

# Variation and covariation in survival, dispersal, and population size in barn owls *Tyto alba*

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## Summary

1. Population dynamics are the result of variation in survival, recruitment, emigration and immigration rates. Covariation between these demographic rates critically affects the dynamics and magnitude of fluctuations in population size. Such covariation can arise by environmental factors affecting several rates in similar ways. Also demographic processes, such as the source–sink and the balanced dispersal process, are expected to lead to covariation between demographic rates.

2. Here, we study variation and covariation in survival, emigration, immigration, and the size of a Swiss barn owl (*Tyto alba*) population, and examine the factors associated with this variation. For practical reasons, survival and emigration are often confounded in studies of natural populations. We overcome this problem by jointly analysing live-recapture and dead-recovery data using recently developed statistical methods.

3. Mortality, emigration, the number of known immigrants, and population size were positively correlated over time. Neither the source–sink nor the balanced dispersal process is expected to lead to this pattern.

4. Survival was lower for juveniles than adults (mean 17% vs. 72%), and highly variable across years in both age classes. Snow cover, mean annual temperature and population density accounted for 32–47% of the variation in survival of juveniles and adults. Emigration was higher for juveniles than for adults, and adults emigrated more often when the population size was higher.

5. Our results showed that local population dynamics were affected by density dependence and the stochastic environmental factors snow cover and temperature. Rather than lending support to one of the two dispersal hypotheses, the patterns of correlation between survival, dispersal, and population size suggest strong fluctuations in environmental conditions that influence the dynamics of barn owl populations at a larger spatial scale.

*Key-words:* combined live-recapture and dead-recovery model, natal dispersal, breeding dispersal, environmental stochasticity, program MARK.

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## Introduction

Local population size is determined by the balance between recruitment of new breeders through reproduction and immigration, and loss of individuals through mortality and emigration. Variation in these

demographic parameters, due to stochastic events or density-dependent processes, determines the dynamics of local populations. Whether fluctuations in the demographic parameters compensate each other to reduce the variance in population numbers, or amplify each other to increase this variance depends on the covariation between them.

Covariation between demographic parameters can arise if fluctuations in different demographic parameters are governed by the same external variables, such as weather. Alternatively, demographic processes can lead to such covariation. For example, two different processes governing dispersal between local populations,

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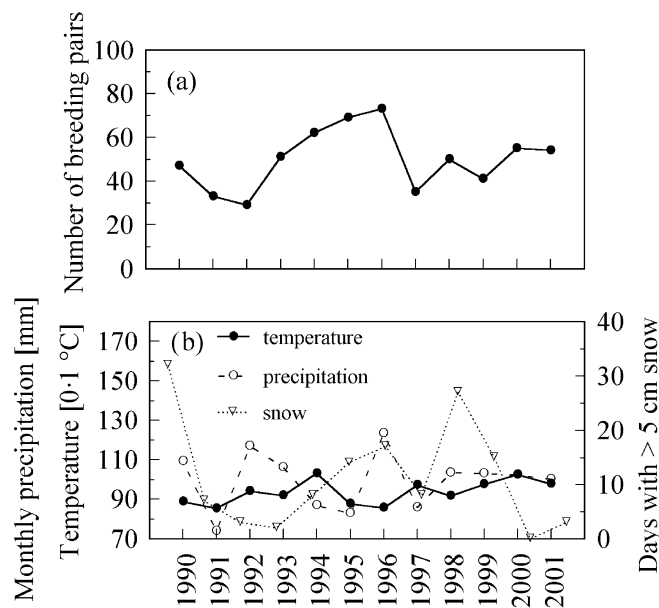
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the source–sink hypothesis and the balanced dispersal hypothesis (Pulliam 1988; McPeck & Holt 1992), both predict temporal patterns of covariation between survival, immigration, emigration and population size at the local scale. According to the source–sink hypothesis, dispersal between populations is driven by population processes and results in a net flow of individuals from more productive to less productive areas (Pulliam 1988; Dias 1996). Emigration rates are expected to increase with population density and survival, because more individuals are produced that cannot settle in their native area when density and survival are high. The balanced dispersal hypothesis considers dispersal as a strategy for habitat selection employed by individuals, and theory predicts an equal number of individuals to move between any two areas (McPeck & Holt 1992; Lemel *et al.* 1997). This model further predicts a positive correlation between immigration and emigration rates, and a negative correlation between the proportion of individuals dispersing and local population size. To deepen our understanding of the processes that govern natural population dynamics, data on variation and covariation in survival, emigration, immigration and population size are urgently needed. Such data require detailed long-term studies of natural populations, and are thus still rare.

A common problem in studies of natural populations is that individuals can go undetected during sampling occasions, or that they move out of the study area where they cannot be observed during subsequent surveys. Using simple enumeration techniques, both kinds of individuals would falsely be counted as having died. Capture–mark–recapture methods allow us to control for variation in recapture success (Lebreton *et al.* 1992). These methods estimate the recapture

probability (probability that a given individual is recaptured at time  $t$ , given that it was alive and in the study area at time  $t$ ) independently of the local survival rate (probability of surviving and staying in the study area). However, true survival and permanent emigration cannot be teased apart using these models alone. A second class of models, so-called dead-recovery models, considers the case where marked animals are recovered dead or killed by hunters and the mark is returned to the marking institution (Brownie *et al.* 1985). The area where marks can be recovered is usually much larger than the study area, and therefore this class of models largely overcomes the problem of emigration from the study area. The strengths of both approaches can be combined, and survival can be separated from emigration, if both kinds of data, life recaptures and dead recoveries, are available. Models permitting such analyses have only recently been developed (Burnham 1993), and so far few studies have applied these methods (Frederiksen & Bregnballe 2000; Blums *et al.* 2002).

In this study, we use combined live-recapture and dead-recovery models to separate survival and emigration in a barn owl (*Tyto alba* Scopoli) population in western Switzerland. We investigate temporal variation and covariation in survival, immigration, emigration and population size, and examine factors potentially affecting variation in these demographic rates. Our study was carried out from 1990 to 2002. The population size varied between 29 and 73 breeding pairs during this time, and the geometric mean rate of population change was 1.03, suggesting that the average population size was nearly constant (Fig. 1a). We first investigate the temporal pattern in survival and emigration rates for juveniles and adults. Then we estimate the covariation between these rates and population density. Further,



**Fig. 1.** (a) Breeding population size of barn owls at our study site, and (b) weather: mean annual temperature (calculated for the period 1 March until end of February, solid line and black dots), number of days with snow cover > 5 cm (dotted line and triangles), and mean monthly precipitation between July and November (broken line and open circles).

we investigate the correlation between emigration rate, the number of known immigrants from outside the study area, and population size. Finally, we examine the relationship between survival and the stochastic variables temperature, snow cover and precipitation.

## Methods

### DATA COLLECTION

We studied *Tyto alba*, which is a medium-sized bird that preys mainly upon small mammals captured in pastures and hayfields. A detailed description of the biology of this species can be found in a recent review (Roulin 2002a). Our study was carried out in western Switzerland (46°49' N; 06°56' E; altitude 430–520 m a.s.l.). In an area covering 30 × 7 km, 110 nest-boxes were put up in barns and regularly checked to ring nestlings and breeding adults. Our study area is flanked by suitable habitat for the barn owl to the east and west, and the owls reached similar densities in the whole region. Volunteers regularly ring nestlings throughout most of the breeding range of the barn owl in Switzerland. This ringing activity, which did not include regular monitoring of the adult population, produced 85 immigrants for which we know the place and date of birth. Over the course of the study, we further encountered 249 unringed individuals, for which we have no information on their origin. We therefore define immigrants as birds ringed outside our study area. As the arrival of ringed and unringed birds to our study site was strongly correlated over time ( $r = 0.80$ ,  $N = 12$  years,  $P = 0.002$ ), our analysis was not sensitive to this definition.

We combined data on live recaptures and dead recoveries collected between March 1990 and the end of February 2002. All live recaptures were made within the boundary of our study area (190 km<sup>2</sup>), whereas dead recoveries came from an unrestricted area (birds were recovered between 0 and 758 km from their place of ringing). We used data collected on 2672 individuals (2338 ringed as nestlings and 334 ringed as adults), of which 325 (123 and 202, respectively) subsequently were recaptured at least once (1007 recaptures in total) or found dead ( $n = 205$ ).

### DESCRIPTION OF MODELS AND HYPOTHESES

The models used here consist of four components (Burnham 1993). The first component models the true survival rate,  $S$ . The second component models the recapture rate,  $P$ , which is the probability of capturing an individual at a particular occasion, given that it is alive and in the study area at that time. Thirdly, the recovery rate,  $r$ , describes the probability that a dead animal is recovered and reported. and finally, the emigration rate,  $E$ , is the probability for an individual of leaving the sampling area, given that it survived. Our study population is not particularly isolated from neighbouring barn owl populations, and thus  $E$  can be

regarded as a measure of movement relative to the size of our study area. A second measure of the same phenomenon is the distance of known movement within our study area from one year to the next. We compared the two measures and expected a strong positive correlation. In so doing, we test the correctness of our modelling approach to calculate  $E$ , and its assumption that all individuals within a particular group have the same emigration rate.

Juvenile birds often differ from adults in their propensity to disperse (Greenwood & Harvey 1982), and are subject to different kinds of hazards. Therefore, we considered models that allowed for differences between juveniles (first year of life) and adults in all four model components independently. Even though males appear to be more philopatric than females (Roulin 2002a), we could not treat the sexes differently in the analysis because the sex was unknown for most individuals. In a first step, we examined variation in all four model components between years (models 1–8, Table 1), which we counted from 1 March (onset of breeding, see Roulin 2002b) until the end of February of the following year. We assessed the correlation between survival and emigration by considering a model that constrained survival and emigration rates to fluctuate synchronously (model 9, Table 1).

In a second step, we examined whether the time variation in survival and emigration was related to population density (models 10–13, Table 1 and Fig. 1a), or weather (survival only, models 14–19, Table 1 and Fig. 1b). Several studies suggested that the number of days with significant snow cover (we chose > 5 cm) is one of the most important climatic factors driving barn owl population dynamics, because rodents and shrews become unavailable under the snow (see Roulin 2002a). We could not use prey availability directly because such data were not available. We further hypothesized that low temperature throughout the year and high autumn (July–November) precipitation could cause a higher energy demand (McCafferty, Moncrieff & Taylor 2001) or negatively affect hunting success (Michelat & Giraudoux 1992) and thus lead to higher mortality. All weather data were obtained from a meteorological station near Bern (46.55°N/7.25°E, altitude 565 m).

### STATISTICAL ANALYSIS

Capture–recapture and dead-recovery models make the assumption that each individual marked at time  $t$  has the same probability of surviving to time  $t + 1$  (Lebreton *et al.* 1992). Furthermore, these models assume that the individuals are identical in the probability of being recaptured or recovered dead, respectively (Brownie *et al.* 1985). We verified that the data met these assumptions by assessing the fit of a general, time-dependent model, which we subsequently used as starting point for model selection. As no goodness-of-fit (GOF) test exists for the complete model, we used

**Table 1.** Model selection for combined live-recapture and dead-recovery data. The fit of the models is assessed by Akaike's Information Criterion (AICc); lower values show better fit. Delta AICc gives the difference in AICc between the current model and the best model (in bold). The Akaike weights ( $w$ ) assess the relative support that a given model has from the data, compared to the other models in the set. Num. Par is the number of estimated parameters of a given model. The Deviance is the difference in  $-2 \log$  Likelihood between the current model and the saturated model, the saturated model being the one with the number of parameters equal to the sample size. *Model notation:*  $S$ , survival parameters,  $P$ , recapture parameters,  $r$ , recovery parameters,  $E$ , emigration parameters. Age dependence is symbolized by 'a-x/x', where  $x$  is a place holder for the effects on juveniles, in front of the slash, and on adults, after the slash. Both age classes are modelled as unconstrained time-dependent (t), constant over time, (.), or dependent on a covariate. The covariates were population density (= dens), days with snow cover > 5 cm (= snow), average temperature (= temp), and monthly precipitation (= precip). Some models assume that age classes vary synchronously over time, denoted by double slash (//). In model 9, survival and emigration rates vary synchronously, as indicated by brackets [ ]

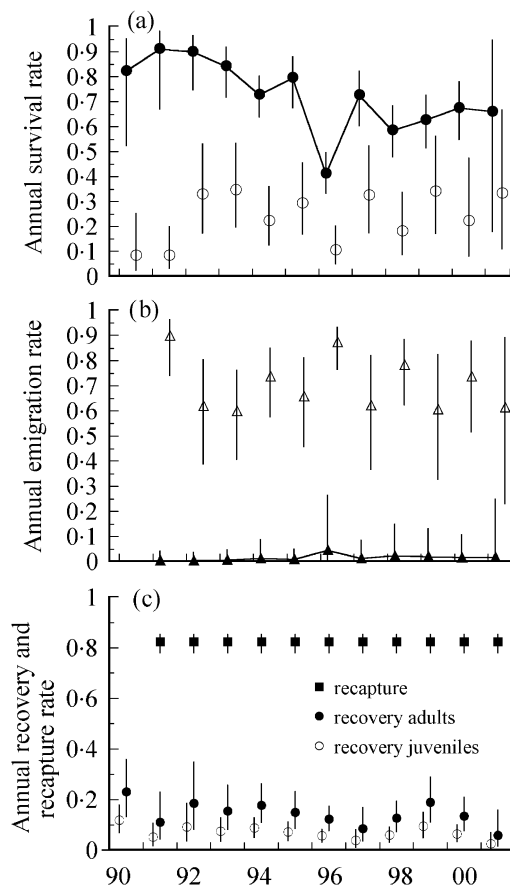
Model	AICc	Delta AICc	$w$	Num. Par	Deviance	
<b>(a) Modelling time variation in all four model components</b>						
1	$S_{a-t/t} P_{a-t/t} r_{a-t/t} E_{a-t/t}$	4330.10	40.48	0.000	88	572.12
2	$S_{a-t/t} P_{a-t/t} r_{a-t/t} E_{a-./}$	4292.78	3.16	0.126	40	634.61
3	$S_{a-t/t} P_{a-t/t} r_{a-t/t} E_{a-./}$	4301.34	11.72	0.002	29	665.63
4	$S_{a-t/t} P_{a-t/t} r_{a-t/t} E_{a-./}$	4311.09	21.47	0.000	29	675.38
5	$S_{a-t/t} P_{a-t/t} r_{a-t/t} E_{a-./}$	4346.52	56.90	0.000	29	710.81
6	$S_{a-t/t} P_{a-t/t} r_{a-t/t} E_{a-t/t}$	4295.66	6.04	0.030	49	618.99
7	$S_{a-t/t} P_{a-t/t} r_{a-t/t} E_{a-./}$	4308.17	18.56	0.000	49	631.50
8	$S_{a-t/t} P_{a-t/t} r_{a-t/t} E_{a-t/t}$	4295.85	6.23	0.027	49	619.18
9	$[S_{a-t/t} E_{a-t/t}] P_{a-t/t} r_{a-t/t}$	<b>4289.62</b>	<b>0.00</b>	<b>0.613</b>	<b>40</b>	<b>631.44</b>
<b>(b) Effect of population density on survival and emigration</b>						
10	$S_{a-dens/t} P_{a-t/t} r_{a-t/t} E_{a-./}$	4305.56	15.94	0.000	30	667.82
11	$S_{a-t/dens} P_{a-t/t} r_{a-t/t} E_{a-./}$	4334.18	44.56	0.000	30	696.43
12	$S_{a-t/t} P_{a-t/t} r_{a-t/t} E_{a-dens/}$	4294.82	5.20	0.045	41	634.59
13	$S_{a-t/t} P_{a-t/t} r_{a-t/t} E_{a-./dens}$	4292.96	3.34	0.115	41	632.74
<b>(c) Effect of weather (alone and in combination with density) on survival</b>						
14	$S_{a-snow/t} P_{a-t/t} r_{a-t/t} E_{a-./}$	4298.57	8.95	0.007	30	660.82
15	$S_{a-temp/t} P_{a-t/t} r_{a-t/t} E_{a-./}$	4301.01	11.39	0.002	30	663.26
16	$S_{a-precip/t} P_{a-t/t} r_{a-t/t} E_{a-./}$	4312.95	23.33	0.000	30	675.20
17	$S_{a-t/snow} P_{a-t/t} r_{a-t/t} E_{a-./}$	4328.24	38.62	0.000	30	690.50
18	$S_{a-t/temp} P_{a-t/t} r_{a-t/t} E_{a-./}$	4341.93	52.31	0.000	30	704.18
19	$S_{a-t/precip} P_{a-t/t} r_{a-t/t} E_{a-./}$	4321.12	31.50	0.000	30	683.37
20	$S_{a-dens+snow/t} P_{a-t/t} r_{a-t/t} E_{a-./}$	4295.80	6.18	0.028	31	656.02
21	$S_{a-t/dens+snow} P_{a-t/t} r_{a-t/t} E_{a-./}$	4318.90	29.28	0.000	31	679.12

separate GOF tests provided by program RELEASE (Burnham *et al.* 1987), and program ESTIMATE (Brownie *et al.* 1985) for the live recapture and dead recovery data, respectively. For both data types, the GOF test showed that models taking into account age effects fitted the data well (live recaptures: Tests 2 + 3, excluding Test 3.SR for birds ringed as nestlings, in program RELEASE:  $\chi^2 = 52.6$ , d.f. = 44,  $P = 0.18$ ; dead recoveries: model 0 in program ESTIMATE:  $\chi^2 = 21.0$ , d.f. = 35,  $P = 0.90$ ). We found no evidence for overdispersion in our data (combining the GOF test statistics for both data types ( $\Sigma\chi^2/\Sigma df = \hat{c}$ ):  $73.6/78 = 0.94$ ) and thus no evidence for deviation from the assumption that the fates of the individuals are independent of each other, i.e. that the data follow a multinomial distribution (Anderson, Burnham & White 1994).

All models were run in program MARK (White & Burnham 1999). We followed basic capture-mark-recapture methodology (Lebreton *et al.* 1992), and based model selection on the small-sample-size adjusted Akaike's information criterion (AICc) (Burnham & Anderson 2002). The model with the lowest AICc is the most parsimonious model, and provides the best

description of the structure in the data as it is the best balance between overfitting (hence loss of precision) and underfitting (hence bias) of the data (Burnham & Anderson 2002).

We used two different methods to calculate the amount of variation in survival or emigration explained by the covariates population density, snow cover, temperature and precipitation. As a first method, we used the analysis of deviance (Skalski, Hoffmann & Smith 1993):  $V = [\text{deviance}(\text{constant model}) - \text{deviance}(\text{covariate model})] / [\text{deviance}(\text{constant model}) - \text{deviance}(\text{time-dependent model})]$ . This method estimates the proportion (V) of total variance in time explained by a particular covariate. As a second method, we used random effects models, which partition the total variance into its two components, process variance and sampling variance (Link & Nichols 1994; see Burnham & White 2002; Loison *et al.* 2002; [http://www.cnr.colostate.edu/class\\_info/fw663/Mark.html](http://www.cnr.colostate.edu/class_info/fw663/Mark.html) for details). Using this method, we calculated the proportion of process variance explained by a particular covariate. Each of these two approaches has its weaknesses. The analysis of deviance fails to distinguish between process and sampling variance, whereas the



**Fig. 2.** (a) Survival rates, (b) probability of leaving the study area during one year (emigration), and (c) probability of being recaptured alive (recapture rate) or found and reported dead (recovery rate). Filled symbols are for adults, open symbols for juveniles, except for recapture rates, which were equal between the age classes. Vertical bars give the 95% confidence interval of the estimates. Estimates are from model [ $S_{a-t/t}$ ,  $F_{a-t/t}$ ],  $P$ ,  $r_{a-t/t}$ ] (Table 1).

random effects based method is subject to estimation uncertainty, especially when short time series are used. We therefore used both methods and supported those estimates for which both methods agree.

## Results

### TEMPORAL PATTERNS IN SURVIVAL AND EMIGRATION

Model selection clearly favoured the model with time-dependent survival, emigration and recovery rates, and constant recapture rates (model 9, Table 1, Fig. 2a–c). This model constrained survival and emigration rates to vary synchronously, and was 20 times (ratio of  $w$ :  $0.613/0.030 = 20.4$ ) better supported than a model with unconstrained time variation in the two demographic rates (model 6). Model selection therefore clearly favoured the hypothesis that survival and emigration rates were correlated over time (Fig. 3a). The selected model also shows that survival and recovery rates were lower, and emigration rates higher for juvenile compared to adult birds (Fig. 2a–c).

Survival rates of juvenile and adult owls showed considerable time variation around a mean of 0.172 (SE = 0.045) and 0.720 (SE = 0.044), respectively (Fig. 2a). The probability of juvenile birds leaving the study area varied around a mean of 0.746 (SE = 0.048, Fig. 2b), whereas adults hardly moved out of the study area at all (emigration rate 0.010, SE = 0.014). Models constraining survival or emigration to be constant in either age class (e.g. models 4, 5, 7 and 8 compared to model 9, Table 1) had a markedly higher deviance, and were poorly supported by the data.

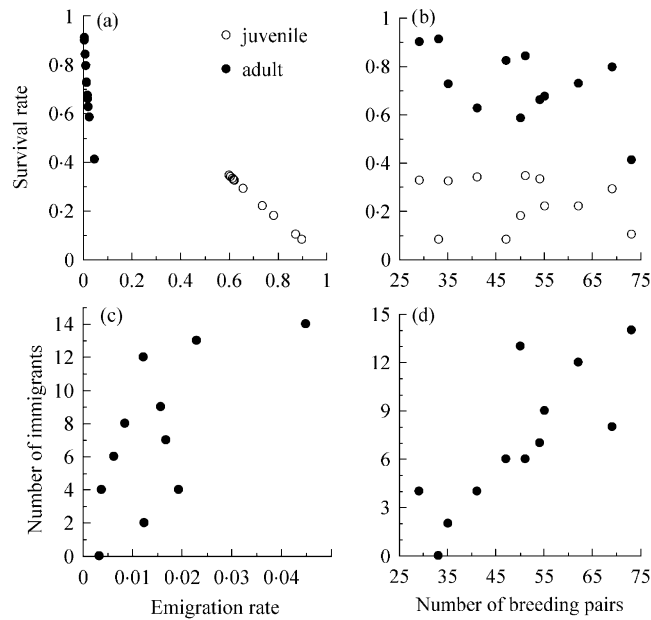
### EMIGRATION, IMMIGRATION AND POPULATION SIZE

Over the 12 years of our study, 85 adult individuals, which were ringed outside our study area, immigrated. They had travelled 6–155 km from their place of ringing, and 59 of them had been ringed as nestlings in the previous year. The number of immigrants arriving each year positively correlated with breeding population size (Fig. 3d,  $N = 12$ ,  $r = 0.80$ ,  $P = 0.002$ ). We incorporated the number of immigrants as a covariate into the modelling framework (using model 2, Table 1) and found that it was positively related to adult emigration (Fig. 3c, coefficient on the logit scale: 11.35, SE = 0.78; model AICc = 4291.65), indicating that factors associated with variation in dispersal acted synchronously at a larger spatial scale.

We compared the estimates of adult emigration rate to the average distance between the breeding sites of the same individual in two consecutive years within our study area (breeding dispersal). Incorporation of local movement as a covariate into the modelling framework (using model 2, Table 1) yielded a close correspondence between local movement and the adult emigration rate (coefficient on the logit scale: 40.34, SE = 7.65; model AICc = 4293.05).

### ENVIRONMENTAL AND DENSITY EFFECTS ON SURVIVAL AND EMIGRATION

The covariates population density, snow cover, temperature, and precipitation explained up to half of the variation in survival and emigration (Table 2), even though the inclusion of these covariates did not result in a better supported model (models 10–21). The analysis of deviance and the method based on random effects models suggested that snow cover and temperature were important for juvenile survival, and autumn precipitation and population density for adult survival (Table 2). The joint effect of snow cover and population density did not explain more variation than one of the covariates alone in either case. According to both methods, autumn precipitation had very little effect on juvenile survival. In some cases, the random effects method yielded negative estimates or higher estimates than the analysis of deviance. This probably



**Fig. 3.** Correlations between demographic variables: (a) survival rate vs. emigration rate, (b) survival rate vs. breeding population size, (c) number of immigrants vs. adult emigration rate, and (d) number of immigrants vs. breeding population size. Survival and emigration rates were estimated by model  $[S_{a-t} F_{a-t}] P, r_{a-t/t}$  (Table 1).

**Table 2.** Proportion of the temporal variance in survival explained by snow cover, annual temperature, precipitation during the autumn, and population density. We used two methods for calculation. (1) The residual variance ( $\sigma_{res}^2$ ) of the respective random effects models is shown. The proportion of process variance explained by a particular covariate is then  $(\sigma_{res, unconstrained\ time\ dependence}^2 - \sigma_{res, covaria}^2) / \sigma_{res, unconstrained\ time\ dependence}^2$  (Loison *et al.* 2002). (2) The proportion of total variance (process variance + sampling variance) explained by a covariate was calculated by analysis of deviance (Skalski *et al.* 1993)

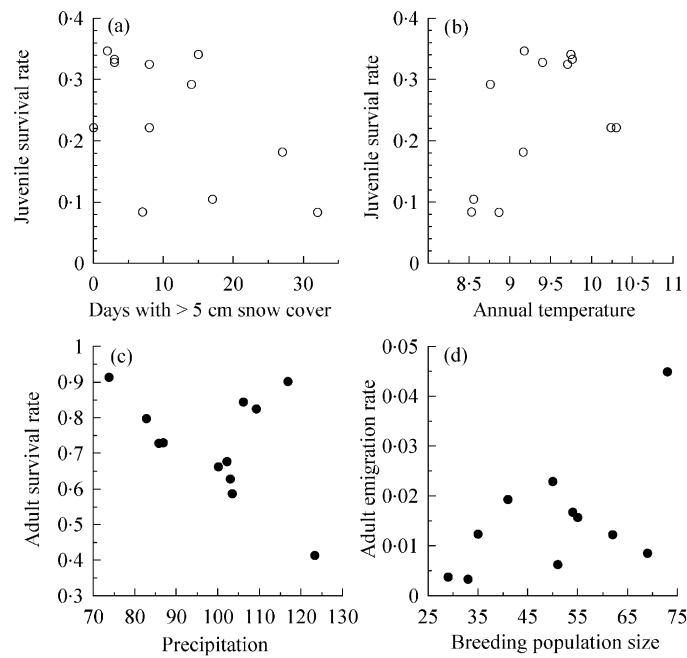
Covariate	Juvenile survival			Adult survival		
	$\sigma_{res}^2$	Proportion of process variance	Proportion of total variance	$\sigma_{res}^2$	Proportion of process variance	Proportion of total variance
Unconstrained time dependence	0.008			0.018		
Snow	0.004	0.469	0.357	0.017	0.059	0.267
Temperature	0.004	0.420	0.297	0.020	-0.110	0.087
Autumn precipitation	0.009	-0.234	0.004	0.016	0.104	0.360
Density	0.008	-0.024	0.185	0.013	0.307	0.189
Density + snow	0.004	0.424	0.475	0.012	0.320	0.416

reflects imprecise estimation of the random effects method as a result of the short time series, which may be at the lower limit for applying this method (Burnham & White 2002). The analysis of deviance showed that population density explained 1% and 60% of the variation in juvenile and adult emigration, respectively.

Survival of juveniles and adults was negatively related to population density (Fig. 3b, coefficient, on the logit scale:  $-1.5$ , SE = 0.56, and  $-0.16$ , SE = 0.04) and to the number of days with snow cover (Fig. 4a,  $-4.16$ , SE = 1.14, and  $-4.31$ , SE = 0.97), and positively related to temperature (Fig. 4b, 5.8, SE = 1.74, and 3.0, SE = 1.25). Autumn precipitation negatively correlated with adult survival (Fig. 4c,  $-2.9$ , SE = 0.57), and the effect of population density on adult emigration was 22.96 (SE = 0.76) (Fig. 4d).

### Discussion

This study investigates the temporal patterns in survival and dispersal in a Swiss barn owl population. Using live-recapture and dead-recovery data simultaneously, we were able to tease apart survival and emigration (Burnham 1993), and to examine the factors that potentially cause variation in the two demographic rates separately. Our estimates of annual survival rates are thus estimates of true survival and not confounded with variation in emigration tendencies. We found that juvenile survival was worse and they were more likely to emigrate than adults. Juvenile and adult survival and emigration rates varied over time. Population density and winter harshness explained up to 48% of this variation. There was a strong covariation between



**Fig. 4.** Correlations between survival and environmental variables (a–c), and adult emigration and population size (d). Survival and emigration rates were estimated by model  $[S_{a-t}/F_{a-t}] P_{a-t/t}$  (Table 1).

survival and emigration as more owls emigrated in years when survival was low. Furthermore, the emigration rate positively correlated with the number of immigrants in any year, and with population size.

Our estimates of annual survival, on average 72% for adults and 17% for juveniles, correspond well with earlier studies, which reported estimates between 40% and 80% for adults and between 15% and 35% for juveniles (Sauter 1956; Bairlein 1985; De Bruijn 1994; Taylor 1994). Also in agreement with these studies, which analysed recoveries of dead barn owls, we found that survival rates fluctuate markedly over time. However, our study further showed that the variation in the probability of recovering dead birds has to be accounted for in order to get correct estimates for survival and its temporal variation. We found that the recovery rates varied over the years and were lower for juvenile birds than for adults (see Fig. 2c). A possible reason for variation in recovery rates is variation in death causes and seasonal occurrence of mortality (e.g. in years when many owls starve inside barns, the probability of recovery by humans is higher).

In our population, up to 48% of the time variation in both juvenile and adult survival was attributable to variation in weather or population density (see Table 2). When we attempted to account for sampling variation, our analysis suggested that variation in juvenile survival was mainly affected by snow cover and temperature, whereas variation in adult survival was mostly affected by population density. These results were confirmed by the analysis of deviance. However, the length of our study may be at the lower limit to reliably attribute the variance in survival to external factors. Nevertheless, our findings add to

the studies showing that natural populations are driven by a combination of density dependence and stochastic environmental factors, and often different factors affect different parts of the population (Leirs *et al.* 1997; Dennis & Otten 2000; Gaillard *et al.* 2000; Sæther *et al.* 2000; Coulson *et al.* 2001). In our study, survival was generally lower in years with long-lasting snow cover and low temperatures. The consequences of such environmentally mediated variation in survival for population dynamics depends on how sensitive the dynamics are to variation in the affected fitness component. The sensitivity of population dynamics to the various fitness components is determined by the life history of a species (Caswell 2001). In barn owls and other bird species with early age at maturity and a large clutch size, the population growth rate is more sensitive to variation in adult than juvenile survival (Sæther & Bakke 2000; Hone & Sibly 2002). Our results thus suggest that weather mostly affected a fitness component that is more loosely related to population dynamics, whereas population density affected a fitness component with a stronger relation to dynamics.

Survival significantly decreased with increasing population size. This result, however, hinges primarily on the association between the particularly high population size in 1996 and the lowest observed survival rate in that year. Any unobserved variable could have caused the high mortality which led to a population crash and introduced apparent density dependence into our data. One candidate for this unobserved variable is rodent density, which has been shown to be important for barn owl population dynamics (Taylor 1994; Hone & Sibly 2002).

In the middle of the last century, European barn owl populations crashed following severe winters (Schifferli 1949; Sauter 1956; Güttinger 1965; Bairlein 1985). It was therefore suggested that barn owl population dynamics are strongly affected by winter harshness. Our results showed that a considerable amount of variation in at least juvenile survival is explained by variation in snow cover. Our estimate is likely to be lower than the true long-term effect, because the winters covered by our study were all relatively mild. Our findings are consistent with the hypothesis of Güttinger (1965), who proposed that only extraordinarily harsh winters cause high mortality and that the population dynamics are driven by other factors, such as vole abundance, in normal years (Taylor 1994). The effect of harsh winters promotes synchronized population dynamics at the regional scale, whereas a dependence on local factors tends to desynchronize dynamics (Ranta *et al.* 1995; Koenig 1999). Apparently, in some years barn owl populations of several European countries crashed simultaneously, suggesting some degree of large-scale synchrony in the population dynamics of this species (Giraudoux, Michelat & Habert 1990).

Young owls emigrated out of our study area far more often than adult individuals. Natal dispersal therefore occurred more often than breeding dispersal, which is typical for birds (Greenwood & Harvey 1982). Emigration of juvenile and adult owls varied between years, and the variation in adult emigration was mirrored by variation in dispersal within the study area. This suggests that our method of estimating emigration worked well, and that dispersal at the local and regional scale were correlated over the years.

We found strong positive correlations between the temporal patterns of emigration, immigration, mortality and population size. This result is consistent with the observation that some years with especially harsh winter conditions lead to low survivorship, high mobility and subsequent crashes in barn owl populations (Schifferli 1949; Sauter 1956; Bairlein 1985; De Bruijn 1994). A positive correlation between emigration and population size is predicted to lead to faster colonization of empty habitat patches and to a higher population growth rate at the regional scale (Sæther, Engen & Lande 1999). On the other hand, a positive correlation between immigration and population size, as observed in our study, is predicted to have the opposite effect. The pattern of dispersal in our study population is thus unlikely to greatly alter the regional population dynamics compared to the case of random dispersal.

Two slightly different processes affecting dispersal are predicted to lead to different patterns of covariation between emigration, immigration, survival and population size. The source–sink hypothesis predicts a net flow of individuals from highly productive areas to low productive areas, whereas the balanced dispersal hypothesis predicts the exchange of an equal number of individuals between any two areas (Pulliam 1988; McPeck & Holt 1992). Under the source–sink process,

years with good survival and high population size would produce a higher proportion of individuals that cannot settle locally, and thus lead to a higher emigration rate. In contrast, the balanced dispersal process always produces a similar number of migrants, and therefore in years with high population sizes, the proportion of emigrants and immigrants is relatively low. The positive associations between emigration, immigration, mortality and population size in our study population are not fully compatible with either of these hypotheses. Rather our results suggest that barn owl populations in western Switzerland are subject to fluctuating environmental conditions causing high mortality and forcing individuals to leave the area in some years. During the years of our study, this happened when population sizes were high, and the correlation between emigration and immigration suggested that the driving environmental factors operate at the regional rather than the local scale. Our results indicated that temperature, snow cover and precipitation may, in part, be responsible for these fluctuations.

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