

available at [www.sciencedirect.com](http://www.sciencedirect.com)

ELSEVIER

journal homepage: [www.elsevier.com/locate/biocon](http://www.elsevier.com/locate/biocon)

## Sex-specific roost movements and population dynamics of the vulnerable long-fingered bat, *Myotis capaccinii*

Eleni Papadatou<sup>a</sup>, Roger K. Butlin<sup>b</sup>, Roger Pradel<sup>c,d</sup>, John D. Altringham<sup>a,\*</sup>

<sup>a</sup>Institute of Integrative and Comparative Biology, Faculty of Biological Sciences, University of Leeds, Leeds LS2 9JT, United Kingdom

<sup>b</sup>Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, United Kingdom

<sup>c</sup>Centre d'Ecologie fonctionnelle et Evolutive/Centre National de la Recherche Scientifique (CEFE/CNRS), BP 5051, 34293 Montpellier Cedex 5, France

<sup>d</sup>Institut Mediterrani d'Estudis Avançats IMEDEA (CSIC-UIB), Miquel Marqués 21, 07190 Esporles, Mallorca, Spain

---

### ARTICLE INFO

**Article history:**

Received 18 April 2008

Received in revised form

6 October 2008

Accepted 17 October 2008

Available online 3 December 2008

---

**Keywords:**

MARK

Capture-recapture

*Myotis capaccinii*

---

### ABSTRACT

The roosts of many IUCN-listed cave-roosting bat species are under threat from tourist development in SE Europe and other regions of the world. Much-needed conservation strategies require, among other information, an understanding of their roost movements and population dynamics, which can now be obtained relatively quickly using advanced models. We have studied the long-fingered bat, *Myotis capaccinii*, an obligate cave-dweller, in Dadia National Park, Greece. The species formed colonies of up to a few thousand individuals and was highly mobile, frequently switching summer roosts up to 39 km apart, even during late pregnancy. The bats migrated to distant hibernacula including a cave in Bulgaria 140 km NW of the Park. Adult recapture probabilities varied with season and sex: low female recapture rates in autumn, relative to spring and summer, indicated non-random temporary emigration following nursery colony dispersal. The opposite pattern was seen in males: increasing recapture rates in the autumn suggest that males gather in these roosts to mate with females in transit. Adult survival (0.86–0.94) was similar in females and males, similar in winter and summer, and comparable to recent estimates for other bats based on similar modelling techniques. Sex-based differences in juvenile recapture suggest female philopatry and male-biased dispersal. Our work shows that protection of *M. capaccinii* roosts must extend beyond the Park's and indeed the country's boundaries: its conservation requires large-scale, trans-national integrated conservation plans. Our results will apply to many other warm-temperate species with similar life history cycles.

© 2008 Elsevier Ltd. All rights reserved.

---

### 1. Introduction

Migratory and intra-seasonal movements are common in highly mobile animals such as birds and bats. The movement of birds has been extensively studied but much less is known about the role of intra- and inter-seasonal movements between roosts in the ecology of bats (e.g., Fleming and Eby,

2003; Kerth et al., 2006; Popa-Lisseanu et al., 2007). Roosts protect bats from predation and adverse weather, promote energy conservation and facilitate social interactions and information transfer (Kunz, 1982; Kunz and Lumsden, 2003). Temperate bats use roosting sites for rearing pups in summer, mating in late summer and autumn and hibernation in winter. Throughout the world caves and mines host large bat

\* Corresponding author. Tel.: +44 113 343 2832; fax: +44 113 343 2835.

E-mail addresses: [Elena.papadatou@gmail.com](mailto:Elena.papadatou@gmail.com) (E. Papadatou), [R.K.Butlin@sheffield.ac.uk](mailto:R.K.Butlin@sheffield.ac.uk) (R.K. Butlin), [roger.pradel@cefe.cnrs.fr](mailto:roger.pradel@cefe.cnrs.fr) (R. Pradel), [j.d.altringham@leeds.ac.uk](mailto:j.d.altringham@leeds.ac.uk) (J.D. Altringham).

0006-3207/\$ - see front matter © 2008 Elsevier Ltd. All rights reserved.

doi:10.1016/j.biocon.2008.10.023

colonies and the high fidelity shown to just one or a few sites makes bats particularly vulnerable (e.g., Tuttle, 1976). Caves serve as nursery colonies in tropical and warm-temperate regions and hibernacula in both cool and warm-temperate zones. In warm-temperate regions, cave use is often complex, with bats moving from site to site (e.g., Kunz, 1982). The loss or degradation of any of these sites may reduce reproductive success or increase mortality (Fleming and Eby, 2003).

Because roosts with different functions are needed to complete the yearly cycle, protecting only those sites with large numbers of bats may be insufficient: management for conservation requires an understanding of roosting ecology (e.g., Kurta and Kennedy, 2002). Nursery colonies in underground sites are widespread in southern Europe, but the same (and many other) sites are used at other times of year. For example, Koyunbaba Cave in NW Turkey is home to nursery colonies totalling 23,000 bats of six species (Furman and Ozgul, 2004), but the cave is used by a wider range of species throughout the year. Unfortunately, Koyunbaba and many other caves surveyed by Furman and Ozgul are under threat, primarily from tourist development, despite the threatened status of the bats using them. The situation is similarly unsettling in several other countries in the region (e.g., Paragamian et al., 2004) and beyond (e.g., Mexico, Arita, 1996; China, Niu et al., 2007). Of the sites under study here, Maronia Cave is threatened by tourist development and Koufovouno is unprotected and subject to frequent disturbance, which can lead to roost abandonment.

Understanding the dynamics of animal populations is also of great importance in conservation management. The probability of adult survival is usually the major determinant of population growth or decline in long-lived species (e.g., Prévot-Julliard et al., 1998), such as bats: estimates of survival rate and the identification of the factors affecting it are therefore vital (Morris and Doak, 2002). Capture-mark-recapture models have been among the most important methods for the study of population dynamics, particularly of cryptic animals (Burnham et al., 1987; Pollock et al., 1990; Lebreton et al., 1992). The recent development of sophisticated models and flexible software has facilitated the modelling of complex dynamics (Lebreton et al., 1992; Cooch and White, 2006). By identifying factors involved in the survival and recapture processes, these models can help us understand the dynamics, ecology and behaviour of animal populations (Pollock et al., 1990; Lebreton et al., 1992), estimate trends and assess their viability in time, as well as evaluate the impact of threats and management practices on survival (Lettink and Armstrong, 2003; Pryde et al., 2005).

Capture-mark-recapture has been applied in bats to track movements between sites (e.g., Humphrey and Cope, 1976; Tuttle, 1976; Fleming and Eby, 2003; Rivers et al., 2006), to study social systems and population structure (e.g., McCracken and Bradbury, 1981; Park et al., 1998; Entwistle et al., 2000; Senior et al., 2005) and to estimate population size (e.g., Vonhof and Fenton, 2004; Senior et al., 2005; Rivers et al., 2006). Many older attempts to estimate survival rates used demographic techniques (e.g., life tables; see review by Tuttle and Stevenson, 1982) subject to several sources of bias and error. Only a few recent studies have investigated demographic parameters and population dynamics using more ro-

bust modelling techniques (Hoyle et al., 2001; Lettink and Armstrong, 2003; Senior and Simon, 2003; Pryde et al., 2005, 2006).

The long-fingered bat (*Myotis capaccinii*, Bonaparte, 1837) is a cave-roosting species that uses underground sites throughout its life cycle (Spitzenberger and von Helversen, 2001; Papadatou et al., 2008). Females form large maternity colonies in spring and summer to give birth and rear their young. Few adult males are present in these colonies. At the end of summer, maternity colonies disperse and the number of males increases (Papadatou et al., 2008). In winter, most bats move to different caves to hibernate (Spitzenberger and von Helversen, 2001; Papadatou et al., 2008). The species is widely but sparsely distributed around the Mediterranean (Mitchell-Jones et al., 1999; Spitzenberger and von Helversen, 2001). Classified as Vulnerable by the World Conservation Union (IUCN, 2007), it has undergone substantial declines in the western part of its distribution (Mitchell-Jones et al., 1999). Although rare overall, population density can be locally high (Spitzenberger and von Helversen, 2001) suggesting its distribution may be dependent on the availability of suitable underground roost sites. As a regional migrant (Hutterer et al., 2005) it is believed to cross national boundaries between summer and winter roosts, but evidence for this remains sparse and anecdotal. Although the ecology of *M. capaccinii* is now being investigated (e.g., Biscardi et al., 2007; Papadatou et al., 2008), we still have much to learn.

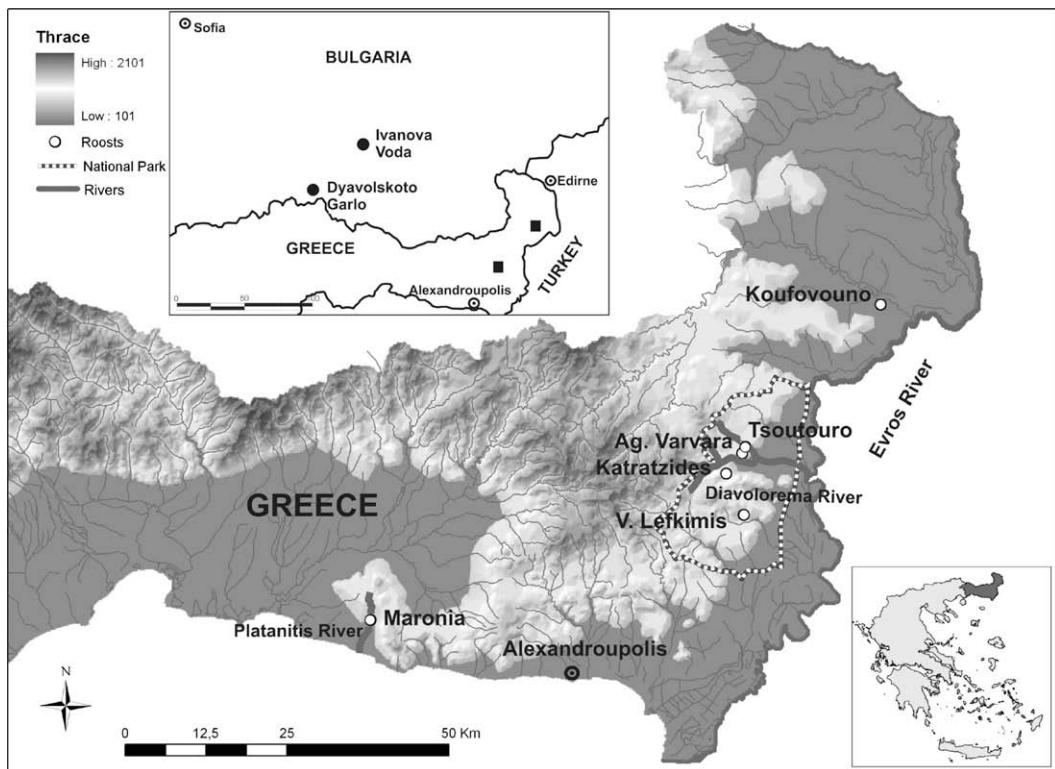
Using a ringed bat population and mark-recapture modelling we aimed to: (a) study the seasonal movements of *M. capaccinii* and determine whether roosting sites within the boundaries of a protected area are adequate for the protection of this species, (b) obtain primary population parameter estimates (survival and population size) and identify factors affecting them and (c) determine whether differences between adult female and male biology (see Papadatou et al., 2008) were reflected in differences in these parameters and in recapture probabilities.

The study was conducted in and close to the National Park of Dadia-Lefkimi-Soufli, Greece, but the results are likely to be applicable to other populations of the species across its geographical distribution, since it uses similar roosts throughout its distribution. Indeed it is likely to be relevant to other temperate cave-roosting bats, including several IUCN ‘red book’ species.

## 2. Materials and methods

### 2.1. Study sites

One volcanic cave (Vouva Lefkimis) and three disused chromium mines (Agia Varvara, Tsoutouro and Katrätzides) were used by *M. capaccinii* in the National Park of Dadia-Lefkimi-Soufli (Fig. 1). The species was also found in two limestone caves near to the park, Maronia and Koufovouno (Fig. 1). Early recaptures of ringed bats showed that Koufovouno was used by the park’s population and it was included in the analysis. The Diavolorema River (Fig. 1) was used regularly by foraging *M. capaccinii* from all of the roosts studied and hence it was also included in the analysis. Roosting sites are described in detail in Papadatou et al. (2008).



**Fig. 1 – The National Park of Dadia-Lefkimi-Soufli and study roosts. Inset: caves Ivanova Voda and Dyavolskoto Garlo (solid circles), used by hibernating bats, in the western Bulgarian part of the Rhodope Mountain range and summer roosts in Dadia National Park and Koufovouno cave (solid squares).**

## 2.2. Data collection

Data were obtained from bats captured at roost entrances during evening emergence using a harp trap (Faunatech, Australia) or mist nets (BTO, UK) and occasionally over the river. Fieldwork was carried out between October 2002 and October 2004. No bats were captured from December to March, since most had migrated to their hibernacula (Papadatou et al., 2008). Visits were made on a regular basis, at intervals (10 or 14 days) aimed at minimising disturbance. Maternity colonies were visited only once in June. All individuals were released within 2 h of capture. Captured bats were identified, their sex, age, reproductive condition and time of capture recorded, and their weight and length of forearm measured. Three age categories were defined, juvenile (J), sexually immature (I) and adult (A) bats (for further details see Papadatou et al., 2008). Bats were ringed on the forearm using individually numbered aluminum rings (The Mammal Society, UK).

## 2.3. Data analysis

### 2.3.1. Data considerations

Only adult bats were used in the analysis, divided into females and males. Immature individuals were excluded to reduce data heterogeneity, since their year of birth was uncertain, and preliminary analysis showed that the number of sampling periods was insufficient for juveniles. However, bats first captured and marked as juveniles in 2003 and recaptured as adults in 2004 were included in the analysis the first

time they were recaptured as adults. Capture data for each group within each of the two years of the study were pooled into seasons based on the bats' seasonal roosting habits (Papadatou et al., 2008) and capture effort. The reasons for pooling were: (a) reduction of data sparseness, (b) reduction of capture heterogeneity since only one roost was sampled on each occasion, and (c) it was biologically meaningful to examine population parameters in seasons. Seasons were spring (April–May), summer (June–August) and autumn (September–October or November), a similar approach to that followed by Hoyle et al. (2001). Winter was considered an interval, as no captures took place and most bats had left the sites. In total, there were seven capture seasons, each representing a capture occasion in the analysis: AU02 (autumn 2002), SP03 (spring 2003), SU03 (summer 2003), AU03 (autumn 2003), SP04 (spring 2004), SU04 (summer 2004) and AU04 (autumn 2004). Multiple recapture of a bat within a season, was considered a single recapture (Hargrove and Borland, 1994). Survival ( $\phi$ ) was estimated for intervals between seasons and recapture rate ( $p$ ) and population size (N) for each season.

### 2.3.2. Model construction and goodness of fit testing

Data analysis was carried out using MARK (Cooch and White, 2006; White and Burnham, 1999). The Cormack-Jolly-Seber (CJS) model based on live recaptures of animals in an open population (Lebreton et al., 1992) was selected initially. The main effects were sex and time, and their interaction was included, giving the starting model:  $\phi_{\text{sex}} \cdot \text{time} \cdot p_{\text{sex}} \cdot \text{time}$ , where ( $\phi$ ) is the survival and ( $p$ ) the recapture rate. Model notation follows

the approach recommended by Lebreton et al. (1992). The starting model was based on the biology of the population, as well as statistical considerations such as goodness of fit (GOF) testing (Lebreton et al., 1992). GOF Tests 2 and 3 were applied using the program U-CARE (Choquet et al., 2005) to see whether the data set violated the assumptions underlying the starting model (Pollock et al., 1990; Lebreton et al., 1992). GOF tests are made up of four different components: TEST2.CT + TEST2.CL + TEST3.SR + TEST3.SM. Any systematic variation in the data set that is not accounted for by the starting model reflects capture (assumption 1) and (or) survival heterogeneity (assumption 2) and results in significance mainly in the TEST2.CT and/or TEST3.SR, respectively (Pradel et al., 2005). Tests 3.SM and 2.CL have no simple biological interpretation (Choquet et al., 2005). U-CARE also provides “directional” tests for immediate trap dependence (specific capture heterogeneity; Pradel, 1993) and transience (specific survival heterogeneity; Pradel et al., 1997). Transience is an extreme case of individual heterogeneity resulting from the capture of animals travelling through the study area at the time of sampling (Pradel et al., 1997). To incorporate transient individuals, a TSM (time since marking) model is used as the global model instead of the CJS model. This model, denoted  $\varphi_{\text{sex}^*M^2t}/\varphi_{\text{sex}^*t}$  where “M2” indicates the classification variable for the newly and previously marked groups and “t/t” indicates full time-dependence for survival ( $\varphi$ ) for each group, respectively, allows survival to differ between newly and previously marked individuals (Pradel et al., 1997; Cooch and White, 2006). The survival of previously marked individuals is an unbiased estimate of the survival of residents, while the survival of newly marked individuals (initial survival including both transient and resident individuals) can be used to estimate the proportion of transients using the formula (Pradel et al., 1997; Appendix):

$$\%T = (1 - \varphi_{R+T}/\varphi_R) \times U/(U+A)$$

where  $\varphi_{R+T}$  is the first-year or initial survival,  $\varphi_R$  the survival of residents, and U and A the number of unmarked and already marked individuals in the sample, respectively.

A GOF test for the TSM model includes all component tests for both sexes except TEST3.SR (Pradel et al., 1997). Hence, GOF tests can identify biological characteristics of the study population that prevent the CJS model from fitting the data. Although sampling was not instantaneous in relation to the intervals between seasons, this was assumed not to affect survival estimates, given the long life span of bats (Hargrove and Borland, 1994; Barclay and Harder, 2003).

### 2.3.3. Candidate model set and model selection

Following GOF testing and construction of an appropriate starting (global) model, a set of alternative models containing fewer parameters was derived based on preliminary analysis and some *a priori* biological considerations from knowledge of this (Papadatou et al., 2008) and other bat species. The most parsimonious among models was selected based on Akaike's information criterion corrected for small sample size (AIC<sub>c</sub>) (Burnham and Anderson, 2002). The model with the lowest AIC<sub>c</sub> best explains the variation observed in the data set and contains the smallest number of parameters possible. As the most parsimonious model, it is selected as a basis

for inference (Anderson et al., 1994; Burnham and Anderson, 2002). If over-dispersion was detected in the data, the quasi-likelihood adjustment of AIC<sub>c</sub> was used (QAIC<sub>c</sub>), incorporating the over-dispersion coefficient ( $\hat{\epsilon}$ ) (Anderson et al., 1994). We also report the difference ( $\Delta$ ) between QAIC<sub>c</sub> of each model and that of the most parsimonious model and Akaike's weight ( $w_i$ ) for each model. Models with  $\Delta\text{QAIC}_c < 2$  are considered to have substantial support and are thus used for making inferences, models with  $\Delta\text{QAIC}_c$  between 4 and 7 have less support and models with  $\Delta\text{QAIC}_c > 10$  essentially none (Burnham and Anderson, 2002). Akaike's weight is proportional to the relative likelihood of each model and the smaller it is the less plausible is the alternative model (Buckland et al., 1997). To accommodate model selection uncertainty, survival and recapture rates and their associated precision measures were estimated using model averaging over all models (Buckland et al., 1997).

### 2.3.4. Population size estimates

MARK does not calculate population sizes for open, live recapture models. We therefore estimated population size  $N_i$  for capture occasion (season) i, as  $n_i/\hat{p}_i$  (Hoyle et al., 2001; Pryde et al., 2005), where  $n_i$  is the number of bats captured on occasion i including both marked and unmarked individuals and  $\hat{p}_i$  is the estimated capture rate for the same occasion. Approximate 95% confidence intervals were calculated as  $\hat{N}_i \pm 2\text{se}(N_i)$  where  $\text{se}(N_i)$  is the standard error of the estimate given by the equation  $\text{se}(\hat{N}_i) = n(\text{se}[\hat{p}])/\hat{p}^2$  (Lettink and Armstrong, 2003).

## 3. Results

### 3.1. Summary statistics

Overall, 4164 bats were captured, 2499 ringed (60.0%), and 831 individuals recaptured (33.2%) with a total of 1127 recaptures, i.e., including individuals repeatedly recaptured, over 139 capture occasions. Of 1573 adults captured and marked, 453 individuals were recaptured (Table 1) with a total of 737 recaptures. The majority of adults were recaptured at a different roosting site from the original capture site (Table 1). Distance between roosting sites ranged from 1 km (Ag.Varvara-Tsoutouro) to 39 km (V. Lefkimis – Koufovouno) (Fig. 1). Long-distance movements were as likely as shorter movements, as the proportion of bats ringed elsewhere and recaptured at the more distant site (Koufovouno) was no lower than at other sites (42% Koufovouno; 12–20% other sites). Frequent movement between roosting sites allowed us to treat them as a single site for the population parameter estimates.

After pooling capture occasions into seasons, most adult bats were captured once only and, of those marked, most were recaptured once only. The proportion of male recaptures was significantly lower than the proportion of female recaptures (Table 1;  $\chi^2 = 9.919$ , df = 1, P < 0.01).

### 3.2. GOF test and global model

The GOF test showed that the CJS model fitted our data, but the P value was close to significance (Tests 2 and 3, total  $\chi^2 = 43.014$ , df = 30, P = 0.058; Table 2). The directional test for

**Table 1 – Number of adult bats ringed, number and proportion of individuals recaptured and number and proportion of individuals recaptured at the site of original capture only and at different sites at least once. Original capture occasions were used, i.e., data is presented prior to pooling into seasons.**

	Female	Male	Total
No. bats ringed	966	607	1573
Individuals recaptured	306	147	453
% Individuals recaptured	32	24	29
No. recaptured original site	110	67	175
% Recaptured at original site	36	46	39
No. recaptured different site	196	80	272
% Recaptured at different site	64	54	61

transience for both sexes was significant ( $z = 2.208$ ,  $P < 0.05$ ), but the test for trap dependence was not ( $z = -0.944$ ,  $P = 0.34$ ). When the two sexes were examined separately, transience was detected only in females ( $z = 2.354$ ,  $P < 0.01$ ), indicating an excess of newly marked individuals never seen again. The autumn 2003 cohort was primarily responsible for the significant result, but there was a weak effect of transience in all seasons (data not shown). Transience was not detected in males, but this could be the result of the generally low male recapture probabilities and smaller data set. Therefore, both sex groups were examined under a TSM model.

GOF test result for this model was significant ( $\chi^2 = 33.751$ ,  $df = 21$ ,  $P < 0.05$ ), because of the significant TEST2.CT for females (Table 2). However, the specific test for trap dependence was not ( $z = -0.250$ ,  $P = 0.80$ ). This indicates capture heterogeneity resulting from over-dispersion of the data, possibly due to lack of independence between individuals, a feature commonly observed in gregarious species (Burnham and Anderson, 2002). Because the calculated over-dispersion coefficient ( $\hat{c}$ ) was less than 3 (1.61), we concluded that the TSM model fitted our data set adequately.

### 3.3. Candidate model set and model selection

#### 3.3.1. Modelling survival

Temporal or seasonal variations were considered in modelling survival. Differences in energetic demands between

sexes and/or between different reproductive seasons are likely to cause differences in survival. Models with interaction terms between effects ( $\varphi_{\text{sex}} \cdot M_2 \cdot t/t$ ), models constrained by season ( $\varphi_{\text{sex}} \cdot M_2 \cdot \text{season}/\text{season}$ ) and some alternatives including additive effects were applied.

#### 3.3.2. Modelling recapture

Recapture rate ( $p$ ) was considered to be different between sexes and constrained to be affected by season, i.e., the main effects on ( $p$ ) were sex and season. The summary of capture–recapture data ( $m$ -arrays, not shown) showed that recapture varied seasonally and differed between males and females: this was incorporated in the models as an interaction term between the main effects. Exploratory analysis confirmed that sex or season alone did not explain any of the variation in the data, so that models  $p_{\text{sex}}$ ,  $p_{\text{season}}$  and  $p$  (i.e., constant recapture and equal between males and females or between seasons) were not included in the set. However, some models having only additive effects of the main factors (sex + season) were considered, because including them allows a formal test of the interaction effect (sex\*season). Hence, recapture rate was modelled as  $p_{\text{sex} \cdot \text{season}}$  or  $p_{\text{sex+season}}$ .

#### 3.3.3. Intervals

Intervals between seasons (AU02, SP03, SU03, AU03, SP04, SU04, AU04) calculated from the median date of the pooled capture occasions of one season to the median of the next were 0.5, 0.2, 0.3, 0.6, 0.3 and 0.3 years successively. Yearly fractions were used as a mean to estimate an equivalent annual survival for each season.

#### 3.3.4. Model set

Twenty models were constructed. The global model had no support (Table 3;  $\Delta QAI C_c >> 10$ ;  $w_i = 0$ ). According to the most parsimonious model (Table 3), survival was equal in adult males and females, initial survival showed random temporal variation, and survival of resident individuals was constant through time ("/" notation). However, this model had an evidence ratio  $w_1/w_2$  (Burnham and Anderson, 2002) only 1.22 times better than the next best model, which assumed a constant initial survival ("./" notation; Table 3). In other words, evidence for variation over time of the proportion of transients was not clearly supported by the data. There was some evidence for an additive sex effect (model 3) or seasonal variation in survival (models 4 and 5) with their  $\Delta QAI C_c < 3$ . Overall, the two best models ( $\Delta QAI C_c < 2$ ) had 55% of the support from the data and the top 11 ( $\Delta QAI C_c < 7$ ) all of the support. Models with additive effect of sex and season in recapture rate ( $p_{\text{sex+season}}$ ) had no support ( $\Delta QAI C_c >> 10$ ;  $w_i = 0$ ).

### 3.4. Parameter estimates

Estimated adult initial survival was lower than the resident adult survival, as expected (Table 4). Initial and resident survival was similar for adult males and females (Table 4) as suggested by the best models in the set (Table 3). Annual survival of residents varied between 0.862 (SE = 0.275) and 0.943 (SE = 0.169). Estimated seasonal recapture rates were generally low in both sexes (Table 4). Adult female recapture rates

**Table 2 – GOF test results of the CJS model  $\varphi_{\text{sex}} \cdot \text{time}$   $p_{\text{sex}} \cdot \text{time}$  for *M. capaccinii* capture–recapture data.**

	$\chi^2$	df	P
<i>Males</i>			
TEST2.CT	6.568	4	0.16
TEST2.CL	7.763	4	0.10
TEST3.SR	1.878	4	0.76
TEST3.SM	1.540	2	0.46
<i>Females</i>			
TEST2.CT	10.060	4	0.04
TEST2.CL	6.930	4	0.14
TEST3.SR	7.385	5	0.19
TEST3.SM	0.889	3	0.83
Total	43.014	30	0.06

**Table 3 – Candidate model set describing survival and recapture of adult male and female *M. capaccinii* bats in the Dadia National Park and adjacent region. Models are ranked according to their  $\Delta\text{QAIC}_c$  values. Only models with  $\Delta\text{QAIC}_c < 7$  and the global model (in bold) are shown.**

Model	QAIC <sub>c</sub>	$\Delta\text{QAIC}_c$	w <sub>i</sub>	Relative model likelihood	n.p.	Qdev
1 $\varphi_{M2^*}/tP_{\text{sex}} \cdot \text{season}$	1640.24	0.00	0.30	1.00	13	69.26
2 $\varphi_{M2^*}/P_{\text{sex}} \cdot \text{season}$	1640.64	0.40	0.25	0.82	8	79.77
3 $\varphi_{\text{sex}+M2^*}/P_{\text{sex}} \cdot \text{season}$	1642.25	2.01	0.11	0.37	9	79.37
4 $\varphi_{M2^*} \cdot \text{season}/P_{\text{sex}} \cdot \text{season}$	1642.27	2.03	0.11	0.36	10	77.37
5 $\varphi_{M2^*} \cdot \text{season}/P_{\text{sex}} \cdot \text{season}$	1642.70	2.46	0.09	0.29	10	77.80
6 $\varphi_{\text{sex}^*M2^*} \cdot \text{season}/P_{\text{sex}} \cdot \text{season}$	1644.17	3.92	0.04	0.14	11	77.24
7 $\varphi_{\text{sex}^*M2^*} \cdot /P_{\text{sex}} \cdot \text{season}$	1644.19	3.95	0.04	0.14	10	79.29
8 $\varphi_{M2^*} \cdot \text{season}/P_{\text{sex}} \cdot \text{season}$	1646.16	5.92	0.02	0.05	12	77.20
9 $\varphi_{M2^*} t/tP_{\text{sex}} \cdot \text{season}$	1646.64	6.40	0.01	0.04	17	67.52
10 $\varphi_{M2^*} \cdot /tP_{\text{sex}} \cdot \text{season}$	1646.75	6.50	0.01	0.04	12	77.79
11 $\varphi_{\text{sex}+M2^*} t/tP_{\text{sex}} \cdot \text{season}$	1647.19	6.95	0.01	0.03	18	66.03
17 $\varphi_{\text{sex}^*M2^*} t/tP_{\text{sex}} \cdot t$	1668.79	28.55	0.00	0.00	32	58.85

$\varphi$  = survival,  $p$  = recapture, QAIC<sub>c</sub> = Quasi Akaike's Information Criterion,  $\Delta\text{QAIC}_c$  = differences in QAIC<sub>c</sub> between each model and the most parsimonious model, w<sub>i</sub> = Akaike's weight, n.p. = number of estimable parameters, Qdev = deviance.

were highest in spring and summer, whereas adult male recapture rates were highest in the autumn (Table 4).

### 3.5. Proportion of transients

Results for the proportion of transients are shown in Table 5.

### 3.6. Adult population size

Population size was estimated for resident males and females in spring and summer 2003 and 2004. Autumn populations were not estimated, because of the evidence of non-random movements and the low recapture probabilities of bats (Pollock et al., 1990). Estimates of adult population size ranged between 606 (381–830) and 1662 (1045–2278) for the females and between 388 (95–680) and 3447 (846–6048) for the males,

though the latter estimate is less precise (Table 5). Overall estimates ranged between 993 and 5109 individuals. Because male and female CI always overlap (Table 5), there is no evidence for departure from 1:1 sex ratio in the population, but males are less likely to be caught.

### 3.7. Juvenile dispersal and survival

Of 364 bats ringed as juveniles in 2003, 57 (16%) were recaptured as adults in 2004 and 79% of the recaptures were females. Thus 27% (45/164) of females, but only 6% (12/200) of males, were recaptured (contingency test;  $\chi^2 = 31.36$ , df = 1,  $P < 0.001$ ). Similar results were obtained the following year: 7% (19/272) of the juveniles ringed in 2004 were recaptured as adults in early-mid summer 2005 and 74% were females. For comparison, 28% (236/833) of the adult bats ringed in

**Table 4 – Average estimates of survival ( $\varphi$ ) and recapture ( $p$ ) and their standard errors (SE): (a) initial survival, i.e., for the first interval immediately following initial capture including both residents and transients (R + T) and survival for all other intervals, i.e., residents only (R), and (b) seasonal recapture rates. Recapture was not estimated for transients, since these are not recaptured by definition. AU02 = autumn 2002, SP03 = spring 2003, SU03 = summer 2003 and so on.**

Season	R + T survival				R survival			
	Females		Males		Females		Males	
	$\varphi$	SE	$\varphi$	SE	$\varphi$	SE	$\varphi$	SE
<b>(a) Survival</b>								
1    AU02–SP03	0.523	0.207	0.497	0.222	–	–	–	–
2    SP03–SU03	0.332	0.242	0.318	0.311	0.943	0.169	0.910	0.226
3    SU03–AU03	0.587	0.304	0.563	0.331	0.872	0.232	0.870	0.265
4    AU03–SP04	0.466	0.143	0.444	0.160	0.947	0.121	0.934	0.136
5    SP04–SU04	0.494	0.248	0.469	0.261	0.943	0.177	0.903	0.242
6    SU04–AU04	0.461	0.310	0.442	0.327	0.863	0.243	0.862	0.275
<b>(b) Recapture</b>								
	Females				Males			
	$p$		SE		$p$		SE	
1    Spring	0.220		0.041		0.049		0.018	
2    Summer	0.205		0.034		0.092		0.024	
3    Autumn	0.077		0.016		0.142		0.032	

**Table 5 – The proportion of transients (% T) in the population and estimates of *M. capaccinii* male and female population sizes (N) with 95% confidence intervals (CI) across seasons.**

Season	Females			Males		
	% T	N	95% CI	% T	N	95% CI
SP03	64	606	381–830	65	388	95–680
SU03	29	652	438–866	34	1132	40–1725
AU03	47	–	–	47	–	–
SP04	38	1662	1045–2279	44	3447	846–6048
SU04	28	1553	1045–2062	37	1524	727–2322

2003 were recovered in 2004. The proportion of juveniles recovered in 2004 was significantly lower than that of adults (contingency test;  $\chi^2 = 26.11$ , df = 1, P < 0.001).

#### 4. Discussion

##### 4.1. Recapture and transience

Adult recapture probabilities were low and varied with season and sex. Male recapture rates were lower than those of females in spring and summer, since many males roost at unknown sites, when females congregate in maternity roosts to breed (Papadatou et al., 2008). In the autumn, male recapture rate increased and female recapture rate decreased, indicating non-random, temporary emigration following maternity colony dispersal at the end of summer. Increasing male recaptures, combined with a larger proportion of males in the autumn samples (Papadatou et al., 2008), suggest that more males gather in these roosting sites, possibly to mate with females in transit. The capture of many unmarked individuals in the autumn suggests transient animals, confirmed by the significant result of GOF tests for females. Transience was more apparent in the autumn, and also in spring 2003. The non-significant result for males may be a result of low male recapture rates and/or real differences in their dispersal behaviour. Autumn and spring transients are probably bats passing through on their way to their winter and summer quarters, respectively. Females in transit may stop over to rest and refuel (Strelkov, 1969; Fleming and Eby, 2003) and/or to mate with the resident males (Dwyer, 1966; Park et al., 1998).

##### 4.2. Roost fidelity and philopatry

It has been suggested that bats are more faithful to more permanent but scarce sites, such as caves and mines (Kunz, 1982; Lewis, 1995; Kunz and Lumsden, 2003). We observed roost switching among *M. capaccinii* maternity colonies between and within years (Papadatou et al., 2008), but it was less frequent than in many tree-roosting species, e.g., *Myotis bechsteinii* (Kerth et al., 2006) and *Nyctalus lasiopterus* (Popa-Lisseanu et al., 2007). Colonies of these species frequently occupy several roosts simultaneously within their home range as the colony fragments and reforms. *M. capaccinii* also conforms to this fission–fusion model, with regular interchange of bats between roosts over a substantial area, but they move less frequently than the tree-roosting species studied. With the exception of lactating individuals, *M. capaccinii*, moved

between roosting sites from spring through to autumn, covering distances up to 39 km, even during heavy pregnancy (Papadatou, 2006). Movements between caves have also been observed in *M. capaccinii* in southern France (Némoz and Brisorgueil, 2008) and in other cave-species, e.g., *Macroderma gigas* (Hoyle et al., 2001), *Myotis grisescens* (Tuttle, 1976), *Miniopterus schreibersii* (Dwyer, 1966) and *Desmodus rotundus* (Trajano, 1996).

Females usually return to their natal colony after hibernation, but males rarely do (e.g., Tuttle, 1976; Bradbury, 1977; Petit and Mayer, 1999; Castella et al., 2001), a characteristic of many mammals (Greenwood, 1980). Recaptures of adults ringed as juveniles suggest that *M. capaccinii* conforms to this pattern of male-biased dispersal.

##### 4.3. Adult survival

The most parsimonious model suggested that random temporal effects (such as weather and prey availability) have a more significant effect on survival than season. However, a time effect was apparent only in the interval following initial capture, i.e., when there were transients, and thus may be an effect of the different proportion of transients in each capture occasion. The sex effect was relatively weak, perhaps due to the small male sample. Some studies suggest differential survival between male and female bats (e.g., Gerell and Lundberg, 1990; Hoyle et al., 2001; Pryde et al., 2005), but Sendor and Simon (2003) found no sex-specific difference in survival in *Pipistrellus pipistrellus*. Sex-specific differences in summer survival might be expected due to the high energy demands of lactation and also in winter survival, since females may deposit more fat than males in the autumn (Ransome, 1990). However, although adult females were heavier than males in the autumn, this was due only to their larger skeletal size (Papadatou et al., 2008).

Annual equivalent survival (0.86–0.94), estimated within each season, was comparable to values (>0.80) reported in recent studies using similar modelling methods: e.g., *Myotis nattereri* in the UK (Rivers et al., 2006), *P. pipistrellus* in Germany (Sendor and Simon, 2003) and *Chalinolobus tuberculatus* in New Zealand (Pryde et al., 2005). Most older studies used less rigorous techniques (e.g., unknown age-cohort life tables) and failed to take into account capture heterogeneity (e.g., emigration or dispersal). As a consequence, estimated survival was lower, e.g., 0.28–0.75 in *P. pipistrellus* (Gerell and Lundberg, 1990), 0.72–0.86 in *Myotis lucifugus* (Humphrey and Cope 1976) and 0.57–0.82 in *M. grisescens* (Tuttle and Stevenson, 1982).

Survival estimates for black-headed gull increased from less than 0.75 to 0.90 over time, reflecting the improvement in methods (Prévôt-Julliard et al., 1998).

A greater mortality during the winter compared to other seasons might be expected due to the depletion of fat reserves at the end of hibernation. However, in agreement with Sendor and Simon (2003), we found no evidence for this.

The significantly lower proportion of juveniles recaptured in the year following their birth may indicate higher vulnerability and lower winter survival compared to adults (Tuttle and Stevenson, 1982). However, it is more likely to be due to dispersal of juvenile males away from the natal area: only 6% were recaptured as adults, compared to 27% of juvenile females. Furthermore, immature bats and non-reproductive females may roost separately from maternity colonies (e.g., Hamilton and Barclay, 1994; Solick and Barclay, 2006).

#### 4.4. Adult population size

The lack of familiarity with the study population and roosts in 2003 resulted in fewer captures (Lettink and Armstrong, 2003) which in turn affected population estimators. This may explain the large difference between estimated spring 2003 and 2004 populations. Estimates became more reliable later when capture probabilities were relatively high (Lebreton et al., 1992). Nevertheless, our study shows that the *M. capaccinii* adult population reaches several thousand individuals in spring and summer. However, the species may be only locally abundant in Dadia National Park. Distribution and abundance of suitable underground roosting sites may have a significant effect on the distribution, density and colony size of bat populations (Kunz, 1982). As an obligate cave-dweller (Spitzenberger and von Helversen, 2001), patchy roost distribution may lead to patchy distribution of the species across its range, as appears to be the case in Bulgaria (Benda et al., 2003).

#### 4.5. Conservation implications

The high proportion of transient bats and the regular use of roosts outside the national park show that protection must extend beyond the park's boundaries to be effective in conserving its breeding population. However, we do not know where transient bats are when they are not in the park. One bat ringed in Dadia was recovered in September 2005, and five more in February 2006, in Ivanova Voda, a cave hibernation site in the western Rhodope Mountains of Bulgaria (Fig. 1), 140 km north-west of Dadia (T. Ivanova and B. Petrov, pers. comm.), where up to 9000 hibernating *M. capaccinii* have been reported (Benda et al., 2003). At least nine more ringed bats were seen whose numbers could not be read and many more may have gone unobserved in the dense hibernation clusters. We recovered three bats in Dadia that were ringed at Ivanova Voda (T. Ivanova, pers. comm.). Ivanova Voda and the nearby Djavolskoto Garlo are among only a few large hibernacula in the western Rhodopes (B. Petrov and T. Ivanova, pers. comm.) and like Koufovouno lack legal protection. Tens of thousands of bats of several species, including *M. capaccinii*, hibernate in these two caves from summer roosts in Bulgaria and beyond. Only one small hibernation site of *M. capaccinii* is known in NE Greece (Maronia Cave, Paragamian et al., 2004) but no bats

from Dadia have been recovered there. Furman and Ozgul (2004) recorded approximately 1000 *M. capaccinii* in winter and 4000 in spring in caves in NW Turkey, 140 km east of Dadia. Over 90% of the *M. capaccinii* were in a single cave, Dupnisa, and most appeared to hibernate elsewhere. The evidence suggests that *M. capaccinii* spend the summer in underground sites throughout SE Europe, often forming large maternity colonies. The bats gather to hibernate in even larger concentrations in a small number of sites. This pattern is seen in other species: e.g., an estimated 90% of the population of *Myotis grisescens* in the southeastern United States hibernates in only three caves, with 75% in a single cave (Tuttle, 1976). The conservation of *M. capaccinii* and other migratory species requires large-scale, integrated conservation plans with co-operation between several countries. There is an urgent need for action, since multi-species assemblages in underground sites in Europe (e.g., Turkey, Furman and Ozgul, 2004; Greece, Paragamian et al., 2004) and beyond (e.g., Mexico, Arita, 1996; China, Niu et al., 2007) are threatened by tourist development.

#### Note added in proof

A male ringed at Maronia was recently recaptured at Gargina Doupka cave (near Ivanova Voda, Fig. 1: B. Petrov, pers. comm.) in Bulgaria and a female from Koufovouno was recaptured at Koyunbaba Cave in Turkey (see Furman and Ozgul, 2004; B. Ozkan and S. Paksuz, pers. comm.) emphasising the complex, trans-national migration patterns.

#### Acknowledgments

We thank WWF Hellas, especially K. Poirazidis and D. Skartsis for their hospitality and assistance. Thanks to the many people who helped with fieldwork. Bats were caught under license from the Hellenic Ministry of Rural Development and Food and the National Park of Dadia-Lefkimi-Soufli. The research protocols complied with the current laws of Greece. EP was funded by a University of Leeds Research Scholarship with assistance from Bat Conservation International. RP was in a sabbatical with the Spanish Ministry of Science (SAB-2006-0014/Roger Pradel).

#### REFERENCES

- Anderson, D.R., Burnham, K.P., White, G.C., 1994. AIC model selection in overdispersed capture-recapture data. *Ecology* 75 (6), 1780–1793.
- Arita, H.T., 1996. The conservation of cave-roosting bats in Yucatan, Mexico. *Biological Conservation* 76, 177–185.
- Barclay, R.M.R., Harder, L.D., 2003. Life histories of bats: life in the slow lane. In: Kunz, T.H., Fenton, M.B. (Eds.), *Bat Ecology*. The University of Chicago Press, Chicago, pp. 209–253.
- Benda, P., Ivanova, T., Horáček, I., Hanák, V., Červený, J., Gaisler, J., Gueorguieva, A., Petrov, B., Vohralík, V., 2003. Bats (Mammalia: Chiroptera) of the Eastern Mediterranean. Part 3. Review of bat distribution in Bulgaria. *Acta Societas Zoologicae Bohemicae* 67, 245–357.
- Biscardi, S., Russo, D., Casciani, V., Cesarini, D., Mei, M., Boitani, L., 2007. Foraging requirements of the endangered long-fingered

- bat: the influence of micro-habitat structure, water quality and prey type. *Journal of Zoology* 273 (4), 372–381.
- Bradbury, J.W., 1977. Social organization and communication. In: Wimsatt, W.A. (Ed.), *Biology of Bats*. Academic Press, New York, pp. 1–73. III.
- Buckland, S.T., Burnham, K.P., Augustin, N.H., 1997. Model selection: an integral part of inference. *Biometrics* 53 (2), 603–618.
- Burnham, K.P., Anderson, D.R., 2002. *Model Selection and Multimodel Inference. A Practical Information – Theoretic Approach*, second ed. Springer-Verlag, New York.
- Burnham, K.P., Anderson, D.R., White, G.C., Brownie, C., Pollock, K.H., 1987. Design and analysis methods for fish survival experiments based on release-recapture. *American Fisheries Society Monograph* 5.
- Castella, V., Ruedi, M., Excoffier, L., 2001. Contrasted patterns of mitochondrial and nuclear structure among nursery colonies of the bat *Myotis myotis*. *Journal of Evolutionary Biology* 14 (5), 708–720.
- Choquet, R., Reboulet, A.M., Lebreton, J.D., Gimenez, O., Pradel, R., 2005. U-Care 2.2 User's Manual. CEFE, Montpellier, France. <<ftp://ftp.cefe.cnrs.fr/biom/Soft-CR/>>.
- Cooch, E., White, G., 2006. Program MARK: A Gentle Introduction (<[http://www.phidot.org/software/mark/docs/book/mark\\_book.zip](http://www.phidot.org/software/mark/docs/book/mark_book.zip)>).
- Dwyer, P.D., 1966. The population pattern of *Miniopterus schreibersii* (Chiroptera) in North East New South Wales. *Australian Journal of Zoology* 14, 1073–1137.
- Entwistle, A.C., Racey, P.A., Speakman, J.R., 2000. Social and population structure of a gleaning bat, *Plecotus auritus*. *Journal of Zoology* 252, 11–17.
- Fleming, T.H., Eby, P., 2003. Ecology of bat migration. In: Kunz, T.H., Fenton, M.B. (Eds.), *Bat Ecology*. The University of Chicago Press, Chicago, pp. 156–208.
- Furman, A., Ozgul, A., 2004. The distribution of cave-dwelling bats and conservation status of underground habitats in Northwestern Turkey. *Biological Conservation* 120, 243–248.
- Gerell, R., Lundberg, K., 1990. Sexual differences in survival rates of adult pipistrelle bats (*Pipistrellus pipistrellus*) in south Sweden. *Oecologia* 83 (3), 401–404.
- Greenwood, P.J., 1980. Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour* 28, 1140–1162.
- Hamilton, I.M., Barclay, R.M.R., 1994. Patterns of daily torpor and day-roost selection by male and female big brown bats (*Eptesicus fuscus*). *Canadian Journal of Zoology* 72 (4), 744–749.
- Hargrove, J.W., Borland, C.H., 1994. Pooled population parameter estimates from mark-recapture data. *Biometrics* 50 (4), 1129–1141.
- Hoyle, S.D., Pople, A.R., Toop, G.J., 2001. Mark-recapture may reveal more about ecology than about population trends: demography of a threatened ghost bat (*Macroderma gigas*) population. *Australian Ecology* 26 (1), 80–92.
- Humphrey, S.R., Cope, J.B., 1976. Population ecology of the little brown bat, *Myotis lucifugus*, in Indiana and North-Central Kentucky. *American Society of Mammalogy Special Publication No. 4*. Allen Press, Lawrence, Kansas.
- Hutterer, R., Ivanova, T., Meyer-Cords, C., Rodrigues, L., 2005. Bat Migrations in Europe. A Review of Banding Data and Literature. Federal Agency for Nature Conservation, Bonn.
- IUCN 2007. 2007 IUCN Red List of Threatened Species. <<http://www.iucnredlist.org/>> (accessed 08.07.08.).
- Kerth, G., Ebert, C., Schmidtke, C., 2006. Group decision making in fission-fusion societies: evidence from two-field experiments in Bechstein's bats. *Proceedings of the Royal Society B – Biological Sciences* 273, 2785–2790.
- Kunz, T.H., 1982. Roosting ecology of bats. In: Kunz, T.H. (Ed.), *Ecology of Bats*. Plenum Press, New York, pp. 1–55.
- Kunz, T.H., Lumsden, L.F., 2003. Ecology of cavity and foliage roosting bats. In: Kunz, T.H., Fenton, M.B. (Eds.), *Bat Ecology*. The University of Chicago Press, Chicago, pp. 3–89.
- Kurta, A., Kennedy, J. (Eds.), 2002. *The Indiana Bat: Biology and Management of an Endangered Species*. Bat Conservation International, Austin, Texas.
- Lebreton, J., Burnham, K.P., Clobert, J., Anderson, D.R., 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62 (1), 67–118.
- Lettink, M., Armstrong, D.P., 2003. An introduction to using mark-recapture analysis for monitoring threatened species. *Department of Conservation Technical Series* 28A, 5–32 (<<http://www.doc.govt.nz/upload/documents/science-and-technical/docts28.pdf>>).
- Lewis, S.E., 1995. Roost fidelity of bats – a review. *Journal of Mammalogy* 76 (2), 481–496.
- McCracken, G.F., Bradbury, J.W., 1981. Social organization and kinship in the polygynous bat *Phyllostomus hastatus*. *Behavioral Ecology and Sociobiology* 8 (1), 11–34.
- Mitchell-Jones, A.J., Amori, G., Bogdanowicz, W., Krystufek, B., Reijnders, P.J.H., Spitzenberger, F., Stubbe, M., Thissen, J.M.B., Vohralik, V., Jimá, J., 1999. *The Atlas of European Mammals*. Academic Press, London.
- Morris, W.F., Doak, D.F., 2002. *Quantitative Conservation Biology: Theory and Practice of Population Viability Analysis*. Sinauer Associates, Sunderland.
- Némoz, M., Brisorgueil, A., 2008. Connaissance et conservation des gîtes et habitats de chasse de 3 chiroptères cavernicoles: Rhinolophus euryale, Murin de Capaccini, Minioptère de Schreibers. SFEPM, Paris.
- Niu, H., Wang, N., Zhao, L., Liu, J., 2007. Distribution and underground habitats of cave-dwelling bats in China. *Animal Conservation* 10, 470–477.
- Papadatou, E., 2006. Ecology and conservation of the long-fingered bat *Myotis capaccinii* in the National Park of Dadia-Lefkimi-Soufli, Greece. Ph.D. Dissertation, University of Leeds.
- Papadatou, E., Butlin, R.K., Altringham, J.D., 2008. Seasonal roosting habits and population structure of the long-fingered bat *Myotis capaccinii* in Greece. *Journal of Mammalogy* 89, 503–512.
- Paragamian, K., Nikoloudakis, E., Papadatou, E., Sfakianaki, E., 2004. Biological – Environmental Study of Maronia Cave: Analysis of Current Status – Proposals. Greek Institute of Speleological Research.
- Park, K.J., Masters, E., Altringham, J.D., 1998. Social structure of three sympatric bat species (Vespertilionidae). *Journal of Zoology (London)* 244, 379–389.
- Petit, E., Mayer, F., 1999. Male dispersal in the noctule bat (*Nyctalus noctula*): where are the limits? *Proceedings of the Royal Society B – Biological Sciences* 266 (1430), 1717–1722.
- Pollock, K.H., Nichols, J.D., Brownie, C., Hines, J.E., 1990. Statistical inference for capture-recapture experiments. *Wildlife Monographs* 107, 1–97.
- Popa-Lisseanu, A.G., Bontadina, F., Mora, O., Ibanez, C., 2007. Highly structured fission-fusion societies in an aerial-hawking, carnivorous bat. *Animal Behaviour*. doi:10.1016/j.anbehav.2007.05.011.
- Pradel, R., 1993. Flexibility in survival analysis from recapture data: handling trap dependence. In: Lebreton, J.D., North, P.M. (Eds.), *Marked Individuals in the Study of Bird Population*. Birkhauser Verlag, Basel, Switzerland, pp. 29–37.
- Pradel, R., Hines, J.E., Lebreton, J.D., Nichols, J.D., 1997. Capture-recapture survival models taking account of transients. *Biometrics* 53 (1), 60–72.
- Pradel, R., Gimenez, O., Lebreton, J.D., 2005. Principles and interest of GOF tests for multistate capture-recapture models. *Animal Biodiversity and Conservation* 28 (2), 189–204.

- Prévoteau-Julliard, A.C., Lebreton, J.D., Pradel, R., 1998. Re-evaluation of adult survival of black-headed gulls (*Larus ridibundus*) in presence of recapture heterogeneity. The Auk 115 (1), 85–95.
- Pryde, M.A., O'Donnell, C.F.J., Barker, R.J., 2005. Factors influencing survival and long-term population viability of New Zealand long-tailed bats (*Chalinolobus tuberculatus*): implications for conservation. Biological Conservation 126 (2), 175–185.
- Pryde, M.A., Lettink, M., O'Donnell, C.F.J., 2006. Survivorship in two populations of long-tailed bats (*Chalinolobus tuberculatus*) in New Zealand. New Zealand Journal of Zoology 33 (2), 85–95.
- Ransome, R.D., 1990. The natural history of hibernating bats. Christopher Helm, London.
- Rivers, N.M., Butlin, R.K., Altringham, J.D., 2006. Autumn swarming behaviour of Natterer's bats in the UK: population size, catchment area and dispersal. Biological Conservation 127 (2), 215–226.
- Sendor, T., Simon, M., 2003. Population dynamics of the pipistrelle bat: effects of sex, age and winter weather on seasonal survival. Journal of Animal Ecology 72 (2), 308–320.
- Senior, P., Butlin, R.K., Altringham, J.D., 2005. Sex and segregation in temperate bats. Proceedings of the Royal Society B – Biological Sciences 272 (1580), 2467–2473.
- Solick, D.I., Barclay, R.M.R., 2006. Thermoregulation and roosting behaviour of reproductive and non-reproductive female western long-eared bats (*Myotis evotis*) in the Rocky mountains of Alberta. Canadian Journal of Zoology 84 (4), 589–599.
- Spitzenberger, F., von Helversen, O., 2001. *M. capaccinii* (Bonaparte, 1837) – Langfubfledermaus. In: Krapp, F. (Ed.), Handbuch der Säugetiere Europas, Fledertier I. Aula Verlag, Wiebelsheim.
- Strelkov, P.P., 1969. Migratory and stationary bats (Chiroptera) of the European part of the Soviet Union. Acta Zoologica Cracoviensis 14 (16), 393–440.
- Trajano, E., 1996. Movements of cave bats in southeastern Brazil, with emphasis on the population ecology of the common vampire bat, *Desmodus rotundus* (Chiroptera). Biotropica 28 (1), 121–129.
- Tuttle, M.D., 1976. Population ecology of the gray bat (*Myotis griseescens*): philopatry, timing and patterns of movement, weight loss during migration, and seasonal adaptive strategies. Occasional Papers of the Museum of Natural History, the University of Kansas 54, 1–38.
- Tuttle, M.D., Stevenson, D., 1982. Growth and survival of bats. In: Kunz, T.H. (Ed.), Ecology of Bats. Plenum Press, New York, pp. 105–150.
- Vonhof, M.J., Fenton, M.B., 2004. Roost availability and population size of *Thyroptera tricolor*, a leaf-roosting bat, in north-eastern Costa Rica. Journal of Tropical Ecology 20, 291–305.
- White, G.C., Burnham, K.P., 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46, 120–139.