Local population dynamics and the impact of scale and isolation: a study on different little owl populations

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The understanding of how variation of demographic rates translates into variation of population growth is a central aim in population ecology. Besides stochastic and deterministic factors, the spatial extent and the isolation of a local population may have an impact on the contribution of the different demographic components. Using long-term demographic data we performed retrospective population analyses of four little owl (*Athene noctua*) populations with differential spatial extent and degree of isolation to assess the contribution of demographic rates to the variation of the growth rate (λ) of each local population and to the difference of λ among populations. In all populations variation of fecundity contributed least to variation of λ, and variation of adult survival contributed most to variation of λ in three of four populations. Between population comparisons revealed that differences mainly stem from differences of immigration and juvenile local survival. The relative importance of immigration to λ tended to decrease with increasing spatial extent and isolation of the local populations. None of the four local populations was self-sustainable. Because the local populations export and import individuals, they can be considered as open recruitment systems in which part of the recruited breeding birds are not produced locally. The spatial extent and the degree of isolation of a local population have an impact on local population dynamics; hence these factors need to be considered in studies about local population dynamics and for deriving conservation measures.

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Introduction

Understanding changes in population growth rate is one of the basic aims of population ecology and central to the field of conservation (Caughley 1994, Sibly and Hone 2002, Norris 2004). Population growth rates change in response to environmental perturbations or to density-dependence through changes of the underlying demographic parameters. For a detailed understanding of population dynamics it is therefore necessary to assess the impact of changes of demographic parameters on changes in population growth rate and to identify causes of changes of demographic parameters.

A common focus of research is to study the demographic mechanisms underlying growth and decline of a local, open population (Baguette and Stevens 2003). Besides stochastic (environment) and deterministic factors (density), the spatial extent of the local population and the degree of isolation can have impacts on its dynamics (Thomas and Kunin 1999, Steen and Haydon

2000, Serrano and Tella 2003, Bowler and Benton 2005). If an individual moves a certain distance the chances to remain in the local population increase with increasing spatial extent of the population. Therefore effects of immigration and emigration on local population growth are likely to become larger with decreasing spatial extent of the local population. Similarly, effects of dispersal become more important the closer local populations are to each other. Therefore studies carried out at a local scale may be insufficient to understand processes determining abundance over larger areas (Lambrechts et al. 1999, Thomas and Kunin 1999), but finding the appropriate spatial scale for population monitoring is challenging (Petranka et al. 2004), and depends on the research question. One way to overcome this difficulty is to enlarge the study area, such that immigration and emigration only occur within the study area (Camus and Lima 2002). Yet, such studies ignore possible effects due to spatial population structure and may be very difficult to carry out, because the study area could easily become too large for a proper sampling. Another way can be a comparative study including several local populations extending over areas with different sizes and different degrees of isolation.

Despite the potential importance of scale and degree of isolation on local population dynamics, few comparative field studies have quantified their effects and correctly included all gains and losses to population growth. The estimation of immigration is challenging and many population studies have not included immigration (Letty et al. 2001, Reid et al. 2004).

We developed an approach to estimate the immigration rate that does not require the assumption that all animals in the population are marked, but is based on capture-recapture data and on recordings of reproductive success. While correctly including all gains and losses to the local populations, our aim was to understand demographic mechanisms underlying the dynamics of four local populations of little owls (*Athene noctua*) and to assess the impact of their spatial extent and degree of isolation to local population growth. The little owl has declined significantly over much of Europe during the last decades (Juillard 1989, Exo 1992, Tucker and Heath 1994). The demographic mechanisms underlying these declines are unclear, because only few demographic analyses have been carried out. Exo (1983) and Knötzsch (1988) performed key-factor analyses demonstrating that factors not associated with reproduction contributed most to population change. Letty et al. (2001) carried out a prospective perturbation analysis using a matrix population model, but without including immigration resulting in limited conclusions regarding the contribution of all demographic rates to population growth.

Using long-term demographic data, we first estimated the demographic rates for each population. Second, we compared the mean demographic performance of the four populations using a life table response experiment (LTRE, Caswell 2001) analysis. This allowed us to identify demographic differences resulting in differential population performances, and to explore effects of the spatial extent and the degree of isolation on the study populations. Third, we applied LTRE analysis to each population to decompose the observed annual changes in the local population growth rates to the contributions of individual demographic parameters. Two populations were stationary whereas two declined to extinction. We were also interested to learn which demographic mechanisms caused the populations to go extinct.

Methods

Model species, study areas and data collection

The little owl is a sedentary, small-sized owl preying mainly on voles and large insects. It is a cavity breeder and inhabits various kinds of open landscapes (Glutz von Blotzheim and Bauer 1980). We studied four local populations in Switzerland and southern Germany (Table 1). The study area of Genève is characterized by rows of large trees (mainly oaks) and arable fields, and the three other study areas are basically traditionally farmed orchards (see Ullrich 1980, Knötzsch 1988, Meisser 1995, Luder and Stange 2001 for more detailed descriptions of the study areas). The local population Basel had the smallest spatial extent, Friedrichshafen the largest (Table 1). Three local populations were surrounded by unsuitable habitat for little owls, whereas suitable habitat with breeding little owls bordered on one side of the population Göppingen. We regard the population Göppingen as not isolated, whereas the other three were isolated to some degree. The time period for sampling demographic data differed between populations. At the beginning of each study, the study area and the number of nest boxes increased over several years (Ullrich 1980, Knötzsch 1988, Meisser 1995). Because changes of the size of the study area or of the number of nest boxes can result in biased estimates of local survival and immigration rates, we only considered the periods during which the size of the study areas and the number of nest boxes remained constant.

The common feature of the sampling protocol in the four study areas was that each year between March and July at least one inspection of all nest boxes was conducted at the time of pair formation, egg laying or incubation, and at least one more inspection was performed of the occupied nest boxes later when the nestlings were ringed. In practice, however, most nest boxes were checked more frequently during the breeding season. When an adult owl was present, we tried to catch it. Because females are incubating the eggs and brooding the chicks, we frequently could catch females. Captures

Table 1. Description of the four study populations with information about sample sizes.

	Basel	Göppingen	Genève	Friedrichshafen
Coordinates	47°32′N, 7°40′E	48°40′N, 9°38′E	46°12′N, 6°04′E	47°39′N, 9°30′E
Mean altitude (m a.s.l.)	270	380	430	450
Study area size (km^2)	23	40	60	95
Adjacent population	no	yes	no	no
Study period	1978–1994**	1978–2003	1993–2003	1979–2001*
Number of ringed nestlings	267	659	433	791
Number of ringed adults	92	73	52	26
Number of individuals recaptured at least once	71	55	30	171
Number of breeding events	138	353	260	455

*For the statistical analyses only the period 1979–1995 was considered
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of males were less frequent. Adults were ringed individually and the ring number of individuals ringed at a previous occasion was recorded. Sex of adults was determined according to the presence or absence of a brood patch. Each year all nestlings born in the nest boxes were ringed. In order to clean the nest boxes, further visits during winter were conducted. Occasional captures of adults at this time were not considered for these analyses, but we recorded the number of dead nestling that did not fledge, in order to correctly assess the number of fledglings of each brood.

Statistical analyses

The elements of our analyses were the estimation of demographic rates (reproductive success, age-specific local survival rates, immigration rates) and the application of retrospective perturbation analyses to assess the contribution of the variation of the demographic rates to variation of the population growth rates in each population and among populations. We start with the description of the retrospective analyses, and then describe how the demographic parameters needed to parameterise the population model were estimated.

Retrospective perturbation analyses

We used life table response experiments (LTRE) for the retrospective perturbation analyses, which can be an accurate way to identify the demographic parameters relevant for population changes (Brault and Caswell 1993, Horvitz et al. 1997, Caswell 2001, Cooch et al. 2001, Coulson et al. 2005). LTRE estimate the contribution of a demographic parameter to population change from the sensitivity of population growth rate (λ) to changes in the demographic parameter and on the magnitude of this change. These calculations require the formulation of a population model. We used a simple female based model which assumes that little owls start to reproduce at an age of 1 year and that the reproductive performance and survival of reproductive

individuals does not change with age. Both simplifications are realistic for little owls (Ullrich 1980). The number of breeding females in year $t+1$ is given by the sum of the number of females that were already reproducing in year t and that have survived and not emigrated until year $t+1$, the number of young females produced in the year t that were locally recruited in year $t+1$, and the number of female immigrants. Formally, we get

$$N_{t+1} = N_t \phi_{t,ad} + N_t \phi_{t,juv} F_t + I_{t+1} \quad (1)$$

where N_{t+1} is the number of females in year $t+1$ aged at least one year, $\phi_{t,ad}$ is the probability that a female aged at least one year survives and remains in the study population between year t and $t+1$ (adult local survival probability, the complement of death and emigration), $\phi_{t,juv}$ is the probability that a female that is marked as fledgling in year t is still alive and in the study population in year $t+1$ (juvenile local survival probability, the complement of death and emigration), F_t is the number of fledged females per adult female in year t (fecundity) and I_{t+1} is the number of immigrated females. The population growth rate is then calculated as,

$$\lambda_t = \frac{N_{t+1}}{N_t} = \phi_{t,ad} + F_t \phi_{t,juv} + i_t \quad (2)$$

The immigration rate (i_t) is defined as the number of immigrants in year $t+1$ per animal present in year t. The following LTRE analysis requires the calculation of the sensitivities of λ to changes in the underlying demographic parameters. Assuming no temporal variation and autocorrelation in the demographic parameters, they are calculated as the first derivative of λ with respect to the demographic parameters. The sensitivity of λ to changes in local adult survival is $S(\phi_{ad}) = \partial\lambda/\partial\phi_{ad} = 1$, to changes in local juvenile survival it is $S(\phi_{juv}) = \partial\lambda/\partial\phi_{juv} = F$, to changes in fecundity it is $S(F) = \partial\lambda/\partial F = \phi_{juv}$ and to changes in immigration rate it is $S(i) = \partial\lambda/\partial i = 1$.

Life table response experiments: comparative approach

To estimate how much the population-specific demographic rates have contributed to the difference of λ among populations we used a fixed design approach (Horvitz et al. 1997, Caswell 2001). We compared the demography of each population m (λ_m) with an average population ($\bar{\lambda}$). The demographic parameters of the average population were the means of the four population-specific means. The population-specific growth rate is the sum of the growth rate of the average population and a deviation ($\lambda_m = \bar{\lambda} + \Delta_m$). An approximation of the deviation Δ_m is given by the difference of the demographic parameters a_j and the corresponding sensitivities as,

$$\Delta_m \approx \sum_j (a_j^m - \bar{a}_j)\frac{\partial \lambda}{\partial a_j}\bigg|_{\lambda_n} \qquad (3)$$

Because some sensitivities change when the demographic parameters change, they are evaluated halfway between λ_m and $\bar{\lambda}$ (i.e. at $\lambda_n = (\lambda_m - \bar{\lambda})/2$). This first order approximation of Δ_m is usually very accurate if no extreme variation in the demographic parameters occur (Caswell 2001). The results are expressed as the contribution of each demographic parameter of the current population to the difference of λ between the current and the average population.

Life table response experiments: temporal dynamics

To estimate the contribution of the temporal variation and covariation of vital rates to variation of λ over time we used random effects LTRE (variance decomposition; Horvitz et al. 1997). For each population we decomposed the temporal variance of λ into the components of temporal variances and covariances of the underlying vital rates (Caswell 2001). To summarize the results it is useful to calculate the contribution of the variance and covariances involving a particular demographic parameter to the variation in λ. This is the sum of the variance and half of those covariance components in which the vital rate is involved (Horvitz et al. 1997).

Parameterisation of the population model

Estimation of local survival rates
We estimated annual local survival rates from the capture–recapture data using capture–recapture models (Lebreton et al. 1992). These models allow getting separate estimates of age-specific local survival (ϕ_t) and recapture probabilities (p_t-probability that an individual that is alive at time t and in the population is recaptured at time t). The capture–recapture model can

be used in an analogous way as ANOVAs to test the impact of factors on the variation of the survival rate. Because the sex of the nestlings could not be determined, we assumed an even sex ratio of the nestlings to be able to estimate unbiased sex-specific survival rates (Nichols et al. 2004).

We first assessed the goodness-of-fit of a global model capturing variation in survival and recapture due to age, sex and time effects. We then fitted several a priori defined candidate models that considered fewer effects, ranked these models according to their support by the data using information-theoretic approaches and calculated model-averaged survival estimates to be used for the LTRE analyses. Details about modelling of the local survival rates are given in Appendix 1. Temporal variances of survival rates were estimated using random effects methodology (Burnham and White 2002) to the best models with unrestricted time-dependent survival rates.

Estimation of fecundity
We defined the number of fledglings per breeding pair per year as fecundity. For each population the raw data used were for each monitored brood the number of young fledged, an identification identity of the territory and the year. Because adult females often live longer than one year and are quite strongly philopatric to their breeding site, the data were not completely independent, which would result in underestimated standard errors if conventional fixed effects models were used for the analyses. We used linear mixed models where the territory identification identity is considered to be random. Ideally the female identity would be another random factor, yet sample size would have become too small, if we would have included only broods with known females. To estimate the mean and the temporal variance of fecundity, we used the year as an additional random factor. We assumed an even sex ratio and divided the estimated year-specific fecundities by two to obtain the number of fledged females per breeding female needed in the LTRE analyses. To test whether there were linear trends over time in fecundity, we considered the year as a fixed, linear covariate. We performed modelling with restricted maximum likelihood estimation (REML) implemented in GENSTAT 5.4.1 (Payne et al. 1993).

Estimation of immigration rate
If the population growth rate is known, immigration rate can be estimated as:

$$\hat{i}_t = \hat{\lambda}_t - \hat{\phi}_{t,ad} - \hat{F}_t\hat{\phi}_{t,juv} \qquad (4)$$

The population growth rate could be calculated from the number of breeding pairs as N_{t+1}/N_t. However, the number of breeding pairs is not an accurate index of true population size here, as some pairs might have remained

undetected because they nested in natural cavities or because their brood failed at an early stage. Population growth rate can also be estimated from the capture-recapture data of adult owls as the ratio of the local survival rate of the adults ($\phi_{t,ad}$) and the probability that an adult is not a new recruit in the population (γ_{t+1}, Pradel (1996)). The seniority probabilities (γ), can be estimated from reverse-time capture–recapture models (Pradel 1996, see below). Thus, after little algebra, the immigration rate is estimated as,

$$\hat{i}_t = \phi_{t,ad} \frac{1-\hat{\gamma}_{t+1}}{\hat{\gamma}_{t+1}} - \hat{F}_t \phi_{t,juv} \qquad (5)$$

The variance-covariance matrix of i was calculated with the delta method from the point estimates of the parameters needed to calculate i and their variance–covariance matrix (Seber 1982). Temporal variances of i were estimated from the year-specific values and the corresponding variance–covariance matrix with the method developed by Gould and Nichols (1998).

For modelling the seniority probability (γ) we used the same capture–recapture data as for the survival rate estimation, but of the locally born owls only the recaptures were included. We considered similar candidate models as for the estimation of survival (see Appendix 2 for details).

Estimation of covariances

For the decomposition of the temporal variance of λ into the contributions of the vital rates the temporal covariances among vital rates needs to be computed. However, we are not aware of frequentist methods to decompose the total covariance into sampling and temporal covariances. Therefore, we used the total covariance calculated from the year-specific estimates of the four different demographic parameters, although this procedure may have overestimated temporal covariances.

Results

The study populations exhibited substantial temporal fluctuations in size as evidenced by the number of pairs breeding in nest boxes encountered each year (Fig. 1). The populations Genève and Göppingen were fluctuating whereas the populations Friedrichshafen and Basel declined, and finally went extinct.

Estimation of demographic parameters

Local survival rates were rather simple functions of time, sex and age (Appendix 1). The model averaged estimates of adults increased across time in Göppingen, Genève and Friedrichshafen (Fig. 2). Local survival of juveniles

also increased across time in Göppingen and Genève, but declined in Friedrichshafen. Local survival of little owls of both age classes from Basel remained constant over time (Fig. 2). Local survival rates of both age classes were slightly higher in males (geometric mean of model averaged local survival rates: Basel: juv: 0.095 (SE: 0.027), ad: 0.651 (SE: 0.043); Göppingen: juv: 0.083 (0.026), ad: 0.740 (SE: 0.057); Friedrichshafen: juv: 0.190 (0.021), ad: 0.673 (SE: 0.033)) than in females (Table 2), likely reflecting sex-specific differences in dispersal (Exo and Hennes 1980, Ullrich 1980, Gassmann and Bäumer 1993, Knötzsch 1988). The geometric mean of local survival rates of adult females was highest in Genève and lowest in Basel, for juvenile females it was highest in Friedrichshafen and lowest in Göppingen (Table 2). Comparing the temporal variance (Table 2) among age classes is difficult, because the maximum possible variance for a survival rate with mean $\bar{\phi}$ is $\bar{\phi}(1-\bar{\phi})$. Following Gaillard and Yoccoz (2003) and Morris and Doak (2004) we therefore compared the ratio of observed to the maximum possible variance. It appeared that adult survival was relatively more variable than juvenile survival in all populations apart from Basel (Table 2).

The number of fledglings per breeding pair and year was highly variable over time in all populations (Fig. 2). On average, it was highest and fluctuated most in Göppingen and was lowest in Friedrichshafen (Table 2). Fecundity decreased continuously across time in Göppingen (Wald-χ^2 = 4.6, P = 0.03, β = -0.027 (SE: 0.012), n = 269) and Genève (Wald-χ^2 = 9.2, P < 0.01, β = -0.111 (SE: 0.037), n = 201), but not in Basel (Wald-χ^2 = 2.7, P = 0.10, β = -0.061 (SE = 0.037), n = 138) and Friedrichshafen (Wald-χ^2 = 0.0, P = 0.99, β = -0.001 (SE = 0.019), n = 356).

Seniority probabilities were fairly constant across time, but declined in Genève (Appendix 2). The estimates of the year-specific immigration rates based on model-averaged seniority, local survival and fecundity rates appeared to be rather imprecise (Fig. 2). They were on average largest in Göppingen and lowest in Friedrichshafen and the temporal variance was zero in all populations (Table 2).

Life table response experiments

Comparative approach

Using the geometric means for survival and immigration and the arithmetic mean for fecundity, λ of Göppingen and Genève were ≈ 1, those of Basel and Friedrichshafen < 1, and that of the average population was $\bar{\lambda} = 0.95$. The most important demographic parameters contributing to the difference of λ among populations were differences in local juvenile survival and immigration,
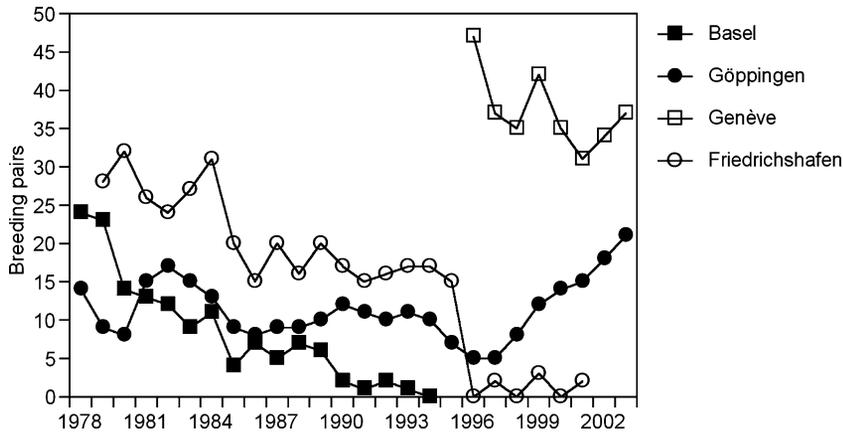
Fig. 1. Dynamics of the number of breeding pairs in nest boxes in four little owl populations. Note that for the population Genève no census was carried out in the years 1993–1995.

whereas differences in adult survival were comparatively less important (Fig. 3). Least important were differences in fecundity.

Temporal dynamics

The temporal variance of adult local survival contributed most to the variation of λ in all populations but Basel (Fig. 4). The contribution of the variation of fecundity, immigration and local juvenile survival to variation of λ were similar and in most populations much smaller than the contribution of the variation of adult local survival. The temporal covariances were always small (<|0.02|), and therefore the impossibility to separate sampling from process covariances had a negligible effects on the results only.

Discussion

Differences in the performance of the four local little owl populations could be largely attributed to differences in local juvenile survival and immigration, and less to differences in adult survival and fecundity. Part of the differences in local juvenile survival and immigration among populations stem from different spatial extents and degrees of isolation of the study populations. Temporal variation in population growth rate was most strongly affected by the variation of local adult survival in three of four local populations, whereas the highly variable fecundity did not contribute significantly in any population, supporting the results of key-factors analyses (Exo 1983, Knötzsch 1988). This pattern can be explained by differential sensitivity of λ to changes in demographic parameters and by the variances of the demographic parameters.

Little owls have comparatively short natal dispersal distances (mean about 3 km, but with records of up to 200 km) and adults are highly philopatric (Ullrich 1980, Knötzsch 1988, Exo 1992, Paradis et al. 1998). Therefore, local adult survival is likely to be close to true adult

survival and immigrants are mainly dispersing juveniles. These immigrants were an important contribution to the growth of all our local populations – all of them would have become extinct if immigration had stopped. In this sense all local populations could be considered as sinks (Dias 1996). True juvenile survival is in the range of about 0.3 – 0.35 in little owls (Exo and Hennes 1980). Because estimated local juvenile survival was much smaller in all populations we can conclude that many juveniles emigrate from the local populations. In this sense, all populations could also be regarded as sources. The source-sink dichotomy is therefore not particularly useful to describe these local populations. Given the spatial scales of the studied local populations, they are better regarded as open-recruitment systems in which an important part of the recruited breeding birds originate from individuals that are not produced by the local populations. Such a system has been described in a number of bird species (Stacey and Taper 1992, Lambrechts et al. 1999, Baillie et al. 2000, Murphy 2001, Franklin et al. 2004) and small mammals (Nichols and Pollock 1990).

Because the immigrants are produced in adjacent populations, the dynamics of the local populations are determined in part by stochastic and deterministic factors operating in neighbouring populations. The relationship between the contributions of immigration (calculated as i/λ; Basel: 0.15, Göppingen: 0.27, Genève: 0.12, Friedrichshafen: 0.09) and the spatial extent of the local populations tended to be negative, suggesting that populations expanding over a small spatial area are more influenced by variation of immigration rate and therefore by factors not operating locally compared to populations expanding over a large spatial area. Moreover, the contribution of immigration was by far highest for the only studied population with adjacent populations (Göppingen), suggesting that the degree of isolation had an impact on the local population dynamics of little owls. However, our sample size was too small to make wide-ranging conclusions. Assessing the relative importance of spatial extent and degree of isolation on
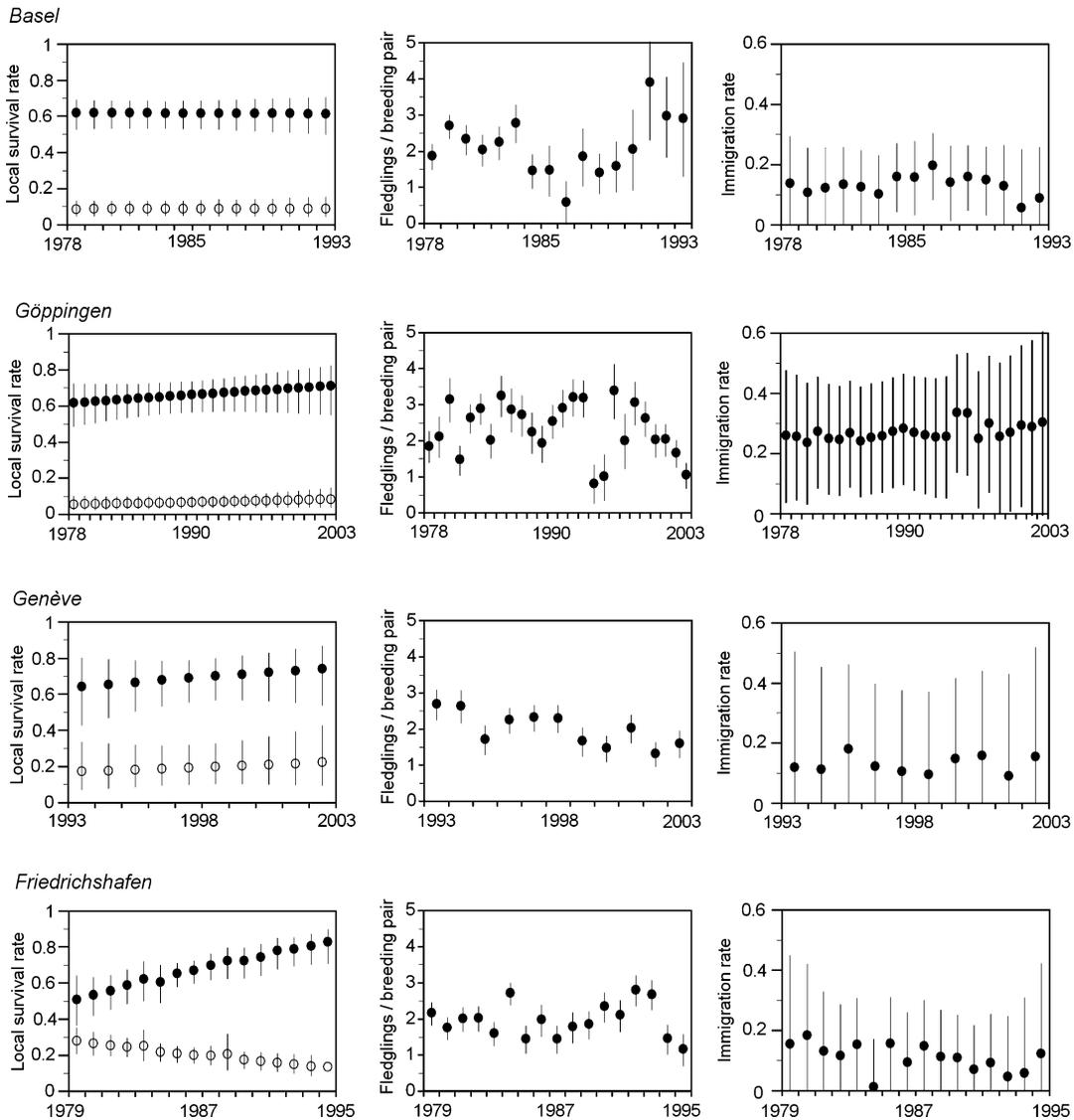
Fig. 2. Model averaged annual local survival rates, fecundity and immigration rates of little owl females in four populations. For the panels with local survival the closed symbols refer to adults and the open symbols to juveniles. The vertical lines show the limits of the unconditional 95% confidence intervals (i.e. including model selection uncertainty). The sample size to estimate fecundity for each year and site is equivalent to the number of breeding pairs (Fig. 1).

Table 2. Estimates of mean and temporal variance (σ^2) of demographic parameters of female little owls from four populations. For the estimation of fecundity a model with the random factors year and nest box identity was used. The other demographic parameters were computed as the geometric means from the model averaged estimates. To compare the variation of survival rates, we computed the proportion of the maximum possible variance P_{max} as $\sigma^2/\text{mean}/(1-\text{mean})$; see Gaillard and Yoccoz (2003) and Morris and Doak (2004).

|	Fecundity		Immigration		Juvenile survival		Adult survival	
	Mean (SE)	σ^2	Mean (SE)	σ^2	Mean (SE)	σ^2 (P_{max})	Mean (SE)	σ^2 (P_{max})
Basel	2.005 (0.177)	0.110	0.123 (0.018)	0.0000	0.082 (0.024)	0.0019 (0.025)	0.610 (0.042)	0.0007 (0.003)
Göppingen	2.265 (0.148)	0.282	0.266 (0.022)	0.0000	0.059 (0.017)	0.0000 (0.000)	0.659 (0.051)	0.0655 (0.292)
Genève	1.947 (0.144)	0.075	0.123 (0.052)	0.0000	0.188 (0.060)	0.0017 (0.011)	0.687 (0.068)	0.0094 (0.044)
Friedrichshafen	1.940 (0.136)	0.080	0.090 (0.025)	0.0000	0.191 (0.016)	0.0064 (0.041)	0.674 (0.026)	0.0391 (0.178)
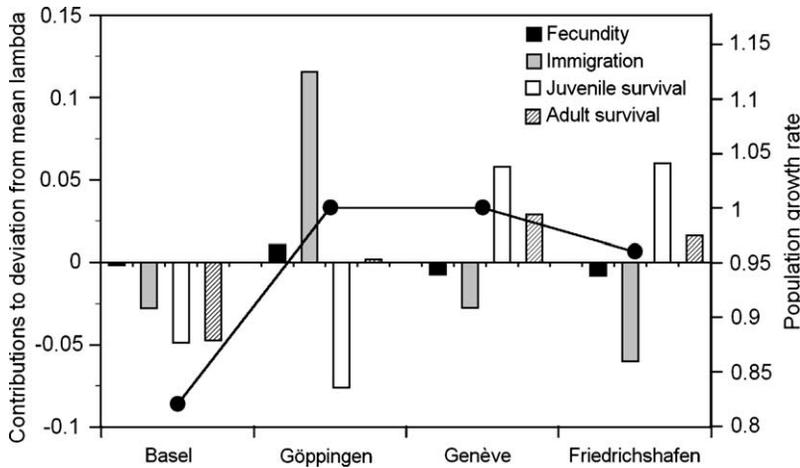
Fig. 3. Contributions of the difference of the four demographic parameters between population m and the average population to the difference of the population growth rates between population m and the average population. Indicated are also the population specific mean growth rates (dots). The populations are sorted by their spatial extent with Basel being the smallest.

local population dynamics would be an important exercise for setting up conservation measures. This would require a larger sample of local populations and more detailed knowledge about the spatial distribution of local populations.

Variation of adult local survival was the most important demographic reason for the variation of population growth rate across time. Consequently, factors that impact adult local survival have a strong impact on the local population dynamics. Adult local survival increased slightly over time in three populations. It is difficult to say why these increases occurred. Because adult little owls are highly philopatric, the increases are more likely to reflect increases of true survival than decreases of breeding dispersal probabilities or distances. Potential environmental factors affecting adult survival are predation by martens (*Martes foina*), variation of food availability and the duration of snow cover during winter (Glutz von Blotzheim and Bauer 1980, Exo 1988, Exo 1992).

Although the temporal variation of fecundity was strong, it did not contribute significantly to variation in population size. Part of the explanation is that the sensitivity of the population growth rate to changes in fecundity was not large. It agrees with the common finding that highly variable demographic parameters have usually low population growth rate sensitivities (Pfister 1998, Gaillard and Yoccoz 2003, Morris and Doak 2004).

Given that immigration is an important contribution for the maintenance of these local little owl populations, it is at first surprising that the temporal variation of immigration had not contributed to the variation of the population growth rate. The sensitivity of the population growth rate to changes in immigration was the same as to changes in adult survival, but the temporal variance of immigration was zero. This may be an artefact due to the imprecise estimates of the year-specific immigration rates. Methods to estimate immigration needs to be improved to assess in a more rigor way whether the
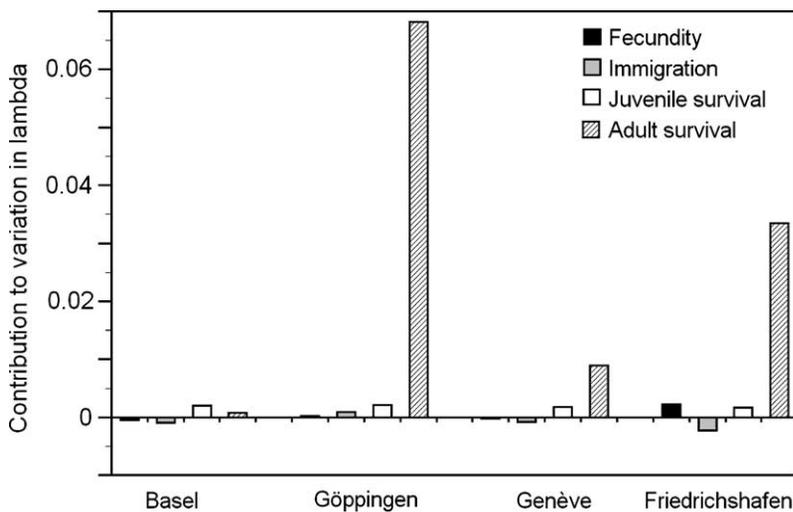

Fig. 4. Contributions of variances and covariances in which demographic rates are involved to the variation of population specific growth rates. The populations are sorted by their spatial extent with Basel being the smallest.

temporal variation of immigration is important for the variation of population growth rate.

Our findings have consequences for conservation. Populations occupying small areas are relatively less prone to variation in fecundity, and relatively more prone to variation in local survival and immigration than populations occupying larger areas. Therefore populations inhabiting small areas can be strongly affected by habitat changes occurring in other areas. The same gradient is apparent for the degree of isolation. Consequently, conservation of little owl populations occupying a small area should focus on expanding the size of the area or on ensuring connections with neighbouring populations, whereas conservation of populations occupying larger area should be more directed towards enhancing or maintaining local recruitment. This conclusion can be generalized qualitatively to other species that have strong natal and week breeding dispersal (e.g. most passerines, Baillie et al. 2000). However, the judgment of the different conservation priorities must be regarded relative to the dispersal behaviour of the species under study (Steen and Haydon 2000, Bowler and Benton 2005).

Methodological issues

The modelling approach we used is based on a number of assumptions, the most critical one is perhaps the restriction to two age classes. Clearly most natural bird populations are more age-structured, in particular longer-lived species (Tavecchia et al. 2001, Reid et al. 2004). However, our data must had included more individuals with exact known age to have reasonable power to detect more age classes, and the simplification to two age classes has given reasonable results in species with a similar life history (Hone and Sibly 2002, Altwegg et al. 2003), and we believe that this is true also for our study.

Our study clearly shows that immigration needs to be included in models for local open populations; otherwise estimates of population growth rate are negatively biased. Traditional ways to estimate immigration is the use of the Jolly-Seber model (Cooch et al. 2001), or to rely on the assumption that all unmarked individuals in the population are immigrants (Möller 2002). We have introduced an alternative approach to estimate immigration rate when only capture–recapture data and data on reproductive success are available, as is the case for many long-term population studies. We have not performed detailed simulation studies to study the performance of this estimator, because the performance of the involved parameters are well studied (Williams et al. 2002) and therefore we expect that it is sensitive to the same assumption violations. Trap response and changes of the spatial extent of the study site are likely to be particularly important assumption violations that result in

substantial bias (Hines and Nichols 2002). These assumptions were met in our study. A disadvantage of our estimators was that it turned out to be rather imprecise. This is likely because the uncertainties in estimating the component parameters are combined. Other statistical methods to estimate immigration would need additional data sampling, such as robust design capture-recapture data (Nichols and Pollock 1990) or independent population surveys (integrated population models; Brooks et al. 2004, Buckland et al. 2004).

Demographic reasons of local extinctions

A specific aim of our study was to understand the demographic reasons for the two local population extinctions (Basel and Friedrichshafen). The demographic estimates from Friedrichshafen did not include the extinction itself, but only the decline until year 1995 (Fig. 1). The decline until 1995 was due to a strong decrease of juvenile local survival resulting in lower local recruitment that could not be halted by increasing adult survival. Hence, there was a decline in the gain component, rather than an increase of the loss component that caused the population to decline. A possible environmental change that could have caused this decline was a decrease of food availability due to changes of farming practices. This was evidenced by declining body mass of the chicks at time of marking (G. Knötzsch, pers. obs.). In Basel, the demographic parameters were not very variable and had no trends over time. Consequently λ remained fairly constant, but as it was less than one the population declined asymptotically. The equilibrium of gain and losses has been disturbed already before the study started, and it is difficult to infer which ones have been involved. However, we can compare the demographic parameters with those from the other populations taking into account that the spatial extent of the populations differed. Fecundity was in the range of the other populations and did not contribute to the difference in λ, suggesting that extinction was not related to a decrease in fecundity. The spatial extent of population Basel was the smallest, thus we expect that the estimates and the contributions of juvenile and adult local survival to the difference of λ among populations to be lower, and the estimate and the contribution of immigration to the difference in λ to be higher than in the other populations. While these expectations are true for juvenile local survival, they were not true for adult local survival and particularly not for immigration. This suggests that the main demographic reasons for the extinction of little owl population in Basel were declines of immigration and adult survival rates that happened already before the study started in 1978. Extinctions of many local populations in the vicinity of the focus population due

to changes of farming practices (Luder and Stange 2001) were probably the reason for the insufficient immigration, and predation of martens on breeding females may have contributed to low survival (Luder and Stange 2001). This comparative analysis showed that the demographic mechanisms resulting in local extinction differed, despite the reason was in both populations changes of farming practices.

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Appendix 1. Modeling annual local survival rates of little owls from four populations.

1. Goodness-of-fit tests

In our global model we assumed that survival was age-specific (2 age classes, the first spanning the time period of the first year after fledgling), time- and sex-specific, and that recapture rate was time- and sex-specific. We denote this model $\phi_{a2 \times s \times t}$, $p_{s \times t}$, where subscript a2 denotes the 2 age classes, s a sex effect, t a time-effect and × denotes an interaction. We assessed the goodness-of-fit of this model with program U-CARE (Choquet et al. 2001). These goodness-of-fit tests were insignificant in all populations (Basel: $\chi^2_{31} = 22.74$, P = 0.86; Göppingen: $\chi^2_{29} = 7.36$, P = 1.00; Genève: $\chi^2_{17} = 9.97$, P = 0.91; Friedrichshafen: $\chi^2_{55} = 16.24$, P = 1.00), showing that this model was a adequate description of the data.

2. Description of candidate models

We defined a priori a set of models and ranked these models according to their support by the data using information theoretic methods (Burnham and Anderson 1998). The recapture rates were always assumed to be sex-specific, because males spend much less time in the nest boxes during the breeding period. Moreover, recapture rates may have been time-specific, because the number of checks of occupied nest boxes during the breeding period varied across time. Possible time-dependence of recapture rates may have been different among sexes (denoted by t × s), or additive (denoted by t + s). We end with three suitable models for recapture rates ($p_{t \times s}$, $p_{t + s}$, p_s). For the local survival rates we always assumed that they were different between the first year of life and later, and that once owls were at least one year old do not change anymore with age. The most complex model considered different survival rates for each age class, sex, and time ($\phi_{a2 \times s \times t}$). The next models considered that survival of both sexes varied in parallel over time ($\phi_{(a2 \times t) + s}$), that survival of both age classes varied in parallel over time ($\phi_{(a2 \times s) + t}$), that survival of both sex-and age classes varied in parallel over time ($\phi_{a2 + s + t}$), or that survival of the sexes do not differ, but still varied over time ($\phi_{a2 \times t}$, $\phi_{a2 + t}$). In order to account for possible directional changes of survival over time, we also included models in which survival rates were constrained to be a linear or quadratic function of time. These effects (denoted by subscripts T and T2, respectively) were used in combination with a sex effect ($\phi_{a2 \times s \times T}$, $\phi_{(a2 \times T) + s}$, $\phi_{(a2 \times s) + T}$, $\phi_{a2 + s + T}$, $\phi_{a2 \times s \times T2}$, $\phi_{(a2 \times T2) + s}$, $\phi_{(a2 \times s) + T2}$, $\phi_{a2 + s + T2}$), and without ($\phi_{a2 \times T}$, $\phi_{a2 + T}$, $\phi_{a2 \times T2}$, $\phi_{a2 + T2}$). The next group of models assumes no time-dependence, but a sex effect on survival ($\phi_{a2 \times s}$, $\phi_{a2 + s}$). The simplest model finally assumes no time- and sex effects on survival (ϕ_{a2}). We used all combinations of the 3 p- and 21 ϕ-models as the set of the candidate models (63 in total). Based on the Akaike's information criteria (AIC) we calculated model averaged estimates of survival rates and used these values for the retrospective modeling.

Because too few males were recaptured in Genève we considered for this population only females, and consequently considered only models without sex effect. We used program MARK (White and Burnham 1999) for modeling and parameter estimation.

3. Modeling results

Table 1. Modeling local survival (ϕ) and recapture rates (p) of little owls in four populations. The model subscript t refers to time dependence (i.e. different in each year), T denotes a liner trend over time, T^2 a squared trend over time, a2 denotes an age effect with 2 age classes, s denotes a sex effect, and. denotes constancy. Given are the deviance of each model, the number of estimated parameters (K), the difference of the AICc value of the current model and of the best model (ΔAICc), and the AICc weight (w_i). For each site the global model and all models with weights ≥ 0.01 are shown.

Model	Deviance	K	ΔAICc	w_i
Basel				
ϕ_{a2}, p_s	307.18	4	0.00	0.23
ϕ_{a2+s}, p_s	305.16	5	0.02	0.22
ϕ_{a2+T}, p_s	307.17	5	2.04	0.08
$\phi_{a2 \times s}$, p_s	305.15	6	2.06	0.08
ϕ_{a2+T+s}, p_s	305.15	6	2.06	0.08
$\phi_{[a2 \times T^2]+s}$, p_s	299.74	9	2.84	0.05
$\phi_{a2 \times T^2}$, p_s	301.84	8	2.87	0.05
ϕ_{a2+T^2}, p_s	306.48	6	3.39	0.04
ϕ_{a2+s+T^2}, p_s	304.51	7	3.48	0.04
$\phi_{[a2 \times T]+s}$, p_s	304.76	7	3.73	0.04
$\phi_{a2 \times T}$, p_s	306.85	6	3.76	0.03
$\phi_{[a2 \times s]+T}$, p_s	305.14	7	4.10	0.03
$\phi_{[a2 \times s]+T^2}$, p_s	304.50	8	5.53	0.01
$\phi_{a2 \times t \times s}$, $p_{s \times t}$	214.85	88	111.77	0.00
Göppingen				
ϕ_{a2+T+s}, p_{s+t}	293.81	30	0.00	0.25
ϕ_{a2+T^2+s}, p_{s+t}	292.10	31	0.45	0.20
ϕ_{a2+T}, p_{s+t}	297.70	29	1.73	0.10
$\phi_{[a2 \times s]+T}$, p_{s+t}	293.53	31	1.89	0.10
$\phi_{[a2 \times T]+s}$, p_{s+t}	293.70	31	2.06	0.09
ϕ_{a2+T^2}, p_{s+t}	296.52	30	2.71	0.06
$\phi_{[a2+T^2]+s}$, p_{s+t}	290.51	33	3.22	0.05
ϕ_{a2}, p_{s+t}	301.41	28	3.29	0.05
$\phi_{a2 \times T}$, p_{s+t}	297.67	30	3.86	0.04
ϕ_{a2+s}, p_{s+t}	301.06	29	5.09	0.02
$\phi_{a2 \times s}$, p_{s+t}	298.93	30	5.12	0.02
$\phi_{a2 \times T^2}$, p_{s+t}	295.15	32	5.68	0.01
$\phi_{a2 \times t \times s}$, $p_{s \times t}$	179.51	141	167.14	0.00
Genève				
ϕ_{a2}, p	106.33	3	0.00	0.41
ϕ_{a2+T}, p	104.81	4	0.55	0.31
$\phi_{a2 \times T}$, p	104.52	5	2.33	0.13
ϕ_{a2+T^2}, p	104.80	5	2.61	0.11
$\phi_{a2 \times T^2}$, p	102.40	7	4.40	0.04
$\phi_{a2 \times t}$, p_t	84.58	29	37.10	0.00
Friedrichshafen				
$\phi_{a2 \times T^2}$, p_{s+t}	453.49	23	0.00	0.56
$\phi_{[a2 \times T^2]+s}$, p_{s+t}	453.48	24	2.09	0.20
$\phi_{a2 \times T}$, p_{s+t}	460.15	21	2.48	0.16
$\phi_{[a2 \times T]+s}$, p_{s+t}	460.10	22	4.52	0.06
$\phi_{a2 \times t}$, p_{s+t}	406.39	49	8.65	0.01
$\phi_{a2 \times t \times s}$, $p_{s \times t}$	351.13	93	54.52	0.00

Appendix 2. Modeling seniority probability of adult little owls from four populations.

We considered all combinations of 3 models for recapture rates ($p_{t \times s}$, p_{t+s}, p_s), and of 10 models for seniority probability ($\gamma_{s \times t}$, γ_{t+s}, γ_t, γ_s, $\gamma_{s \times T}$, γ_{s+T}, γ_T, $\gamma_{s \times T2}$, γ_{s+T2}, γ_{T2}), thus 30 models as our set of candidate models. The estimation and modeling was performed with program MARK (White and Burnham 1999).

Table 1. Modeling seniority (γ) and recapture rates (p) of adult little owls in four populations. The model subscript t refers to time dependence (i.e. different in each year), T denotes a liner trend over time, T^2 a squared trend over time, s denotes a sex effect, and. denotes constancy. Given are the deviance of each model, the number of estimated parameters (K), the difference of the AICc value of the current model and of the best model (ΔAICc), and the AICc weight (w_i). For each site the global model and all models with weights ≥ 0.01 are shown.

Model	Deviance	K	ΔAICc	w_i
Basel				
$\gamma_.$, p_s	230.36	3	0.00	0.40
γ_s, p_s	229.71	4	1.42	0.20
γ_T, p_s	230.36	4	2.07	0.14
γ_{T^2}, p_s	229.03	5	2.84	0.10
γ_{s+T}, p_s	229.71	5	3.51	0.07
γ_{s+T^2}, p_s	228.37	6	4.29	0.05
γ_{s*T}, p_s	229.08	6	5.00	0.03
$\gamma_{s \times T^2}$, p_s	227.30	8	7.52	0.01
Göppingen				
γ_s, p_s	200.26	4	0.00	0.43
γ_{s+T}, p_s	200.23	5	2.11	0.15
$\gamma_.$, p_s	204.63	3	2.25	0.14
$\gamma_{s \times T}$, p_s	198.64	6	2.69	0.11
γ_{s+T^2}, p_s	199.98	6	4.03	0.06
γ_T, p_s	204.55	4	4.29	0.05
$\gamma_{s \times T^2}$, p_s	198.21	7	4.46	0.05
γ_{T^2}, p_s	204.41	5	6.28	0.02
Genève				
$\gamma_.$, $p_.$	65.37	2	0.00	0.63
γ_T, $p_.$	64.85	3	1.65	0.28
γ_{T^2}, p	64.75	4	3.76	0.10
Friedrichshafen				
γ_T, p_{s+t}	237.54	19	0.00	0.35
γ_{T^2}, p_{s+t}	236.43	20	1.18	0.20
γ_{s+T}, p_{s+t}	237.18	20	1.93	0.14
$\gamma_{s \times T^2}$, p_{s+t}	230.79	23	2.50	0.10
γ_{s+T^2}, p_{s+t}	236.27	21	3.32	0.07
$\gamma_.$, p_{s+t}	243.40	18	3.60	0.06
$\gamma_{s \times T}$, p_{s+t}	236.83	21	3.89	0.05
γ_s, p_{s+t}	243.35	19	5.81	0.02