeding season. Differences in survival rates between sexes have been reported previously in many species of birds (Blondel *et al.* 1992, Francis & Cooke 1992, Kanyamibwa *et al.* 1993, Horak & Lebreton

1998). Results on adult survival of Red-necked Nightjars in southern Spain agree with the general pattern described for monogamous birds, males surviving better than females (Breitwisch 1989). However, the influence of rainfall on adult survival differed strikingly between sexes. Although very little is known about sex roles during breeding in Caprimulgiformes (Jackson 1985), several studies suggest that parental investment during incubation and brooding young chicks is higher for females than for males (Tate 1989, Fry *et al.* 1988, Poulin *et al.* 1996, Brigham & Geiser 1997). The influence of rainfall on adult survival could be the direct consequence of higher food availability, reducing the energy investment of adults looking for food and feeding their chicks. However, while this might explain the positive correlation of rainfall with male survival, it cannot explain the negative trend for females. If females spent more time in the nest incubating the eggs and brooding chicks, their vulnerability

Table 3. Estimated recapture and survival probabilities for adult Red-necked Nightjars in South Spain between 1989 and 1995 under the finally selected model (ϕ_{rs} , p_i). Standard deviation (sd) and 95% confidence intervals (CI) are also shown.

Year	Estimate	sd	CI
Recapture			
1990	0.059	0.264 ($\times 10^{-3}$)	0.058–0.059
1991	0.304	0.430 ($\times 10^{-3}$)	0.227–0.394
1992	0.186	0.276 ($\times 10^{-3}$)	0.137–0.246
1993	0.113	0.237 ($\times 10^{-3}$)	0.074–0.168
1994	0.077	0.181 ($\times 10^{-3}$)	0.048–0.121
1995	0.078	0.165 ($\times 10^{-3}$)	0.051–0.117
Male survival			
1989–90	0.706	0.537 ($\times 10^{-1}$)	0.591–0.799
1990–91	0.832	0.525 ($\times 10^{-1}$)	0.704–0.912
1991–92	0.511	0.313 ($\times 10^{-1}$)	0.450–0.572
1992–93	0.874	0.473 ($\times 10^{-1}$)	0.750–0.942
1993–94	0.862	0.492 ($\times 10^{-1}$)	0.735–0.933
1994–95	0.746	0.552 ($\times 10^{-1}$)	0.624–0.839
Female survival			
1989–90	0.775	0.232 ($\times 10^{-1}$)	0.727–0.818
1990–91	0.574	0.475 ($\times 10^{-1}$)	0.479–0.663
1991–92	0.910	0.529 ($\times 10^{-2}$)	0.899–0.920
1992–93	0.465	0.554 ($\times 10^{-1}$)	0.360–0.574
1993–94	0.501	0.533 ($\times 10^{-1}$)	0.398–0.604
1994–95	0.726	0.299 ($\times 10^{-1}$)	0.664–0.781

to predation might be higher than that of males. In the Doñana area there is a rich and dense community of raptors and carnivores which mainly prey upon Rabbits *Oryctolagus cuniculus* (Valverde 1967). It has recently been discovered that in the study area heavy rainfall strongly decreases the availability of rabbits because of the flooding of their burrows (Palomares *et al.* in press). Under low Rabbit densities, predators

Figure 1. Estimated survival probabilities for adult Red-necked Nightjars in southern Spain plotted against rainfall during the breeding season for study period (1989–1995) under the model (ϕ_{rs} , p_i). Mean $\pm$ sd for males (●) and females (○) are represented.

enlarge their dietary niche width increasing the pressure on secondary foraging resources (Fedriani *et al.* 1998), thus potentially affecting more female Nightjars.

Recapture probabilities for adult Red-necked Nightjars varied with time independently of the variable annual catching effort. That variation could be the result of random temporary emigration or dispersal to less accessible areas (see also Sandland & Kirkwood 1981, Pradel 1993), although nightjars seem to show high philopatry (Jackson 1985, Poulin *et al.* 1996). Inter-year variation in recapture probability could also result from heterogeneity in recapture rates between individuals (see also Cézilly *et al.* 1996, Prévot-Julliard *et al.* 1998). Further research is needed on most aspects of the biology and ecology of this and other Nightjar species before these and other basic questions on their life histories can be answered.

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