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Nightingale *Luscinia megarhynchos* survival rates in relation to Sahel rainfall

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Abstract – Survival rates of breeding adult nightingales were estimated by capture–mark–recapture data, collected from 1996 to 2003 at a ringing station in NW Italy. A sample of 256 nightingales provided 338 capture events, obtained with mist–nets operated each year during breeding periods, from May to August. Survival and recapture probabilities were estimated with program MARK and parameterised as a function of annual rainfall indices of three sub–Saharan regions, the main nightingale wintering area. No sex differences in local survival rates were detected, but recapture probabilities were lower for females compared to males. Yearly variations in survival rate were associated with rainfall fluctuations in the Sahel region. In particular, after dryer winter seasons, the survival rates were significantly lower (19% ± 6 SE – 40% ± 5 SE) than in all the others years (50% ± 5 SE). Thus, our results further confirm that the occurrence of drought conditions in the African wintering grounds can negatively affect survival rates of long–distance migratory birds.

Riassunto – *Tassi di sopravvivenza dell'usignolo* Luscinia megarhynchos *in relazione alla piovosità nel Sahel*. Abbiamo studiato, mediante metodi di cattura–marcatura–ricattura, la variabilità interannuale dei tassi di sopravvivenza in usignoli adulti nidificanti presso Villalvernia (Alessandria, Italia nord–occidentale). Dal 1996 al 2003, sono stati inanellati 256 individui, che, con le ricatture, hanno fornito un totale di 338 eventi di cattura in periodo riproduttivo (maggio – agosto). Utilizzando il programma MARK, sono state stimate sia la probabilità di sopravvivenza all'anno successivo sia quella di ricattura. Partendo dal più generale (Cormack–Jolly–Seber), sono stati confrontati diversi modelli, via via più restrittivi. In particolare, si è indagato l'effetto della piovosità sulla sopravvivenza degli usignoli, vincolando tale parametro all'andamento delle precipitazioni in tre possibili aree di svernamento a sud del Sahara (Sahel). Differenze tra i sessi sono state rilevate soltanto per le probabilità di ricattura (inferiore per le femmine rispetto ai maschi), ma non per il tasso di sopravvivenza, mentre il tasso di sopravvivenza locale è risultato correlato con l'andamento delle piogge nel Sahel. In particolare, la sopravvivenza negli anni più aridi è risultata inferiore (19% ± 6 ES – 40% ± 5 ES) rispetto a quella riscontrata negli altri anni (50% ± 5 ES). Pertanto, questo studio dimostra ulteriormente che condizioni di aridità nei quartieri di svernamento africani possono influenzare negativamente i tassi di sopravvivenza di migratori a lunga distanza.

Weather conditions can produce marked effects on bird populations: episodic events like hurricanes, storms, and rapid temperature reductions can be fatal to most birds. In particular, resident birds in temperate regions are more frequently exposed to severe and prolonged cold periods during winter, which may negatively affect food availability. Migratory species can escape this problem by wintering in warmer regions, but, on the other hand, here they can experience severe drought conditions and following habitat and food shortages (Newton 1998, 2004).

Survival and/or population dynamics of several long–distance European migratory birds are known to be influenced by weather conditions in the African wintering areas; in particular, significant effects of annual fluctuations in rainfall levels in sub–Saharan winter quarters on population dynamics have often been highlighted. Drought effects on survival have been detected for marshland birds like purple herons *Ardea purpurea*

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(Cavé 1983), white storks *Ciconia ciconia* (Kanyamibwa *et al.* 1990) and sedge warblers *Acrocephalus schoenobaenus* (Peach *et al.* 1991), but also for aerial feeders, like sand martins *Riparia riparia* (Szép 1995) and barn swallows *Hirundo rustica* (Møller 1989), as well as for species frequenting dryer habitats (e.g. whitethroat *Sylvia communis*, Baillie and Peach 1992). Most of these species as well as other trans–Saharan migrants that winter in the Sahel zone or migrate through it in autumn and spring showed substantial population declines since the late 1960s, when drought conditions in the arid African savannahs have occurred more often and with increasing severity, owing to a failure of the rain–belts to extend towards north (Marchant *et al.* 1990, Newton 2004).

The nightingale *Luscinia megarhynchos* is a trans–Saharan migratory passerine, breeding in warm and temperate areas and commonly found in shrubby habitats and lowland broad–leaved woodland margins. Adult are considered to be highly philopatric, although females show a lower degree of site fidelity than males (Grüll 1988). European populations are generally stable since the late 1980s (Grüll and Fracasso 1997), but declines and range contractions have been reported for some countries, namely Britain (Marchant *et al.* 1990), NE France (Dubois *et al.* 2000) and Switzerland (Schmidt *et al.* 1998). In Italy, the nightingale is a widespread breeding bird (Meschini and Frugis 1993), with a population estimate of 500000–1000000 pairs (Brichetti 1997); spring migration is concentrated in April, while post–breeding migration begins in August and continues until the second decade of September (Licheri and Spina 2002). The winter quarters of the European population (*L. m. megarhynchos*), which are usually reached in late September–October, are located in sub–Saharan Africa between 20°N and the Equator, and as far east as Uganda (Cramp 1988, Keith *et al.* 1992), therefore including some Sahelian areas (mainly western Sahel) and a large area immediately to the south of the Sahel. Here, nightingales occur in savannah woodlands, thorny shrubs, forest edges and second growth forests, feeding chiefly on insects (Cramp 1988). The few African recoveries of European ringed nightingales are mainly on the migration route, but four winter recoveries of birds ringed in Italy from Ghana and Togo suggest that these should be the main winter quarters of at least a part the European breeding population (including Italy) (Fig. 1).

The aim of this study was to estimate survival rates of a nightingale population breeding in NW Italy and to analyse whether this parameter could be affected by drought conditions in the Sahel. The climate of this area, stretching from the Atlantic coast to the Red Sea, between 18°N and 13°N, could affect nightingale survival both on migration and during wintering. The Sahel rainy season, in fact, supports a single annual production of grass, seeds and invertebrates, which rapidly dwindles after the rains and shortly after the autumn arrival of Palaearctic migrants, even in years with average weather conditions (Morel and Morel 1992), and, as suggested by Pilastro and Spina (1997), the ongoing desertification process in sub–Saharan Africa might have a negative impact on species wintering in equatorial Africa.

METHODS

Study area and field protocols

The study area is located in a riparian habitat along the Scrivia river, close to Villalvernia (Alessandria, NW Italy: 44° 49' N – 8° 50' E; 100–110 m a.s.l.). Shrubs and trees commonly found in the study area include *Crataegus monogyna*, *Cornus sanguinea*, *Salix* sp., *Alnus glutinosa*, *Quercus robur*, *Populus nigra*. Birds were captured using 30 mist–nets, scattered in bushes and woodlots in the river bed, for eight consecutive years (1996–2003). Each year we performed 12 24–h capture sessions, from May to August, lasting from dusk to the following evening. All newly captured birds were ringed with metal rings, aged according to Svensson (1992) and sexed by cloacal protuberance and brood patch examination. Only adult sexed birds were used for the analyses. First–year birds were not considered in this study because of the very low sample of recoveries in subsequent years, due to the low natal philopatry, a problem that rarely makes possible juvenile survival estimates with live recaptures (Clobert and Lebreton 1991).

Mark–recapture analysis

Survival estimates derived from analysis of recaptures or resightings of living marked birds are widely used in association with proper stochastic open–population models (Cormack 1964, Seber 1982, Clobert *et al.* 1985, Pollock *et al.* 1990, Nichols 1992). Nevertheless, it is necessary to emphasise that data can be biased if a significant part of the population, even if

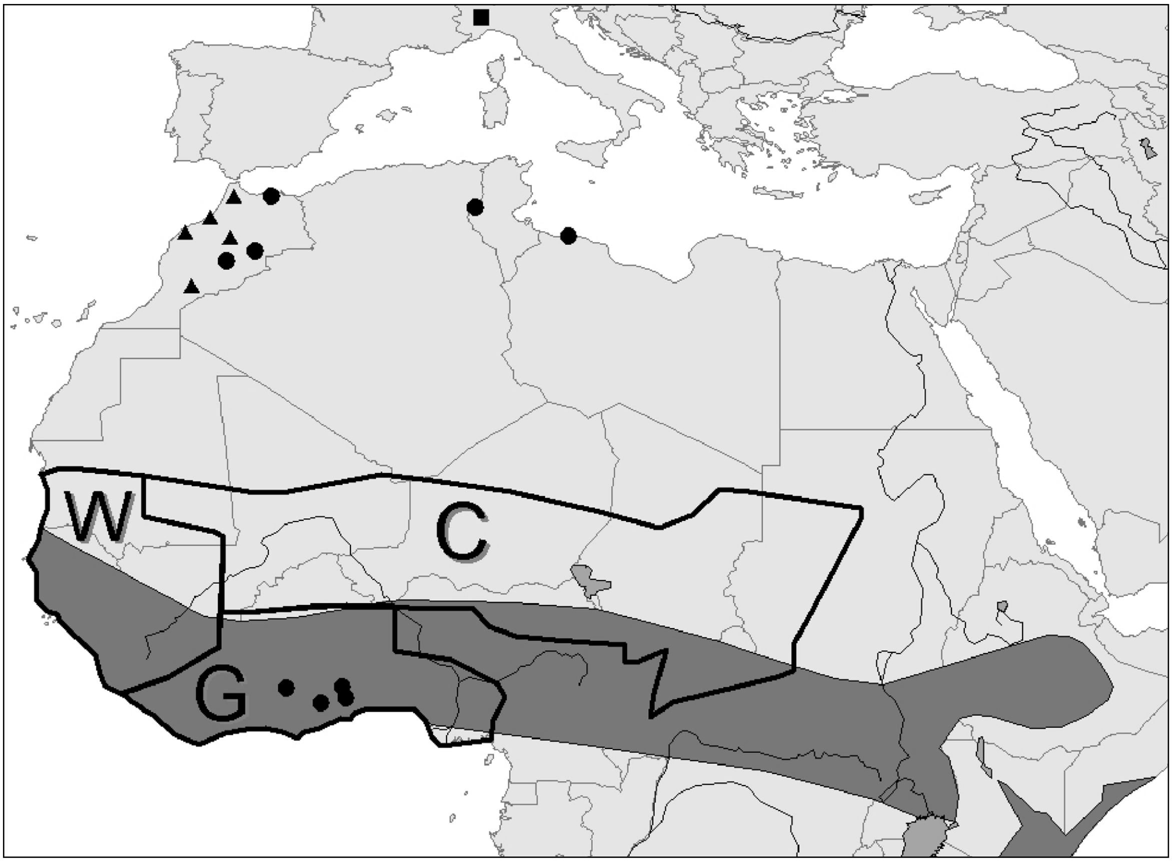

Figure 1. Map of southern Europe and central Africa showing nightingale wintering area (dark grey; after Keith *et al*. 1992), Sahelian regions (according to Landsea *et al*. 1997; W = West; C = Central; G = Guinea Coast), and African recoveries of nightingales ringed in Europe (dots = Italian ringed birds, INFS data–bank, courtesy F. Spina; triangles = other European ringed birds, after Zink 1973). The squared dot in NW Italy indicates the location of the study area. – *Areale di svernamento dell'usignolo (grigio scuro; da Keith* et al. *1992), delimitazione delle regioni climatiche saheliane (da Landsea* et al. *1997; W = Occidentale; C = Centrale; G = Costa della Guinea) e riprese in Africa di usignoli inanellati in Europa (cerchi = individui inanellati in Italia, banca dati dell'INFS, gentilmente forniti da F. Spina; triangoli = individui inanellati in altri paesi d'Europa, da Zink 1973). Il quadrato in Italia nord occidentale indica la posizione dell'area di studio.*

still alive, does not return to the sampling site in subsequent sampling times. Therefore, estimates derived from capture–recapture experiments should be considered as minimal (or "apparent") survival rates, although the bias is frequently negligible for adult philopatric bird species. In this study, capture–recapture data were used in association with open–population models (Cormack–Jolly–Seber, CJS hereafter, and related models) and associated model–selection criteria (e.g. Lebreton *et al.* 1992, Nichols 1994, Williams *et al*. 2002). These models produce survival estimates that are not influenced by variations in recapture probability, and therefore are more reliable than those based on return rates only (Nichols and Pollock 1983, Martin *et al*. 1995).

Survival probability (Φi) is defined as the probability that an animal, living at time i, is still alive and available for recapture at time $i + 1$. Therefore, survival probability complement ($1 - \Phi$) includes both mortality and permanent emigration from the study site. Recapture probability (pi) is the conditional probability that an individual is caught at time i, given that the individual is still alive and within the sampling area. The basic CJS model allows for variability of Φi and pi between different time periods (e.g. successive breeding seasons). To obtain unbiased estimates for the parameters of interest, some basic assumptions must be met (Seber 1982): 1) each marked animal occurring in the population at a given sampling time i has the same capture probability; 2) each marked animal occurring in the population immediately after sampling time i has the same probability to survive until period $i + 1$; 3) marks cannot be lost or overlooked; 4) sampling is simulta-

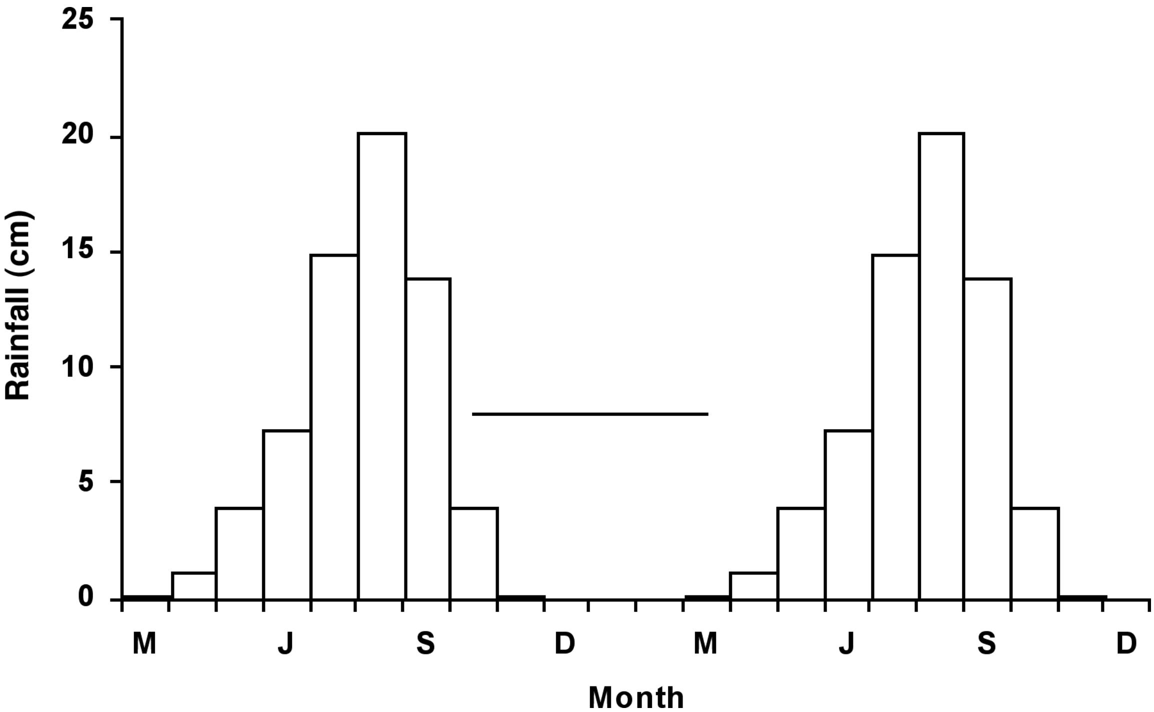

Figure 2. Mean monthly rainfall values in the Sahel (after Mitchell 2003); the horizontal line shows the main period of nightingale presence in wintering areas. – *Piovosità mensile media nel Sahel (da Mitchell 2003); la linea orizzontale indica il periodo principale di presenza dell'usignolo nei quartieri di svernamento.*

neous (i.e. sampling time is negligible in relation to the inter–sampling time). Some of these assumptions may be abandoned with more general models; on the contrary, reduced–parameter models like those adopted in this study make more restrictive assumptions (e.g. survival and/or recapture probabilities are forced to be constant in time). Analyses started with program RELEASE (Burnham *et al.* 1987) to compute the goodness–of–fit test of the most general model (where, for each sex, Φi and p*i* vary only with time). Then, models making further restrictions were fitted with program MARK (White and Burnham 1999, Cooch and White 2002), including models where temporal variation in survival is modelled as a logit–link function of specific weather conditions. This procedure is better than an ordinary regression analysis of the CJS estimates over the variable of interest, because it avoids the pitfalls of the autocorrelation of estimates and the entire variance–covariance structure of the estimates is properly taken into account (Lebreton *et al.* 1992 and references therein). The selection of the most appropriate model was based on the Akaike's Information Criterion (AIC) (Burnham *et al.* 1995, Anderson and Burnham 1999): this procedure allows comparison of not–necessarily nested models and gives a penalty to models according to an increasing number of parameters, in an attempt to select a good approximating model for inference, based on the parsimony principle. The lower the AIC value, the more appropriate the model is, although when the difference in AIC values between two models is < 2, they can be considered to be equally supported by the data (Burnham *et al.* 1995). In this study AICc values (AIC approximated for small samples) were adopted (White and Burnham 1999). To account for model selection uncertainties, model parameters were estimated by the model averaging technique (program MARK), which considers the relative importance of each fitted model (Cooch and White 2002). Parameter estimates are presented with their associated SEs.

Sahel rainfall metrics

To investigate the relationships between survival rates and weather conditions potentially influencing nightingale survival, survival rates were modeled with rainfall data from three Sahel regions, as defined by Landsea *et al*. (1996): the West Sahel (W) extending from the Atlantic coast to about 7ºW, within latitudes from 10ºN to 20ºN; the Central Sahel (C) from 7ºW to about 26ºE, in the latitudes from 10ºN to 20ºN; and the Guinea Coast (G) from the Gulf of Guinea to the Central Sahel region, from 7ºW to about 5ºE (Fig. 1). Rainfall data were expressed by rainfall indices calculated as standardised deviations from the 1950–1990 average conditions (Landsea *et al*. 1996, 1997, Schrage *et al*. 2004). Annual rainfall indices were applied to the cohorts released in the same year, considering that survival of each cohort could be affected by the wet season immediately preceding the wintering period, as rainfalls concentrated between June and September (Fig. 2). To investigate the effect of extreme rainfall values, years were categorised to reflect whether or not a given rainy season was "very dry" or "very wet", following the numerical limits explicitly defined by Landsea *et al*. (1997) for each region (Fig. 3). For example, if a given year was categorised as "very dry" for a given region, it was scored as 1, whereas other years were scored as 0. Both actual rainfall index values and the categorisation ("dry" or "wet" years vs. normal years) were tested in the models.

RESULTS

A total of 256 adult nightingales (143 males and 113 females) was ringed, 82 of which were recaptured in subsequent years, leading to an overall 338 capture events (Tab. 1). The goodness–of–fit test of the general model [Φ(s*t)p(s*t), $\chi^2 = 6.16$, d.f. = 20, $P = 0.99$] and all the test components suggested that the CJS model basic assumptions were nicely met in our dataset. In particular, the test which may indicate transient presence resulted non–significant for both sexes (test 3.SR, males: $\chi^2 = 6.17$, d.f. = 6, $P = 0.99$; females: $\chi^2 = 3.65$, d.f. = 4, $P = 0.45$). The model evaluation procedure started by analysing sex and time effects on variations in recapture probability and survival. According to AIC values, the best fitting model suggested that survival probability varied with time (averaging 44% ± 4 for the entire period), whereas recapture probabilities differed between the sexes, males showing higher recapture probabilities than females (Tab. 2).

To explain temporal variability in survival rates, we constrained survival probabilities to be a function of rainfall indices (Tab. 2). The models depending on West and, to a lower degree, the Central Sahel rainfall indices differed slightly from the model including time effects only [Φ(t)p(s)] (difference in AIC < 2). Therefore, all these models fitted the data relatively

Table 1. Number of adult nightingales released each year and recaptured for the first time in subsequent years. – *Numero di usignoli adulti rilasciati in ciascun anno e ricatturati per la prima volta negli anni successivi*.

Released		Year of first recapture							
Year	*N*	1997	1998	1999	2000	2001	2002	2003	Total
Males									
1996	10	4	1	–	–	–	–	–	5
1997	16		6	–	–	–	–	–	6
1998	35			13	3	–	–	–	16
1999	36				11	2	–	–	13
2000	41					11	2	–	13
2001	33						5	–	5
2002	19							3	3
2003	14								–
Females									
1996	9	1	2	–	–	–	–	–	3
1997	7		–	–	–	–	–	–	–
1998	20			4	2	1	–	–	7
1999	22				3	1	–	–	4
2000	21					2	3	–	5
2001	19						2	–	2
2002	22							–	–
2003	14								–

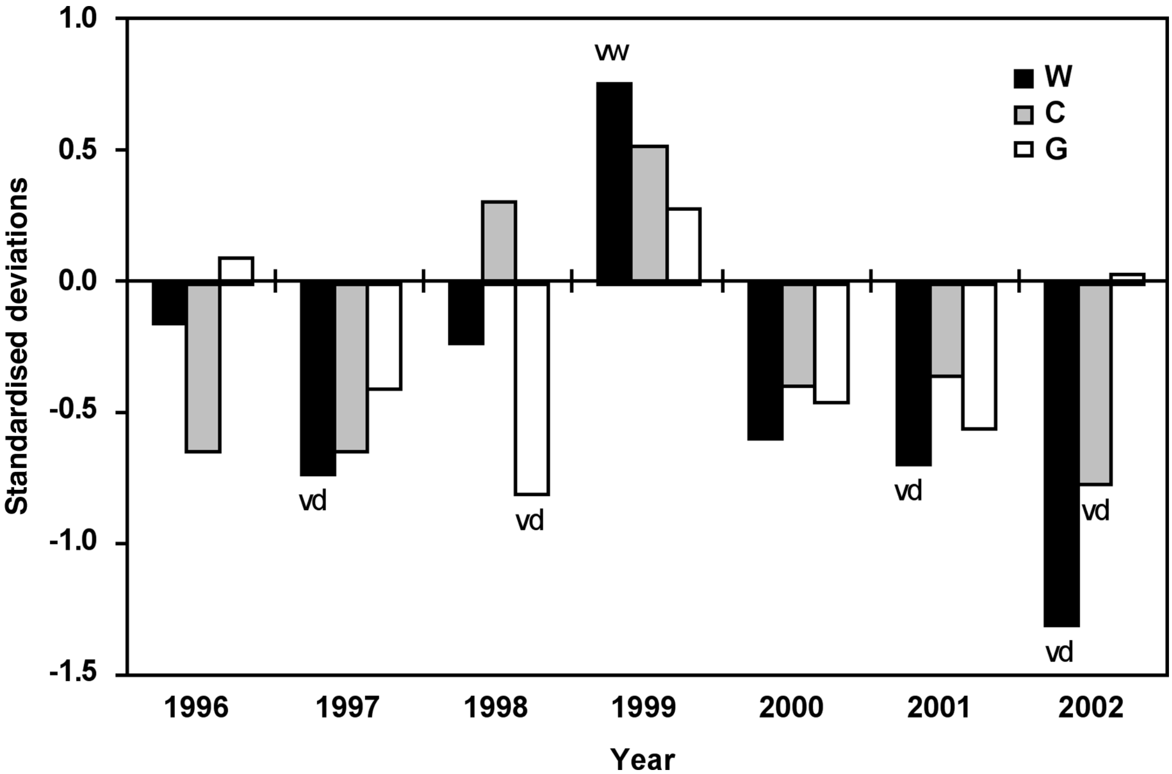

Figure 3. Annual rainfall index anomalies (standardised deviations from the 1950–1990 average conditions) for Central (C) and West (W) Sahel, and Guinea Coast (G). Data gathered in the period 1996–2002, courtesy A.H. Fink (IGM Cologne). Very dry (vd) and very wet (vw) seasons (according Landsea *et al*. 1997) are indicated. – *Indici di anomalia delle precipitazioni annuali, calcolati sul periodo 1996–2002 (deviazioni standardizzate rispetto alla piovosità media nel periodo 1950–1990) per il Sahel Centrale (C), Occidentale (W) e per la Costa della Guinea (G). I dati sono stati gentilmente forniti da A.H. Fink (IGM, Colonia). La designazione delle annate come molto aride (vd) o molto piovose (vw) per ciascuna regione è stata effettuata secondo i criteri indicati in Landsea* et al. *(1997).*

and equally well. However, the models including “very dry” years both for the West and the Central Sahel showed a lower AIC and thus appeared to be the best fitting among all the tested models, revealing that temporal variability in survival rates could be best explained by drought conditions in the West and Central Sahel regions (Tab. 2). Parameter estimates, as obtained by the model averaging technique (see Methods), showed that drought conditions, especially when occurring simultaneously both in the West and Central Sahel regions, resulted in particularly low survival rates and indicated a higher recapture probability in males compared to females (Tab. 3).

DISCUSSION

In this study, we have analysed the temporal variation in recapture and survival probabilities of a breeding population of nightingales, showing that recapture probabilities differed between the sexes and that survival rates were negatively affected by drought conditions in the Western and Central Sahel wintering grounds. The higher recapture probability of males compared to females can be attributed to a lower mobility of females, who are tied to nest sites during the breeding period, whereas males show greater mobility, due to territorial behaviour, which increase the probability of being trapped in mist–nets. This should not be interpreted as a lower site fidelity of females, because a significantly lower female site fidelity would have resulted in a lower “local” survival rather than a lower recapture probability. This result further confirms that sex is a potentially important source of heterogeneity in capture probabilities for passerines, and should therefore be included as a group effect whenever possible, as earlier suggested by Peach *et al*. (1995).

Our overall survival estimate (44% ± 4) compares well with the average survival rate of passerines

Table 2. Model selection results. The first set of models represents variations in survival and recapture probabilities according to time and sex, while the other set of models shows variation in recapture probabilities according to sex and survival probabilities according to different rainfall indices (see Methods for details). The best fitting models according to AIC values are marked with an asterisk. *N* Par. = number of parameters; Φ = survival probability; p = recapture probability; t = time; s = sex; s*t = sex x time interaction; (.) = no effect. G = Guinea Coast rainfall index; C = Central Sahel rainfall index; W = West Sahel rainfall index; vw = very wet seasons; vd = very dry seasons. – *Risultati della selezione dei modelli. La prima serie di modelli analizza la variabilità delle probabilità di sopravvivenza e ricattura in funzione di sesso e tempo, mentre la seconda serie analizza la variabilità nella probabilità di ricattura in funzione del sesso e nella probabilità di sopravvivenza in funzione degli indici di piovosità nel Sahel (v. Metodi per i dettagli). I modelli che mostrano il miglior adattamento ai dati secondo i valori di AIC sono contrassegnati con un asterisco.* N *Par. = numero di parametri; Φ = probabilità di sopravvivenza; p = probabilità di ricattura; t = tempo; s = sesso; s*t = interazione sesso x tempo; (.) = nessun effetto. G = indice di piovosità per la Costa della Guinea; C = indice di piovosità per il Sahel Centrale; W = indice di piovosità per il Sahel Occidentale; vw = annate molto piovose; vd = annate molto secche.*

Model	Deviance	*N* Par.	AICc
Sex and time effects			
Φ(s*t) p(s*t)	51.13	20	441.62
Φ(s*t) p(t)	60.40	17	444.07
Φ(s*t) p(s)	60.76	14	437.76
Φ(s*t) p(.)	71.60	14	448.60
Φ(t) p(s)	67.50	9	433.68*
Φ(s) p(s)	83.26	4	438.97
Φ(.) p(s)	84.57	3	438.22
Sex and rainfall effects			
Φ(G) p(s)	84.42	4	440.13
Φ(C) p(s)	79.63	4	435.34
Φ(W) p(s)	77.15	4	432.85
Φ(W vw) p(s)	83.61	4	439.32
Φ(G vd) p(s)	80.55	4	436.26
Φ(C vd) p(s)	73.70	4	429.41*
Φ(W vd) p(s)	74.32	4	430.03*

(47% ± 2, Boano and Cucco 1991) and to the only previous nightingale survival rate estimate (42%, Martin and Clobert 1996). The model selection process clearly showed a link between nightingale survival rates and the amount of Sahelian rainfall. This is particularly evident below a certain rainfall threshold. Perhaps, this is the reason why the nightingale, in comparison to other European trans–Saharan migrants, is able to maintain a relatively stable population level in absence of prolonged drought periods. The model based on West Sahel data may be considered as more reliable, in that very dry conditions

Table 3. Survival (Φ) and recapture (p) probabilities estimated according to the model averaging technique (program MARK) applied to models Φ(C vd)p(s) and Φ(W vd)p(s) (see Tab. 2). W = West Sahel; C = Central Sahel. – *Stime delle probabilità di sopravvivenza (Φ) e ricattura (p) (*model averaging, *programma* MARK*) ottenute dai modelli Φ(C vd)p(s) e Φ(W vd)p(s) (cfr. Tab. 2). W = Sahel Occidentale; C = Sahel Centrale.*

Parameter	Estimate (SE)
Φ (very dry, in W and C)	0.19 (0.06)
Φ (very dry, only in W)	0.40 (0.05)
Φ (other years)	0.50 (0.05)
p (males)	0.65 (0.09)
p (females)	0.29 (0.07)

occurred in 3 years out of 7, whereas the model based on Central Sahel rainfall indices include only a single very dry season (see Fig. 3).

The observed reduction of survival after very dry seasons could be either due to the deterioration of environmental conditions in the winter quarters or during migration or both. In the first case, the dryer conditions can cause a general reduction of the favourable wintering conditions in Senegal (western Sahel), forcing the birds to move further south, with a resulting longer journey from and to the breeding areas, whereas in the second case birds would not find sufficiently good conditions to accumulate or restore the necessary fuel loads before (spring) or after (autumn) the long crossing of the Sahara (about 1600–1800 km), which can be either made in a single non–stop flight or with an intermittent migratory strategy. According to Biebach (1992), the energy reserves of many trans–Saharan migrants in autumn are just sufficient to reach the Sahel zone only with the aid of tail wind regimes; the safety margin, however, depends entirely on the reliability and strength of these tailwinds. Moreover, fat load of trans–Saharan migrants at arrival in southern Europe after spring migration across the desert and Mediterranean Sea was found to be significantly correlated with the northernmost latitude of the optimal habitat south of the Sahara (Pilastro and Spina 1997). In this conditions, mortality of many birds after very dry years likely result from exhaustion of insufficient fat reserves and subsequent starvation during migration. In fact, it is important to remind that, even if most migrant declines have been attributed to changing events on breeding and/or wintering areas, climate and habitat changes during migration or at pre–migratory stopover fuelling sites may be equally crucial (Newton 2004). Therefore, the conservation of fuelling sites before barrier crossing could be of primary importance for the conservation long–distance migratory birds (Biebach 1992).

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