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Assessing survival in a multi-population system: a case study on bat populations

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Abstract In long-lived animals, adult survival is among the most important determinants of population dynamics. Although it may show considerable variation both in time and among populations and sites, a single survival estimate per species is often used in comparative evolutionary studies or in conservation management to identify threatened populations. We estimated adult survival of the isabelline serotine bat *Eptesicus isabellinus* using capture–recapture data collected on six maternity colonies scattered over a large area (distance 8–103 km) during periods varying from 8 to 26 years. We modelled temporal and inter-colony variations as random effects in a Bayesian framework and estimated mean annual adult survival of females on two scales and a single survival value across all colonies. On a coarse scale, we grouped colonies according to two different habitat types and investigated the effect on survival. A difference in adult survival was detected between the two habitat types [posterior mean of annual survival probability 0.71; 95% credible interval (CI) 0.51–0.86 vs. 0.60; 0.28–0.89], but it was not statistically supported. On a fine scale, survival of the six colonies ranged between 0.58 (95% CI 0.23–0.92) and 0.81 (0.73–0.88), with variation between only two colonies being statistically supported. Overall survival was 0.72 (95% CI 0.57–0.93) with important inter-colony variability (on a logit scale 0.98; 95% CI 0.00–8.16). Survival varied temporally in a random fashion across colonies. Our results show that inference based solely on single colonies should be treated with caution and that a representative unbiased estimate of survival for any species should ideally be based on multiple populations.

Keywords Demography · Mark–recapture · Random effects · Bayesian modelling · *Eptesicus isabellinus*

Introduction

Life history and dynamics of natural populations are determined by vital rates, such as survival and fecundity, and evolutionary changes are generated by individual variation in these rates (Stearns 1992; Skalski et al. 2005). In long-lived animals, growth rate is most sensitive to adult survival (e.g. Lande 1988; Lebreton and Clobert 1990; Saether and Bakke 2000; Gaillard and Yoccoz 2003). Reliable estimates of adult survival are therefore critical for an understanding of population dynamics of long-lived species.

It has well been established that survival in a natural population is often variable over time. However, survival as well as other life-history traits may also be markedly variable among populations and sites of the same species inhabiting heterogeneous environments at various spatial scales (e.g. Paradis et al. 2000; Frederiksen et al. 2005; Grosbois et al. 2008, 2009; Jenouvrier et al. 2009; Sanz-Aguilar et al. 2009). Across the geographical range of a species, these variations are more likely to

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reflect differential climatic conditions (Frederiksen et al. 2005; Grosbois et al. 2009; Jenouvrier et al. 2009). At a finer scale, they may be linked to spatiotemporal variability in habitat availability or quality, food resources, weather, disease, parasites, predator pressure, human activities, and population density (e.g. Jorgenson et al. 1997; Gaillard et al. 1998; Coulson et al. 1999; Dhondt 2001; Ozgul et al. 2006; Sanz-Aguilar et al. 2009). Whatever its origin, the variability in survival, both temporal and spatial, poses a challenge when a unique survival value for the species is desirable, such as in comparative evolutionary studies or when assessing whether a particular population is threatened and in need of conservation management. Interspecific comparative studies of life-history traits, however, often generalise patterns from single populations (Promislow and Harvey 1990; Bennett and Owens 2002), even though some of these traits may be as different within as between species (Dhondt 2001). It has been suggested that to obtain representative estimates of demographic parameters for a given species, different populations in a large area or ideally along the species geographical range should be explored and an average value calculated if significant differences are detected (Bennett and Owens 2002; Frederiksen et al. 2005).

The simultaneous study of survival at multi-population levels using mark–recapture data has recently started to receive attention and, to date, most such studies on mammals have involved large herbivores (e.g. Gaillard et al. 1997; Jorgenson et al. 1997; Loison et al. 1999; but see Graham and Lambin 2002; Ozgul et al. 2006). Although bats constitute up to 20% of all mammal species (over 1,100 species described world-wide to date), their demography is poorly known, and the survival of only a few of them has been systematically studied (see review by O'Shea et al. 2004 for earlier studies; Pryde et al. 2005; Frick et al. 2007; Schaub et al. 2007; Papadatou et al. 2009; Schorcht et al. 2009). To the best of our knowledge, there has been no attempt to assess bat survival at multi-population levels. Unlike other similar-sized mammals, bats have relatively high survival rates (e.g. O'Shea et al. 2004; Papadatou et al. 2009; Schorcht et al. 2009), very long life spans and low reproductive outputs (Barclay and Harder 2003). Most temperate bat species give birth to a single offspring, and females may not reproduce every year. Adult survival of bats is therefore expected to be of major importance for their population dynamics, as in other long-lived animals (Schorcht et al. 2009).

We have studied the potential inter-population variation in annual female adult survival probabilities of the isabelline serotine bat *Eptesicus isabellinus*, with the aim of estimating a representative survival value for the species. The vital rates of this newly discovered bat in the Iberian Peninsula (Ibáñez et al. 2006; García-Mudarra et al. 2009) are not known, and adult females are the most important determinant of bat population demography (Kerth and Petit 2005). We analysed mark–recapture data of individually identified animals from six *E. isabellinus* maternity colonies in the south of Spain and investigated the potential variation in the species' mean annual female adult survival probabilities on two different scales. First, on a coarse scale, we investigated the effect of foraging habitat on survival by grouping the colonies according to the main surrounding habitat type. Second, on a fine scale, we examined the effect of colony on survival. Finally, we estimated the mean value of female adult survival probabilities over all colonies in a joint analysis. One approach to deal with variability in survival is to consider that individual survival values arise from a unique probabilistic distribution with a mean and a variance. This approach has been used to account for temporal fluctuations in survival using models in which temporal variation was modelled as a random effect (Brooks et al. 2002; Burnham and White 2002). We propose to extend the idea of random fluctuations in survival at a multi-population level. We therefore accounted for temporal and inter-colony variations in survival by incorporating random effects in mark–recapture models. We estimated parameters using a Bayesian approach implemented through the use of Markov chain Monte Carlo (MCMC) methods.

Materials and methods

Study species and sites

Serotine bats have only recently been classified as *Eptesicus isabellinus* in the south of the Iberian Peninsula. This species was first described in North Africa (Ibáñez et al. 2006; Dietz et al. 2009). The isabelline serotine *E. isabellinus* is a fairly large bat with a body mass of 19–25 g. Its geographical distribution extends from the south of Spain to the northwest of Africa, and it is also found in the Canary Islands (Dietz et al. 2009). The species forages in open areas like its more common European relative, the serotine bat *E. serotinus*, to which it is most probably ecologically similar (Juste et al. 2009). In our study area, the isabelline serotine selects areas with high relative humidity (e.g. river banks) as preferred hunting sites, most probably because of the higher availability of hard insects, such as Coleoptera and Hemiptera, which represent the largest proportion of its diet (Pérez-Jordá 1994). The species roosts in natural rock crevices as well as in a variety of human constructions (e.g. buildings, bridges, etc.). Maternity colonies typically last from spring to late summer, mostly dispersing by autumn when the bats go to different sites for hibernation (Pérez-Jordá 1994). Preliminary data suggest that these colonies may hibernate in small groups in crevices not very far from their summer roosts (Ibáñez and Juste, unpublished data). In fact, the probably ecologically similar serotine *E. serotinus* is sedentary, and distances between summer and winter roosts are small (Dietz et al. 2009).

We focused on the survival of individually marked female adult *E. isabellinus* at six maternity colonies spread over two provinces: (1) Gadea Bridge, Villarasa (37°25′N, 6°36′W), Molino Duende Bridge, Niebla (37°27′N, 6°41′W) and Sotiel Coronada Tunnel, Calañas (37°36′N, 6°50′W) in Huelva Province; (2) Cañaveroso Bridge, Aznalcóllar (37°32′N, 6°18′E), Alcalá del Río Dam (37°31′N, 5°58′E) and Trajano Bridge, Las Cabezas de San Juan (37°02′N, 5°55′E) in Seville Province. All of these roosts are in man-made constructions at low altitude (ranging from 10 to 120 m a.s.l.) that are used partially or completely by the maternity colonies. Mean distance between colonies was 52 ± 26.2 km [mean ± standard deviation (SD)] and the range was 8–103 km (Fig. 1). The colonies in Gadea, Alcalá del Río and Trajano are much larger in size (200–300 adult females and juveniles) than the other three colonies (40–90). Alcalá del Río and Trajano are both located in the Guadalquivir valley and are surrounded by agricultural fields and transformed marshes. The main land use type surrounding the two colonies is irrigated agriculture (87 and 91% of total land use types, respectively, at an average foraging distance of 5 km from each colony), which presumably offers suitable foraging areas with high prey availability. The remaining four sites are located in habitats consisting mainly of Mediterranean shrub (range 44–93% at distances of 5 km) with forest patches that have been replaced over large areas by *Eucalyptus* sp. plantations interspersed with dry cultures (e.g. wheat).

Data collection

Capture projects were initiated on different years at each of the colonies, the earliest starting in 1983 and the latest in 2001. The duration of each project differed among colonies (range 8–26 years; Table 1). Bats were not captured in certain years at some of the colonies (Table 1) due mainly to incompatibility with other research activities. Some road constructions in 2003 forced the colony to abandon Gadea Bridge until 2006. Similarly, the colony in Cañaveroso fled the bridge in 2004 after a devastating fire in the area and did not return to the roost until 2007.

In most sites and for most of the duration of each study, field protocols consisted of one capture session per year and colony. This took place during the breeding season in July, when most adult males are absent and juveniles start flying. The colony in Gadea was more intensively studied over a number of years because it was used for the study of the species ecology (Pérez-Jordá 1994). Bats were mist-netted during emergence from their diurnal roosts at dusk (Alcalá del Río, Cañaveroso, Gadea, Molino Duende) or when entering their nocturnal roosts (Molino Duende, Sotiel Coronada) or captured manually with hand-nets within their diurnal roosts (Cañaveroso, Gadea, Trajano). Each captured bat was fitted with a 4.2-mm uniquely numbered aluminium alloy ring (Lambournes, Birmingham and Porzana, Icklesham, UK) and assessed for sex, age (two age classes: juveniles and adults) and reproductive condition. Juveniles are considered to be individuals born in the year of capture and are identified by the infused cartilaginous plates in the metacarpal phalangeal joints (Anthony 1988), a character which is still obvious in most individuals at least until early autumn. Adults are individuals captured any year other than their year of birth. All bats were released shortly after handling.

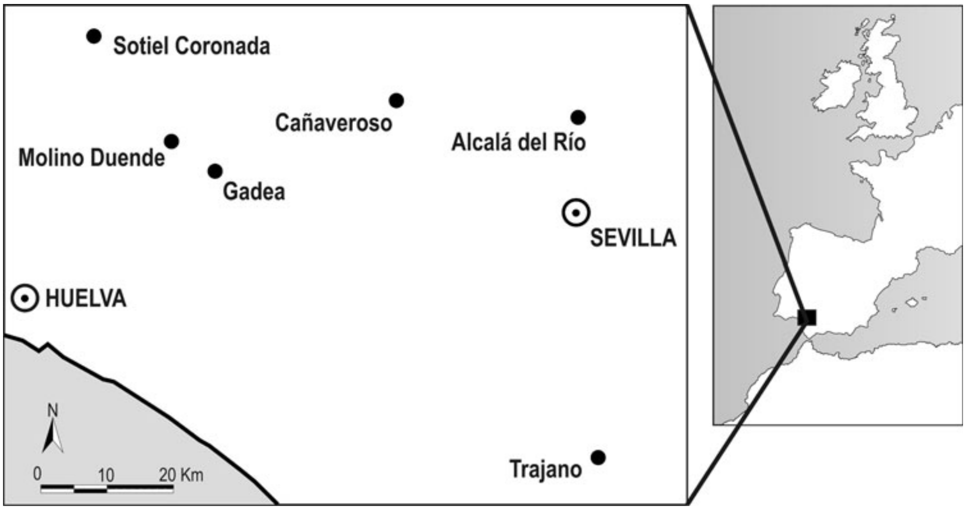

Fig. 1 Map of the six study colonies of the isabelline serotine bat *Eptesicus isabellinus* in the south of the Iberian Peninsula

Table 1 Number of adult female bats ringed, number (and proportion) of individuals recaptured, total number of recaptures (including individuals repeatedly recaptured), length of study period and years when no capture occasions took place at six *Eptesicus isabellinus* colonies in the south of the Iberian Peninsula

Colony	Bats ringed (*n*)	Individuals recaptured (*n*)	Total recaptures (*n*)	Study period	Years without capture occasions
GAD	429	194 (45%)	413	1983–2008 (26)	1986–1987, 2003–2005 (5)
MOD	94	46 (49%)	103	1993–2008 (16)	1994–1995 (2)
SCO	69	32 (46%)	53	1996–2008 (13)	–
CAN	171	44 (26%)	50	1992–2008 (17)	1996–1997, 2004–2006 (5)
H1	763	316 (41%)	619	–	–
ALR	241	27 (11%)	36	2001–2008 (8)	–
TRA	136	24 (17%)	28	2001–2008 (8)	–
H2	377	51 (14%)	64	–	–

[a] GAD, Gadea; MOD, Molino Duende; SCO, Sotiel Coronada; CAN, Cañaveroso; ALR, Alcalá del Rio; TRA, Trajano; H1, Habitat 1; H2, Habitat 2 (see text for details)

[b] Proportion of recaptured individuals among total number of captured individuals is given in parenthesis

[c] Number of years the without capture is given in parenthesis

Data analysis

In addition to using data from adult females, we also used data from female bats initially captured and marked as juveniles to increase sample size. To do so, we removed the first year from their capture histories and considered their first year of capture to be the year when they were first recaptured as adults.

Survival or recapture heterogeneity may induce bias in survival estimates. To check for heterogeneity in survival (transience effect; Pradel et al. 1997) and recapture probabilities (trap dependence effect; Pradel 1993) prior to modelling, we assessed the fit of the general time-dependent CJS model for each colony using the U-CARE software programme (Choquet et al. 2009).

Recaptures of ringed bats have shown that there is no switching between roosts, even between those closest to each other, and that females are strongly philopatric. These observations are reinforced by the results of a recent study which showed that these colonies show high genetic variation and restricted female-mediated gene flow, suggesting no contacts between them (Juste et al. 2009). We therefore did not consider movements between colonies into modelling procedures.

We estimated mean annual female adult survival probabilities using the general framework of random effects. A major advantage of this approach is the flexibility it provides in estimating biological process variance separately from sampling variance. We investigated the potential variation in survival at two different scales, where scale refers to the magnitude of the sampling unit (Liebhold et al. 2004). First, to investigate variation on a coarse scale, we grouped maternity colonies based on the differences in surrounding habitat types (Gadea, Molino Duende, Sotiel Coronada and Cañaveroso vs. Alcalá del Río and Trajano; hereafter called Habitat 1 and Habitat 2, respectively), and we tested for an effect of habitat on their survival probabilities. Because breeding females have increased energy demands, a less suitable habitat (e.g. lower insect abundance) may result in lower survival. Habitat 2 (irrigated agricultural land and transformed marshes) presumably is more predictable and offers higher prey availability; hence we predicted that survival at colonies within this habitat type would be higher than that at colonies in Habitat 1. Second, to investigate variation in survival on a fine scale, we estimated the survival probability of each colony separately and compared estimates between pairs of colonies. Differences in survival among colonies may be related to a variety of colony-specific factors, such as quality of foraging and roosting habitat, density-dependent processes, human disturbance, road kills (Russell et al. 2009), age structure and senescence effects (Festa-Bianchet et al. 2003) and immunological response to disease (Allen et al. 2009). To estimate survival probabilities at each different habitat type or colony we treated temporal variation as a random effect ε_t following a normal distribution with mean 0 and variance σ^2. We estimated the mean survival probability μ per habitat or colony and the temporal process variance in survival probability σ^2 (Gould and Nichols 1998; Burnham and White 2002) on the logit scale following the model:

$$\begin{aligned} \operatorname{logit}(\varphi_t) &= \mu + \varepsilon_t \\ \varepsilon_t &\sim N(0, \sigma^2) \end{aligned} \tag{1}$$

where φ_t is the probability that an individual survives to occasion $t + 1$ given that it is alive at time t. We used the logit link function in order to ensure obtaining survival estimates in the interval [0; 1].Third, to estimate overall survival across all colonies taking into account both temporal and inter-colony variability, we considered the model:

$$\begin{aligned} \mathrm{logit}(\varphi_{ct}) &= \mu + \varepsilon_{ct} + \varepsilon_c \\ \varepsilon_{ct} &\sim N(0, \sigma^2) \\ \varepsilon_c &\sim N(0, \sigma_c^2) \end{aligned} \qquad (2)$$

where μ is the logit mean survival probability across all colonies, ε_{ct} are independent identically distributed random variables drawn from normal distributions with mean 0 and site-specific temporal variances σ^2 and ε_c is a random variable drawn from another normal distribution with mean 0 and inter-colony variance σ_c^2. Both variances σ^2 and σ_c^2 are estimated on the logit scale. Mean values of survival in all models are calculated as the inverse logit of μ, i.e. $S = \mathrm{logit}^{-1}(\mu)$.

Recapture was treated as a fixed effect and was time dependent in all models (see Electronic Supplementary Material 1). Recapture probabilities for years without captures were fixed to zero, while the survival rates of the respective intervals were arbitrarily set to be equal to ensure identifiability and interpretability.

Analysis was performed in a Bayesian framework using MCMC algorithms (Gilks et al. 1996) to take advantage of the flexibility they offer in implementing random effects models. In contrast with the maximum-likelihood approach, using MCMC algorithms we did not obtain point estimates but posterior distributions of the parameters, and this information was summarised as interpretable point estimates (posterior means or medians) and uncertainty intervals (credible intervals) (McCarthy 2007). Because there was no strong prior information on the parameters, we used vague prior distributions, namely a normal distribution with mean 0 and large variance (100) for mean logit survival, a uniform distribution between 0 and 5 for the standard deviation of a random effect and a uniform distribution between 0 and 1 for recapture probabilities. We used the WinBUGS programme (Lunn et al. 2000) to fit models by calling it from software R through the package R2WinBUGS (Sturtz et al. 2005). Priors and likelihoods were specified within WinBUGS, while *R* was useful for setting initial values and post-processing the results (Gimenez et al. 2009). Posteriors were calculated using two Markov chains. The number of iterations applied in model (1) was 1,000,000 with a burn-in of 250,000 iterations; in model (2), it was 4,000,000 with a burn-in of 800,000 iterations. Mixing of the chains was found to be satisfying. Convergence was assessed using the Brooks–Gelman–Rubin criterion (Brooks and Gelman 1998). Model (2), estimating overall survival accounting for colony and time variation, was specified in WinBUGS, as shown in the WinBUGS code (Electronic Supplementary Material 2).

In a Bayesian analysis, there is no predefined threshold of significance to which the probability of an event is compared. To test for the effect of habitat or colony on survival, we calculated the difference in posterior survival means between habitats and between colonies, respectively with the respective 95% credible intervals (CI) of each difference. We considered an effect of habitat or colony as statistically supported when 0 was outside the 95% credible interval of the difference.

Results

A total of 1,140 ringed and 367 recaptured adult female bats were included in the analysis. Of these, 763 and 377 were ringed at sites in Habitat 1 and Habitat 2, respectively (Table 1). The number of bats ringed at each of the six colonies ranged from 69 to 429, and the number of individuals recaptured at each colony varied from 24 to 194 (Table 1). A higher proportion of bats were recaptured at Habitat 1 than at Habitat 2 (41 vs. 14%, respectively; Table 1), presumably because of the shorter duration of the capture projects and the respective larger colony sizes at Habitat 2. Bats were not captured on certain years at half of the colonies (Table 1).

The CJS model fitted the data adequately for all colonies (Gadea: $\chi^2_{52df} = 31.51$, $P = 0.99$; Molino Duende: $\chi^2_{38df} = 31.99$, $P = 0.74$; Sotiel Coronada: $\chi^2_{25df} = 12.08$, $P = 0.99$; Cañaveroso: $\chi^2_{25df} = 9.83$, $P = 1.00$, Alcalá del Río: $\chi^2_{15df} = 2.20$, $P = 1.00$; Trajano: $\chi^2_{11df} = 4.51$, $P = 0.95$). No heterogeneity in recapture probabilities due to trap dependence or in survival probabilities due to transience was detected, since none of the specific tests were significant (results not shown).

Posterior means of annual survival probabilities at Habitats 1 and 2 were 0.71 [95% CI 0.51; 0.86] and 0.60 [95% CI 0.28; 0.89], respectively. The difference between habitats was not statistically supported [95% CI −1.25; 2.24]. Mean annual survival of colonies ranged between 0.58 [95% credible interval (CI) 0.23–0.92] (Alcalá del Río; Seville) and 0.81 (95% CI 0.73–0.88) (Molino de Duende; Huelva) (Table 2). The difference in survival between most of the pairs of the colonies was not statistically supported, except for Molino Duende and Cañaveroso (0.81 vs. 0.61, respectively; Tables 2, 3), which are 35 km apart (Fig. 1). Colonies exhibited various patterns of temporal variation of annual survival estimates across years (Fig. 2), and temporal variances of colony survival probabilities were highly varied (Table 2). The overall posterior mean survival estimate across all colonies was 0.72 (95% CI 0.57–0.93), with an inter-colony variance estimate on the logit scale of 0.98 (95% CI 0.00–8.16). Estimates of colony-specific temporal variances from the model estimating overall survival ranged between 0.57 (95% CI 0.00–3.64) and 6.24 (95% CI 0.22–21.73).

Table 2 Parameter estimates [95% CI] per *E. isabellinus* colony: mean survival probabilities S, temporal process variances σ^2 and geometric means p of recapture probabilities

Estimated parameter[a]	Colony					
	GAD	MOD	SCO	CAN	ALR	TRA
S	0.71/0.70	0.81/0.81*	0.71/0.71	0.61/0.61*	0.58/0.59	0.61/0.61
	[0.62–0.82]	[0.73–0.88]*	[0.58–0.82]	[0.42–0.76]*	[0.23–0.92]	[0.41–0.85]
σ^2	0.69/0.47	0.31/0.13	0.77/0.42	0.95/0.17	3.55/2.34	1.17/0.36
	[0.13–3.02]	[0.00–1.56]	[0.01–3.43]	[0.00–5.85]	[0.02–15.26]	[0.00–8.05]
p	0.45/0.45	0.41/0.41	0.38/0.37	0.25/0.25	0.16/0.16	0.15/0.15
	[0.38–0.52]	[0.33–0.48]	[0.27–0.48]	[0.16–0.35]	[0.07–0.29]	[0.08–0.26]

Abbreviations of colonies as in Table 1

* Statistically different survival estimates

[a] See text Data analysis for definition of parameters. Survival and recapture probabilities are reported on the [0; 1] scale and variances on the logit scale. All parameters are expressed as means and medians (mean/median) of the posterior distributions

Table 3 Credible intervals (95%) of the differences in posterior survival means between pairs of the six *E. isabellinus* colonies in the south of the Iberian Peninsula

Colony	GAD	MOD*	SCO	CAN*	ALR	TRA
GAD		NS	NS	NS	NS	NS
MOD*	[−1.17; 0.18]		NS	–[a]	NS	NS
SCO	[−0.74; 0.82]	[−0.16; 1.28]		NS	NS	NS
CAN*	[−0.34; 1.36]	[0.16; 1.98]*	[−0.50; 1.45]		NS	NS
ALR	[−1.61; 2.18]	[−1.09; 2.82]	[−1.77; 2.32]	[−2.05; 1.78]		NS
TRA	[−0.91; 1.43]	[−0.36; 1.99]	[−1.03; 1.43]	[−1.57; 1.11]	[−2.04; 2.18]	

NS not statistically supported; other abbreviations as in Table 1

* Colonies statistically supported difference in survival estimates

[a] Statistically supported

Discussion

Mean annual survival estimates for the six adult female isabelline serotine colonies (range 0.58–0.81) fall within the range of annual adult survival estimated for single colonies of other bat species, such as *Pipistrellus pipistrellus* [0.80 ± 0.05 (standard error); Sendor and Simon 2003] and *Nyctalus leisleri* (0.76 ± 0.04; Schorcht et al. 2009). These are apparent survival estimates, meaning that permanent emigration and mortality are confounded. However, they are considered to be close to the species' real survival rate because female adults are highly philopatric (Juste et al. 2009), hence permanent emigration is limited. In terrestrial mammals, survival has been shown to be affected by senescence, which means that the mortality of adult individuals increases after a certain age (Caughley 1966; Festa-Bianchet et al. 2003; Descamps et al. 2008). This may lead to underestimation of pooled "adult" survival (Festa-Bianchet et al. 2003). However, markedly different patterns of age-specific survival have been reported in birds (Crespin et al. 2006). In bats, age effects on adult survival have not been detected (Schorcht et al. 2009), and published information on potential senescence effects is lacking; therefore, age effects were not included in the modelling procedures of our study.

The aim of our study was to investigate potential variations in mean annual survival probabilities of adult female isabelline serotines across different sites on two scales and to provide an overall estimate for the species accounting for these variations. Survival estimates varied on both scales. First, on the coarse scale, survival differed between colonies grouped in two different habitat types (Habitat 1 0.71; Habitat 2 0.60). However, as this difference was not statistically supported, we did not use a model to estimate overall survival with a random effect of habitat. Second, on the fine scale, survival differed among colonies, and the difference in one of the 15 pairs of colonies was statistically supported (Molino Duende 0.81 vs. Cañaveroso 0.61). We then used a model to estimate overall survival using inter-colony variability as a random effect. A model fitted while ignoring inter-colony variability had no support from the data according to the Deviance Information Criterion (DIC; Spiegelhalter et al. 2002). DIC is the Bayesian equivalent of the Akaike Information Criterion (AIC;

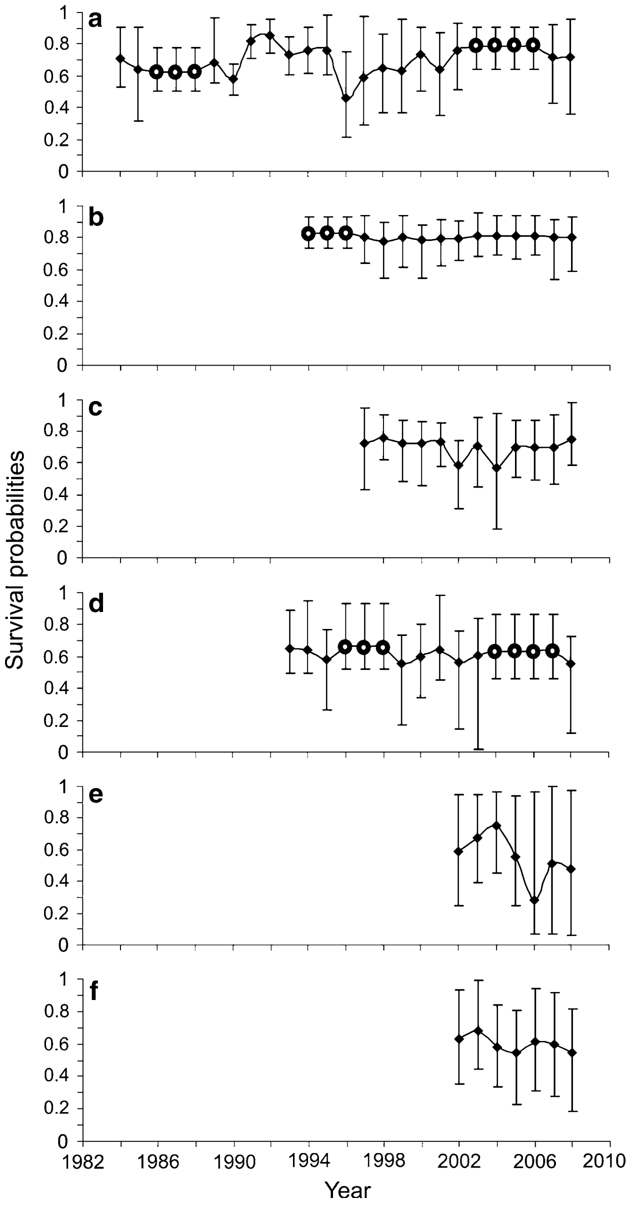

Fig. 2 Temporal variation with 95% credible intervals in annual survival estimates of six *E. isabellinus* colonies in the south of the Iberian Peninsula. Survival probabilities for intervals between recapture probabilities fixed to 0 were set to be equal and are indicated by *circles*. Colonies: **a** Gadea, **b** Molino Duende, **c** Sotiel Coronada, **d** Cañaveroso, **e** Alcalá del Rio, **f** Trajano

Burnham and Anderson 2002) used in the maximum-likelihood approach for model selection. Overall mean annual survival estimated by this model was almost similar to—but more precise than—the value obtained by the model accounting for inter-colony variability (0.71; 95% CI 0.66–0.77 vs. 0.72; 95% CI 0.57–0.93, respectively), However, it was derived by a model that was not selected by formal model selection procedures, such as the DIC. Such models result in misleading, spurious precision measures and/or point estimates. Even if point estimates were found to be similar between the two models in our case (with and without colony effect), the true value may fall outside the narrower precision measures estimated by the "bad" model. We therefore conclude that inter-colony variation is important and that to estimate an overall survival value for the species, we should use the model with the additional random effect of inter-colony variation.

Inter-population variability in survival has been detected and stressed by a number of researchers (e.g. Gaillard et al. 1997; Dhondt 2001; Frederiksen et al. 2005; Ozgul et al. 2006; Sanz-Aguilar et al. 2009), and reported differences often fall within the range of differences found in this study. We suggest that a representative survival value for any species should be based on a number of different populations and that estimates from single populations should be treated with caution. Because vital rates are site-specific (Blondel et al. 1992) and there may be large-scale spatial heterogeneity across a species' geographical range, populations used for survival estimates should ideally cover the species geographical range. The number of populations to be considered in order to obtain a representative "typical" survival estimate with its respective inter-population variance depends on the species, the degree of spatial heterogeneity and the size of the targeted populations. Because we do not yet have the theoretical knowledge, it is not possible to suggest guidelines for choosing the right number for any species. The necessary theoretical knowledge will be gradually acquired through accumulated experience with many species and geographical areas. The minimal contribution of our study is that more than one site per species should be used to obtain less biased survival estimates.

Although our approach accounts for differences among populations and sites, it does not aim to explain their causes. In contrast to our prediction, survival in Habitat 2 (0.60) was lower than survival in Habitat 1 (0.71), but this difference was not statistically supported. It is likely that this difference is due to variation in colony-specific characteristics that may have a more significant effect on survival than foraging habitat, as also shown by the among-colony variation. Colony-specific characteristics include summer and winter habitat, immunological response to disease and spatiotemporal dynamics of viruses, road kills and, potentially, age structure. For example, one of the two colonies in Habitat 2 roosts in a highway bridge that may increase mortality risk by motor vehicles (Russell et al. 2009). The most common bat rabies virus in Europe (EBLV1; Davis et al. 2005; Vázquez-Morón et al. 2008) has been found in some of our study colonies, and colonies may show differential temporal patterns of virus circulation (Vázquez-Morón et al. 2008). In some large long-lived mammals, increased population density may affect population age structure and thus lead to a higher proportion of senescent females which have a lower probability of survival than prime-aged individuals (Festa-Bianchet et al. 2003). However, to date, data on density effects on the age structure of bat colonies as well as senescence effects on bat survival are, as already mentioned, lacking. Because our ultimate aim was to obtain a single unbiased survival estimate for isabelline serotine bats and not to investigate the potential causes of inter-colony and temporal variations, further studies at the multi-population level should be made in order to test for specific biological hypotheses. In such studies, either the random or fixed effects approach could be applied.

Conclusion

Our study contributed to the accumulation of insights into the estimate of survival at multi-population levels. Our data collected over the course of up to 26 years from six colonies of an insectivorous bat species revealed evidence for colony effects and some evidence for a habitat effect on the mean annual survival of adult females, the most important determinant of bat population demography. To estimate an unbiased representative value of survival for any species for comparative studies or conservation purposes (e.g. when a reference value is needed to assess potentially threatened populations), we propose that a number of different populations or sites ideally covering the species geographical range should be examined and a model accounting for inter-population variation be used.

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