Variation of adult survival drives population dynamics in a migrating forest bat

Wigbert Schorcht[1]†, Fabio Bontadina[2,3]† and Michael Schaub[2,4]*†

[1]*NACHTaktiv – Bat Research – Kleffelgasse 6, D-98639 Walldorf/Werra, Germany;* [2]*Institute of Ecology and Evolution, Conservation Biology, University of Bern, Baltzerstrasse 6, CH-3012 Bern, Switzerland;* [3]*SWILD, Urban Ecology & Wildlife Research, Wuhrstrasse 12, CH-8003 Zürich, Switzerland; and* [4]*Swiss Ornithological Institute, CH-6204 Sempach, Switzerland*

Summary

1. Variation of survival across time, between sex and ages strongly affect the population dynamics of long-lived species. Bats are extremely long-lived, but the variation of their survival probabilities is poorly studied with reliable methods.

2. We studied annual local survival probabilities of the migratory Leisler's bats *Nyctalus leisleri* based on capture–recapture data from 1119 individuals sampled in bat boxes over 20 years in eastern Germany. We assessed variation in survival between sex and age classes, estimated the temporal variance of survival and tested whether survival was affected by weather during hibernation or pregnancy.

3. Among females, our analyses revealed two groups of individuals present with different roosting occupancy, survival and/or dispersal. Local survival of locally born females increased with age [first year: 0·45 ± 0·04 (SE); later: 0·76 ± 0·04] and the high recapture probabilities indicate regular presence in the roosts. Recapture probabilities and local survival of foreign adult females were significantly lower, indicating less frequent presence in the roosts and stronger dispersal from the study area.

4. In adult males, locally born and foreign individuals were nearly identical regarding survival and recapture, indicating a more homogenous group. Local survival was very low in the first year (0·04 ± 0·08), most likely caused by strong natal dispersal. It further increased with age (second year: 0·55 ± 0·20, later: 0·69 ± 0·07).

5. Survival probabilities of all females varied significantly and in parallel across time, suggesting that a common environmental factor was operating which affected all individuals similarly. Spring temperature and winter North Atlantic Oscillation explained maximally 9% each of the variation in first year and adult female survival. In contrast to our expectations, the temporal variance of first-year survival was lower than that of adult survival.

6. We found evidence of a complicated social population structure of female Leisler's bats. Our analyses suggest that their population dynamics are driven to a large amount by variation of survival, in particular by adult survival. The reason for the major temporal variations remains to be identified.

Key-words: capture–recapture, Chiroptera, Cormack–Jolly–Seber model, life-history strategy, *Nyctalus leisleri*, temporal variance

Introduction

Much of the diversity of life histories of mammals can be explained by the fast–slow continuum (Stearns 1983; Gaillard *et al*. 1989; Promislow & Harvey 1990), although the existence of one single fast–slow continuum has recently been challenged (Bielby *et al*. 2007). Species with late ages at first reproduction tend to have high probabilities of juvenile and adult survival and low reproductive output (slow species), whereas species with early ages at first reproduction tend to have low survival probabilities and high reproductive output

*Correspondence author. E-mail: michael.schaub@iee.unibe.ch
†All authors contributed equally to the study.

(fast species). The sensitivity of the population growth rate to changes in the different demographic parameters differs among species according to their position along the fast–slow continuum. While population growth of slow species is particularly sensitive to changes in adult survival, population growth of fast species is more sensitive to changes in recruitment (Gaillard, Festa-Bianchet & Yoccoz 1998; Saether & Bakke 2000; Fujiwara & Caswell 2001; Schmidt, Feldmann & Schaub 2005). Adult survival is therefore expected to be an important determinant for the dynamics of long-lived species. Consequently, the understanding of population dynamics of long-lived species requires good knowledge about adult survival as well as its temporal variation.

Bats (*Microchiroptera*) have the typical feature of slow species within the fast–slow continuum of life histories (Gaisler 1989; Bielby *et al.* 2007). They are very long-lived, some individuals reach an age of more than 30 years (Tuttle & Stevenson 1982; Jones & MacLarnon 2001; Brunet-Rossinni & Austad 2004), and they have an extremely low reproductive output (Barclay & Harder 2003). As a consequence, adult survival potentially strongly affects their population dynamics. Despite its potential importance for population dynamics, relatively little is known about survival probabilities of bats (O'Shea, Ellison & Stanley 2004). For only a small number of the more than 1100 bat species do estimates of survival probabilities exist that were obtained with reliable methods (Keen & Hitchcock 1980; Hitchcock, Keen & Kurta 1984; Boyd & Stebbings 1989; Gerell & Lundberg 1990; Hoyle, Pople & Toop 2001; Sendor & Simon 2003; O'Shea *et al.* 2004; Pryde, O'Donnell & Barker 2005; Frick, Rainey & Pierson 2007; Schaub *et al.* 2007; Papadatou *et al.* 2009). Most of these studies have shown that survival from birth until 1 year of age is lower than in subsequent years (O'Shea *et al.* 2004; Papadatou *et al.* 2009). More complicated age structures have not been supported, but they were studied by Sendor & Simon (2003) only. With respect to sex, there is some evidence that females have higher survival (Boyd & Stebbings 1989; Gerell & Lundberg 1990; Hoyle *et al.* 2001; Pryde *et al.* 2005), whereas others found no difference (Hitchcock *et al.* 1984; Sendor & Simon 2003). Survival was often variable across time (Hoyle *et al.* 2001; Sendor & Simon 2003; Pryde *et al.* 2005; Frick *et al.* 2007), suggesting that environmental factors play an important role. This variation could be partially explained by temperatures during winter in some studies (Gerell & Lundberg 1990; Hoyle *et al.* 2001; Pryde *et al.* 2005), but not always (Sendor & Simon 2003).

Survival can be studied reliably from capture–recapture data using the Cormack–Jolly–Seber model which allows to separately estimate survival and recapture probabilities (Lebreton *et al.* 1992). A challenge is the estimation of the temporal variance from such data. The year-specific estimates are subject to sampling variation, because the estimates stem from a finite sample from the population. The calculation of the variance of the year-specific estimates is therefore not a valid estimate of the temporal variance (Gould & Nichols 1998). Rather, the sampling variance has to be subtracted from the total variance to get the desired temporal

(or process) variance. Based on the method of moments, Burnham & White (2002) developed an approach which performs well if data from more than about 10 years are available.

Using Cormack–Jolly–Seber models, we analysed capture–recapture data spanning 20 years of 1119 individuals of the migratory Leisler's bat *Nyctalus leisleri* Kuhl from Germany to study their survival probabilities. Knowledge about survival in this endangered species (Hutson, Mickleburgh & Racey 2001) are limited to longevity data records (eastern Europe: 9 years, Panjutin 1970; central Europe: 12 years, this study). However, longevity provides little information about survival (Krementz, Sauer & Nichols 1989). Our basic aims were to estimate how strongly survival probabilities differ between sexes and age classes and to study the temporal variance of survival probabilities. According to previous studies we expect male survival to be lower than female survival, and survival not to change after bats reached maturity at age 1 year. We expect the temporal variability of adult survival to be smaller than that of juvenile survival. The sensitivity of the population growth rate in long-lived species to changes in adult survival is higher than to changes in juvenile survival. Adult survival should therefore be under stronger selection against temporal variability than juvenile survival (canalization; Gaillard & Yoccoz 2003). We estimated how much of the temporal variation of survival is explained by the variation of spring and winter weather, which are likely to be sensitive periods. We discuss our findings in the light of the potential population dynamics of the species.

Materials and methods

STUDY SPECIES

The Leisler's bat is a medium-sized bat with a body mass of 13–20 g. The main foraging and breeding habitat in Continental Europe are all types of woodland (Schorcht 2002). Leisler's bat has the characteristic phenology of a migratory species in temperate regions; individuals arrive until May in their summer areas where they assemble in roosts, such as tree cavities or bat boxes and form a summer colony of mostly breeding females for reproduction. A colony utilizes a large cluster of neighbouring roosts and individuals change often daily and independently from each other among roosts (Schorcht 2005). As a consequence, the composition of individuals within roosts changes frequently, similarly to the colonial system called fission–fusion society detected in other tree-dwelling bats (Kerth & König 1999; Popa *et al.* 2008). Only few adult males are present in a summer colony, and they do not tolerate each other in the same roost. Mature females do not rear offspring every year, yet if they do, about half produces twins (Schorcht 1998), which is relatively uncommon in bats (Hayssen, van Tienhoven & van Tienhoven 1993). High reproductive output in bats is characteristic for some migratory species and regarded as an adaptation to the presumed higher mortality in migratory compared with resident bat species. After reproduction, the summer colonies break up in August and the bats migrate over 1000–1500 km towards south-western Europe (Steffens, Zöphel & Brockmann 2004) where they spend the non-reproductive period during which mating and hibernation takes place. In the harem mating system of Leisler's bats, males monopolize tree cavities in semi-open wood-

lands, perform song-flights in the vicinity and try to attract females to their roosts (von Helversen & von Helversen 1994).

STUDY SITE AND DATA SAMPLING

We studied a population of Leisler's bat in a forest near Wasungen, situated in southern Thuringia (Germany, 10°20′E, 50°40′N, 350–450 m. a.s.l.). The forest is dominated by coniferous trees (mainly *Pinus sylvestris* L. and *Picea abies* L.), while the natural vegetation would be beeches (*Fagus sylvatica* L.). Because all of the trees are cultivated and relatively young, these extensive forests contain nearly no natural cavities suitable for this bat (Beck & Schorcht 2005). In 1985, we installed different types of 70 flat wooden bat boxes (Schorcht 1994) covering an area of about 200 ha. The spatial extension of the area covered with bat boxes as well as their number remained fairly constant since then. We checked all bat boxes at least twice during each reproduction period usually in the afternoon and all bats found in the boxes were handled. We recorded sex and age (two classes: juveniles up to 1 year old and adults that are ≥1 year old) and marked all individuals with one forearm band (Dresden bat-banding centre, ring type B, Steffens *et al.* 2004). All bats were released shortly afterwards in their roost.

Because we marked all young individuals born in our bat boxes, all adults that were unmarked at first capture were not born in our bat boxes. Furthermore, because only few natural cavities were available in the studied artificial coniferous forest, the majority of them were likely to have been born even outside our study area. Therefore, we call them 'foreign' thereafter. These individuals were at least 1 year old, but the exact age remained unknown. In contrast, the age of the individuals born in our study area was known and we call these individuals 'local' thereafter.

From the capture–recapture data obtained from 1989 to 2008, we constructed individual capture histories. We only considered individuals that were captured between the 1 July and the 31 August in each year to ensure a homogenous sample. For this analysis, we considered the capture histories of 472 local females (from which 181 individuals were recaptured at least once), of 211 foreign females (55 recaptured), of 417 local males (10 recaptured) and of 19 foreign males (11 recaptured, see also Supporting Information, Table S1).

CAPTURE–RECAPTURE ANALYSES

We analysed the data with the Cormack–Jolly–Seber model which allows separate estimates of local survival (ϕ) and recapture (p) probabilities (Lebreton *et al.* 1992). Local survival probability ϕ_i is the probability that a marked individual in the population in year i is still alive and in the population in year $i + 1$, thus true survival and permanent emigration are confounded. The recapture probability p_i is defined as the probability that a marked individual that is alive and in the population in year i is captured at time i.

These parameters may vary over time and may differ between sex and age classes. The estimation of these parameters requires several assumptions to be met (Lebreton *et al.* 1992), which can be tested with a goodness-of-fit test. Once a fitting general model has been found, lower-parameterized models that are nested within the general model are fitted. Each model represents a specific hypothesis about the variation of the parameters of interest. Using the Akaike's information criterion adjusted for small sample sizes (AIC_c), we ranked these models according to their support by the data (Burnham & Anderson 2002). We report AIC_c-differences [$\Delta AIC_{ci} = AIC_{ci} - min(AIC_c)$] to compare different models and calculated Akaike's weights [$w_i = \exp(-0.5 \times \Delta AIC_{ci})/\Sigma\exp(-0.5 \times \Delta AIC_c)$] to assess

the likelihood that the current model is the best given the data and the set of candidate models. Using these weights, we calculated model averaged parameter estimates and unconditional confidence intervals under consideration of all fitted models. Multi-model inference is superior to best-fitting model inference, because the uncertainty of model selection is accounted for explicitly (Burnham & Anderson 2002).

We performed the goodness-of-fit of a general model that accounts for sex and time-specific variation in local survival and recapture probabilities of foreign individuals and for sex-, time- and age- (two age classes) specific variation in local survival and for sex- and time-specific variation in recapture probabilities for local individuals. We used program U-CARE (Choquet *et al.* 2001), and found no indication of lack of fit ($\chi^2 = 89.21$, d.f. $= 103$, $P = 0.83$).

CANDIDATE SET OF MODELS

We considered several hypotheses about variation in recapture, as well as in female and male local survival probabilities, each represented in a different model segment. A complete model fitted to the data is a combination of these three different segments. Considering all possible combinations would have resulted in an undesired large number of candidate models. To reduce this number, we first modelled recapture probability while keeping the survival parts of the model at a general structure. We then continued modelling by keeping the recapture part of the model at the best structure, and then fitted all combinations of male and female survival models (Lebreton *et al.* 1992).

When a bat box was checked, we were usually able to catch all individuals that were in the boxes at that time. Thus, a significant deviation of the estimated recapture probability from 1 must be due to temporal roost changes either to roosts outside the study area or to natural, unknown hiding places within the study area. Owing to the fission–fusion social system, we expected that some individuals will be temporally (i.e. during the same season) absent and thus not catchable. This temporal absence was random, as evidenced by the non-significant goodness-of-fit test and caused therefore no bias in the survival estimates (Schaub *et al.* 2004). In a fission–fusion society, it is unlikely that all individuals show the same behaviour regarding temporal absence (Popa *et al.* 2008). We, therefore, expected differential behaviour among groups of individuals (sex and place of birth), indicating a more complicated structure in the fission–fusion social system. To assess this hypothesis, we formulated models with sex- and/or group-specific recapture probabilities. Moreover, bats of age 1 year may have a lower recapture probability than older bats, because some of them may not yet be mature or have not yet been recruited into the breeding population. Therefore, we also considered models with age-dependent recapture probabilities for individuals of known age. Finally, we supposed that recapture probabilities could vary between years, that they may be a linear function of the number of bat box checks conducted during the sampling period of a year, or that they may be constant over time. These main factors were used separately or in combination to define 13 different recapture models (Supporting Information, Table S2).

We supposed that survival could differ between age classes and that it could be different between years. First-year survival has been found to be consistently lower than adult survival in bats (Sendor & Simon 2003; O'Shea *et al.* 2004; Schaub *et al.* 2007; Papadatou *et al.* 2009), thus we always considered at least two age classes for survival modelling. In some mammals, survival changes with increasing age (Loison *et al.* 1999). This may be possible also in the Leisler's bat, and we therefore considered models in which the survival probability

in the second year of life was different from survival in later years (three age classes). Because the exact age of foreign individuals was unknown, a separate survival probability had to be estimated for them. Only in models in which survival of local individuals does not differ after they are 1 year old could we constrain adult survival probabilities of both groups to be identical.

We had different hypotheses concerning the temporal variation of survival probabilities. Firstly, it is possible that survival of all age classes was differentially variable over time. This may be expected if bats of different age classes are differentially sensitive to environmental variation (e.g. severity of winter). Secondly, survival of all age classes could vary in parallel over time. This can occur if bats of all age classes were similarly sensitive to environmental variation. It has often been reported that survival probabilities of juvenile animals are more sensitive to environmental variation and that they, therefore, are more variable over time (Gaillard & Yoccoz 2003; Schaub, Kania & Köppen 2005; Altwegg, Schaub & Roulin 2007). Thus, we thirdly considered models in which only the survival probabilities of juveniles varied over time while those of all adults remained constant. In long-lived animals, temporal variation in survival is often small (Gaillard *et al.* 1998). Thus, we fourthly formulated models that did not impose temporal variation in any parameter.

Because of the small sample size of recaptured males, it was very unlikely to detect significant temporal variation in their survival, even if it was present. Hence, we did not consider models in which adult male survival was variable over time. We also did not consider models in which survival probabilities of the two sexes were identical. A sex effect was enforced because there is a strong sex difference in natal dispersal in bats (Kerth, Mayer & Petit 2002). Females are very philopatric while males often disperse to other areas and thus juvenile local survival almost certainly differs between sexes. Moreover, because sample size of adult males was lower than that of adult females, male survival estimates would have been dominated by the female survival estimates, if they had been constrained to be the same. Hence, tests about sex differences would not have been very conclusive. A summary of all model segments considered for survival modelling is presented in Table S3 (Supporting Information).

We used random effects models to estimate the temporal variance (σ_t^2) of survival probabilities of females and to estimate how much the variation of weather has contributed to the temporal variance. Random effects models partition the total variance into its two components, process and sampling variance (Burnham & White 2002). Because the variance of a probability is determined by its mean, it is difficult to compare the temporal variances of survival probabilities of different age classes. We therefore calculated the proportion of the maximal possible variance as $P_{max} = \sigma_t^2/\text{mean}/(1 - \text{mean})$ (see Gaillard & Yoccoz 2003). We hypothesized that survival of Leisler's bats is negatively affected by spring temperatures. Bats are exhausted after hibernation and spring migration (Fleming & Eby 2003), gestation is initiated and consequently low temperatures in spring with low availability of flying insects may be detrimental (Ransome & McOwat 1994).

We used the mean of the daily temperatures during the period of pregnancy between mid-April and mid-June as a correlate of the environmental conditions in spring (data from the meteorological station Meiningen, 10 km from the study site; http://www.dwd.de). Furthermore, we hypothesized that the strength of winter could negatively impact survival. As it is unknown where exactly the majority of individuals from our study population hibernated, we used a large scale variable, the winter North Atlantic Oscillation (NAO, Hurrell 1995, obtained from http://www.cgd.ucar.edu/cas/jhurrell/indices.html, accessed: 1 October 2008) as a correlate of the strength of winter. Large values of the NAO indicate warm and wet winters, low NAO values indicate cold and dry winters. We calculated the proportion of the temporal variance in survival explained by the variation of the two weather variables. To do so, we used the best model without constraints on the survival probabilities.

We estimated mean life span (MLS) of females from the average age-dependent survival rates according to (Brownie *et al.* 1985) as,

$$MLS = (1 - \phi_{juv})\frac{-1}{\ln(\phi_{juv})} + \phi_{juv}\frac{-1}{\ln(\phi_{ad})}. \tag{1}$$

The variance was calculated using the delta method (Seber 1982). Modelling of all recapture and survival probabilities were conducted with program MARK (White & Burnham 1999).

Results

Modelling recapture probabilities were remarkably unambiguous (Table 1), with the best model including a sex and a group effect (i.e. local vs. foreign individuals), as well as an additional age effect for the local males. The second best model that also considered an age effect for the local females had almost three times less support (w_i ratio: 0·73/0·27). Model averaged recapture probabilities of local females and of all males older than 1 year were high, whereas recapture probabilities of foreign females and of 1-year-old local males were clearly lower (Table 3).

The common feature of the six top ranked survival models that combine an Akaike's weight of 0·99 was that local survival probabilities of females of all age-classes and origin varied in parallel over time, and that first-year local survival of males was constant (Table 2). The only difference between

Table 1. Summary of model selection results for recapture rates of Leisler's bat in Thuringia, Germany, 1989–2008, with models ranked by ascending ΔAIC_c

Model	Deviance	K	ΔAIC_c	w_i
pFl:., Ff:., Ml: a2, Mf:.	721·19	100	0·00	0·73
pFl: a2, Ff:., Ml: a2, Mf:.	720·92	101	1·99	0·27
$p$sex × group	734·25	99	10·80	0·00
$p$sex × group + effort	733·02	100	11·82	0·00
pFl: a2, Ff:., Ml:., Mf:.	733·98	100	12·79	0·00
$p$sex + group	741·73	98	16·01	0·00
$p$sex × group + year	711·93	117	29·70	0·00
$p$group	759·72	97	31·74	0·00
$p$sex	763·35	97	35·36	0·00
p.	773·57	96	43·34	0·00
$p$effort	772·58	97	44·60	0·00
$p$year	747·05	114	57·89	0·00
$p$sex × group × year	664·62	167	102·18	0·00
General model	663·31	172	118·29	0·00

In all models, the survival model was the same $\{\phi$Fl: a3 × year, Ff: year, Ml: j: year, ad: a2, Mf: .$\}$, and this is not stated in the model notation. For each model we report the deviance, the number of estimated parameters (K), the difference of the AIC_c values of the current and the best model (ΔAIC_c), and the Akaike weight (w_i). We also show the general model $\{\phi$l: a2 × year × sex, f: year × sex, pl: sex × year, f: sex × year$\}$ that was used for the goodness-of-fit test. See Table S2 (Supporting Information) for model notations.

Table 2. Summary of model selection results for local survival rates (ϕ) of Leisler's bat in Thuringia, Germany, 1989–2008, with models ranked by ascending ΔAIC_c

Model	Deviance	K	ΔAIC_c	w_i
$\phi_{Fl:\ a2\ +\ year\ +\ Ff:\ year,\ M:\ a2}$	817·81	27	0·00	0·35
$\phi_{Fl:\ a2\ +\ year\ +\ Ff:\ year,\ Ml:\ a3,\ Mf:\ .}$	814·45	29	0·78	0·24
$\phi_{Fl:\ a3\ +\ year\ +\ Ff:\ year,\ M:\ a2}$	817·71	28	1·97	0·13
$\phi_{Fl:\ a2\ +\ year\ +\ Ff:\ year,\ Ml:\ a2,\ Mf:\ .}$	817·77	28	2·03	0·13
$\phi_{Fl:\ a3\ +\ year\ +\ Ff:\ year,\ Ml:\ a3,\ Mf:\ .}$	814·35	30	2·76	0·09
$\phi_{Fl:\ a3\ +\ year\ +\ Ff:\ year,\ Ml:\ a2,\ Mf:\ .}$	817·67	29	4·00	0·05
[a] $\phi_{Fl:\ a3\times year,\ Ff:\ year,\ M:\ a2}$	753·77	80	49·27	0·00
[b] $\phi_{Fl:\ a3\times year,\ Ff:\ year,\ Ml:\ j:\ year,\ ad:\ a2,\ Mf:\ .}$	721·19	100	61·46	0·00

In all models, the recapture model was the same (best model from Table 1: $p_{Fl:.,\ Ff:.,\ Ml:\ a2,\ Mf:.}$) and is not shown in the model notation. For each model we report the deviance, the number of estimated parameters (K), the difference of the AIC_c values of the current and the best model (ΔAIC_c), and the Akaike weight (w_i). Of the 50 fitted models we show models with $w_i \geq 0.005$, the model that was used to estimate the temporal variance[a] and the best model from Table 1[b]. See Table S3 (Supporting Information) for model notations.

Table 3. Mean and temporal variances of annual local survival and recapture probabilities of Leisler's bat in Thuringia, Germany, 1989–2008

Sex-/age group	Local survival probability			Recapture probability
	Mean (SE)	σ_t^2	P_{max}	Mean (SE)
1st year, local females	0·454 (0·037)	0·0114	0·046	–
2nd year, local females	0·728 (0·045)	0·0059	0·030	0·705 (0·023)
3rd[+] year, local females	0·756 (0·042)	0·0214	0·116	0·705 (0·023)
2nd[+] year, foreign females	0·548 (0·056)	0·0367	0·148	0·414 (0·050)
1st year, local males	0·042 (0·076)	–	–	–
2nd year, local males	0·554 (0·199)	–	–	0·429 (0·187)
3rd[+] year, local males	0·690 (0·072)	–	–	1·000 (0·000)
2nd[+] year, foreign males	0·672 (0·058)	–	–	0·914 (0·057)

All mean estimates given are model averaged estimates. σ_t^2 is the temporal variance of the corresponding local survival probabilities estimated with model $\{\phi_{Fl:\ a3\ \times\ year,\ Ff:\ year,\ M:\ a2}\}$, and P_{max} is reflecting the proportion of the variation relative to the maximally possible variation of 1. Notation of age classes: 1st year, from birth until 1 year old; 2nd year, from age 1 year to age 2 years; 2nd[+] year, from age 1 year onwards; 3rd[+] year, from age 2 years onwards. SE denotes standard error.

these models was whether or not they considered two or three-age classes.

Model averaged local survival probabilities of female Leisler's bats were highly variable across time (Fig. 1). Second year and adult local survival of local females was nearly identical while local survival during the first year was lower. Local survival of foreign females was similar to local survival of local females during their first year (Fig. 1, Table 3). First-year local survival of males was very low (Table 3). Adult local survival was similar for local and foreign individuals, while second-year survival of local males tended to be lower.

Using the model averaged survival estimates, the MLS of a local female was 2·26 years (95% confidence interval: 1·74–2·78 years), thus a new born Leisler's bat can be expected to reproduce at least twice, provided that it starts reproducing when 1 year old.

Temporal variance of local survival was highest for adult local females (Table 3). The ratio of the observed to the maximally possible temporal variance showed that adult survival was more variable than first- and second-year survival. The temporal variance of survival of foreign females was larger than that of the local females of similar age.

Spring temperatures explained 8·2% of the variation of juvenile local survival, but nothing of adult survival. In contrast to our expectations, juvenile local survival tended to decrease with increasing spring temperatures (logit scale: $\beta = -0.029$, SE: 0·022). Winter NAO explained 7·9% of the variation of adult survival and 9·1% of the variation of juvenile survival. Survival increased with increasing NAO (juveniles: $\beta = 0.021$, SE: 0·015, adults: $\beta = 0.025$, SE: 0·017).

Discussion

This study on Leisler's bats revealed that local survival was best described by an age structure with two classes and much lower probabilities at first year, that males had lower local survival probabilities compared to females and that foreign females were less frequently present at the nursery colonies within the study area during the reproducing period and also dispersed more often than local females. This suggests the existence of a complex population structure in females. Temporal variation in survival of females was large, higher for older age classes, and therefore likely to be of importance for the population dynamics of Leisler's bats. Variation of survival could only to a small amount be explained by spring temperature and winter NAO.

Our study confirms that Leisler's bat is a long-lived mammal with survival probability clearly higher than that of similar or slightly larger sized mammals like mice or dormice (Yoccoz & Ims 1999; Schaub & Vaterlaus-Schlegel 2001), but slightly lower than those of large ungulates or seals (Gaillard & Yoccoz 2003; Beauplet *et al.* 2006; Hadley, Rotella & Garrott 2007). Compared to other bat species, it appears that local survival of Leisler's bat was similar to the long-tailed bat *Chalinolobus tuberculatus* Forster (Pryde *et al.* 2005), a similar sized forest bat. Local survival was higher than in the smaller pipistrelle bat *Pipistrellus pipistrellus* Schreber (Gerell & Lundberg 1990), but lower than in the cave-dwelling yuma myotis *Myotis yumanensis* Allen (Frick *et al.* 2007), long-fingered bat *M. capacinii* Bonaparte (Papadatou *et al.* 2009) and greater horseshoe bat *Rhinolophus ferrumequinum* Schreber (Schaub *et al.* 2007). Survival of the brown long-eared bat *Plecotus auritus* L. (Boyd & Stebbings 1989) which is of
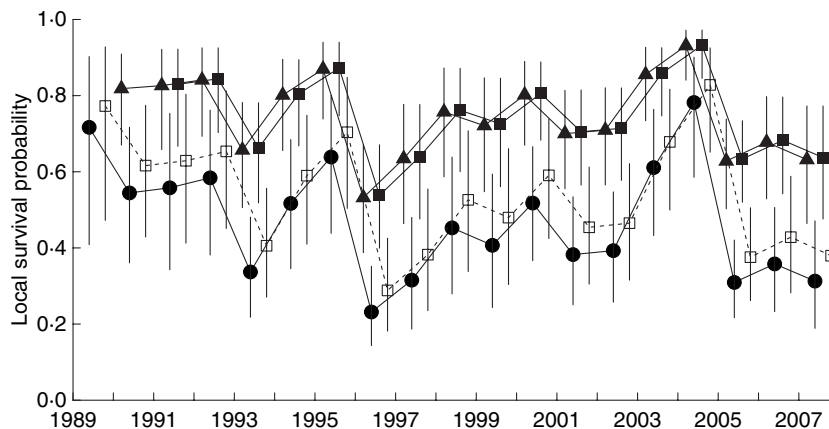
Fig. 1. Model averaged estimates of annual local survival probabilities of female Leisler's bats from 1989 to 2008. Closed symbols refer to local and open to foreign individuals. Closed dot: first-year survival, closed triangle: second-year survival, closed square: third- and later-year survival. The vertical lines show the unconditional 95% confidence intervals.

similar size and lives in the same habitat as the Leisler's bat, but is sedentary, was similar, suggesting that the migratory behaviour of Leisler's bat does not induce particularly high mortality. The higher reproductive output of the migratory Leisler's bat compared to sedentary bat species may therefore be an adaptation not to increased mortality, but rather to the large temporal variability of survival (see below), which has a negative impact on population growth (Tuljapurkar & Orzack 1980).

POPULATION STRUCTURE

The estimates of local survival probabilities obtained from capture–recapture data are the product of the probabilities of survival and permanent emigration (Burnham 1993). Thus, variation of local survival probability among groups of individuals or across time may be due to variation of survival, of permanent emigration or both. This needs to be considered in the interpretation of our findings.

The high local survival probability of adult local females suggests that it is close to true survival and that these females do not emigrate permanently from the study area. If we assume that adult females would have the same survival probabilities regardless of their origin, we can infer that foreign females observed in the study area often disperse permanently after some time. The recapture probabilities were lower than 1, although we could usually catch all individuals that were in the bat boxes at the time of the checks. Given that there were virtually no alternative, natural roosts in the coniferous plantation of our study area, this suggests that the bats were not always present in the bat boxes during the reproductive season either because they used temporally different roosts in the vicinity of the study area or because they were completely absent from the study area for one or several years. The former explanation is in accordance with the fission–fusion social system and we believe it is much more likely to be true that the latter. Recapture probabilities of foreign females were much lower than those of local females. Based on the same argument about capture efficiency, we conclude that foreign females were more often absent from the study area. The less frequent presence of these females is still in agreement with the fission–fusion

social system, but the members of the two groups of females use partially different roosts. Hence, the bat boxes in the study area have been used for roosting by a larger fraction of local than of foreign females. Clearly, more studies about the social system will be necessary to confirm or reject these hypotheses and to uncover more of the details.

Adult males appeared to be a more homogenous group than females. Local and foreign males had similar local survival probabilities which were lower than those of females. They had higher recapture probabilities than females, indicating that they changed roosts less often. In contrast, younger males had lower recapture probabilities than females of the same age, suggesting that a fraction of males that later recruited into the population was not yet in the bat boxes when 1 year old.

The local survival probabilities of juvenile females were relatively high, suggesting that most of the locally born females did not emigrate from the study area. By contrast, local survival probabilities of juvenile males were very low, and consequently a large fraction of juvenile males dispersed from the study area. Even in the second year local survival in males was lower, suggesting that dispersal does not only occur in the first year. Strong natal dispersal in males is a typical behaviour observed in many bat species (McCracken & Wilkinson 2000; Kerth *et al.* 2002). If it is assumed that true survival of juvenile males and females are identical, emigration probability of males is 0·91 (1−0·042/0·454). Overall only a small number of adult males were captured in our study area, indicating that many males settle outside the main area of the colony.

TEMPORAL VARIATION OF SURVIVAL

Local survival probabilities of females from all age classes and origin varied considerably, but in parallel across time (Fig. 1), indicating that these variations are caused by environmental factors to which all females were similarly sensitive. We found that their local survival was weekly negatively impacted by increasing spring temperatures. As this finding does not follow our expectations and the relationship was week, we regard it as a spurious result. In accordance with our expectations, we identified winter NAO to positively

impact female local survival. Both young and adult females survived better when winters were warm and wet, compared to when they were cold and dry. Hibernation in bats is not without interruption: during warmer phases in winter when insects are active bats can become active too and start foraging (Lausen & Barclay 2006). Therefore, more frequently foraging opportunities occur in warmer winters which in turn allow the bats occasionally to replenish their body reserves. However, as the NAO explained at most 9% of the temporal variance of survival, there must be other important mortality factors. In other bat studies, survival was enhanced when the temperatures during wintering were reduced (Pryde *et al.* 2005), while Sendor & Simon (2003) and Hoyle *et al.* (2001) did not find a relationship between winter weather and survival. Leisler's bat are migratory, thus environmental conditions encountered along the migratory flyways could also have a significant impact on annual survival, in a similar way as in birds (Sillett & Holmes 2002). As the migratory flyway and wintering locations are only poorly known, it is not yet possible to test this hypothesis.

The temporal variance of survival was larger in adult than in juvenile females. This result was not expected, because adult survival should be under stronger selection against temporal variability than juvenile survival in long-lived species (Gaillard & Yoccoz 2003). Compared to large ungulates (average across several species), which have similarly high adult survival probabilities as Leisler's bats, the amount of possible temporal variance of adult survival of Leisler's bats was higher (0·116 vs. 0·035, Gaillard & Yoccoz 2003), and that of juvenile survival lower (0·046 vs. 0·099, Gaillard & Yoccoz 2003). Given the high sensitivity of population growth rate to changes in adult survival, this suggests that population dynamics of Leisler's bats is strongly driven by variation of adult survival. If this is true in bat populations generally, it would mean that bat population dynamics works differently from population dynamics of large herbivores, which is mainly driven by the variable recruitment (Gaillard *et al.* 1998). It remains to be seen whether the suggestion that variation of adult survival is relatively more important for population dynamics in bats compared to large ungulates is a general trend and how this life history tactic has evolved. As this is, to our knowledge, the first study that estimated temporal variance of fitness components in bats, it is too early to make general statements. We suggest conducting comparative analyses of many bat species along the gradient of fast–slow continuum (Gaisler 1989; Saether & Bakke 2000).

DIFFERENCES BETWEEN AGE AND SEX CLASSES

While survival during the first year of life was lower than later, there was only a marginal difference of survival between the age classes once the bats were at least 1 year old. This difference was more pronounced in males, but the uncertainty was considerable. In the only other study on age structures of bat survival with reliable methods, there was no indication of complicated age structures (Sendor & Simon 2003). In long-lived species, age-specific survival typically increases over few years and declines thereafter (Loison *et al.* 1999), and we would expect the same for bats. Detecting fine age structures is difficult because it requires very large data sets including many old individuals. We think that our data set was reasonably large to detect strong patterns. Thus, if survival was nevertheless more structured according to age, differences must have been relatively small.

Because of very unequal sample sizes, we did not explicitly test whether survival differs between sexes. Regarding the estimates of each sex, it appears that juvenile males have much lower local survival probabilities than juvenile females, most likely caused by differential dispersal. In addition, local survival probabilities of adult males were lower than those of locally born adult females, in agreement with results from other studies (Boyd & Stebbings 1989; Gerell & Lundberg 1990; Hoyle *et al.* 2001; Pryde *et al.* 2005; Papadatou *et al.* 2009). This might be caused by sex-specific life histories: in the harem mating system of Leisler's bats (von Helversen & von Helversen 1994) few males occupy central resources for reproduction and therewith attract a majority of females. Therefore, the competition among males for access to females is likely to be very high, which could promote risky behaviour. An alternative explanation would again be dispersal from the studied roosts. Older individuals may no longer be able to compete for roosts, and may be forced to leave.

Conclusions

Our findings have implications for conservation of bat populations. The dynamics of Leisler's bat populations are likely to be driven by variation of adult survival. Little is known about mortality factors, yet for the understanding of proximate causes of Leisler's bat population changes, it is of importance to identify them. This need is even more accentuated as variation of survival of different age classes are positively correlated, suggesting common mortality causes. Positive correlation among vital rates reduces the persistence probability of populations (Palmqvist & Lundberg 1998). Recently, there is a growing interest to assess the impact of environmental modifications in the modern landscape. It was recognized that infrastructures such as wind turbines or roads may affect bats populations (e.g. Kunz *et al.* 2007). We concur that these risk assessments are of great importance, because such environmental changes are likely to affect mainly survival, and thus may potentially have a strong impact on bat population dynamics.

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Supporting Information

Additional Supporting information may be found in the online version of this article:

Table S1. Total number of marked and recaptured individual Leisler's bats between 1989 and 2008 for each sex and age group.

Table S2. Notation and hypotheses of the models for recapture probability.

Table S3. Notation and hypotheses of the models for survival probability.

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