Demographic Processes Underlying Population Growth and Decline in *Salamandra salamandra*

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Abstract: *Human activity commonly has negative impacts on wildlife. Often, however, only a single element of the life cycle is affected, and it is unclear whether such effects translate into effects on population growth. This is particularly true for research into the causes of global amphibian declines, where experimental research focuses primarily on the aquatic larval stages but theory suggests these stages have only minor importance for population growth. We used data from long-term mark-recapture studies of two natural populations of the salamander* Salamandra salamandra *to confirm the predictions of population models. One population remained stable (i.e., stationary) throughout the 20 years of the study whereas the other declined to local extinction. We used mark-recapture models to break down population growth rate into its two main components, recruitment and adult survival. Survival of postmetamorphic salamanders was constant over time in the stable population, whereas the declining population was characterized by a decrease in survival and constant recruitment. Population growth was most sensitive to variation in adult survival. Current amphibian research focuses on preadult stages, and researchers assume recruitment is the most important determinant of population growth. This may not be the case. A better understanding of amphibian population dynamics is possible only through the integration of experiments, theory, and data from natural populations. Our results also suggest that amphibian conservation efforts should focus on all stages of the life cycle and their associated habitats.*

Key Words: adult survival, amphibian, demography, global amphibian decline, multistate mark-recapture model, population growth, recruitment

Procesos Demográficos Subyacentes en el Crecimiento y Declinación Poblacional de *Salamandra salamandra*

Resumen: *La actividad humana comúnmente tiene impactos negativos sobre la vida silvestre. Sin embargo, a menudo solo se afecta a un elemento del ciclo de vida, y no es claro si tales efectos se traducen en efectos sobre el crecimiento de la población. Esto aparentemente es cierto para la investigación sobre las causas de las declinaciones globales de anfibios, donde la investigación experimental enfoca primariamente a las etapas larvarias acuáticas pero la teoría sugiere que estas etapas solo tienen poca importancia para el crecimiento de la población. Utilizamos datos de estudios de marcaje-recaptura de largo plazo de dos poblaciones naturales de la salamandra* Salamandra salamandra *para confirmar las predicciones de los modelos poblacionales. Una población permaneció estable durante los 20 años del estudio mientras que la otra declinó hasta la extinción local. Utilizamos un modelo de marcaje-recaptura para desagregar a la tasa de crecimiento poblacional en sus componentes principales, reclutamiento y supervivencia de adultos. La supervivencia de salamandras postmetamórficas fue constante en el tiempo en la población estable, mientras que la población declinante se caracterizó por un decremento en la supervivencia y un reclutamiento constante. El crecimiento de la población fue más sensible a la variación en la supervivencia de adultos. La investigación actual sobre anfibios se centra en etapas preadultas, y los investigadores asumen que el reclutamiento es el factor determinante del crecimiento poblacional. Este puede no ser el caso. Un mejor entendimiento de la dinámica poblacional de anfibios sólo es posible mediante la integración de experimentos, teoría y datos de poblaciones naturales.*

Nuestros resultados también sugieren que los esfuerzos para la conservación de anfibios deben abarcar a todas las etapas del ciclo de vida y sus hábitats asociados.

Palabras Clave: anfibio, crecimiento poblacional, declinación global de anfibios, demografía, modelo multiestado de marcaje-recaptura, reclutamiento, supervivencia de adultos

Introduction

Human activity often has negative effects on wildlife. Many human activities such as fishing and hunting, use of pesticides, killing of animals on roads, or contamination of the environment with endocrine disruptors often affect only a single vital rate or a single life-history stage. For example, hunting affects only mortality, whereas exposure to endocrine disruptors alters fertility through changes in morphology or physiology. Whether these negative effects matter from a conservation point of view depends on whether and how strongly they affect population growth rate (e.g., Burnham & Anderson 1984; McPeek & Peckarsky 1998; Forbes & Calow 2002). If density affects population growth, then the negative effects of human activity may be buffered or cancelled out completely (Forbes & Calow 2002; Sutherland & Norris 2002; Vonesh & De la Cruz 2002). Much experimental work in conservation biology, however, focuses on single elements of the life history of the species under study, and little attention is paid to effects on population growth rate (Biek et al. 2002; Forbes & Calow 2002; Vonesh & De la Cruz 2002) even though population growth is the focus of population viability analyses (Crouse et al. 1987; Fujiwara & Caswell 2001; Forbes & Calow 2002).

Experimental research into the causes of global amphibian population declines (Alford & Richards 1999; Houlahan et al. 2000; Collins & Storfer 2003) has focused primarily on individual- rather than population-level effects (e.g., Kiesecker et al. 2001; Boone & Bridges 2003). Experimental research probably focuses on the egg and larval stages either because experimental research on terrestrial amphibian life stages is difficult or because most amphibian ecologists assume tacitly or explicitly that the aquatic stage (i.e., variation in gains) drives amphibian population dynamics (Wilbur & Collins 1973; Wilbur 1980; Pechmann & Wilbur 1994; Alford & Richards 1999; Kiesecker et al. 2001; Boone & Bridges 2003; Semlitsch 2003). For example, Semlitsch (2003) writes that the success of amphibian populations is believed to be determined primarily by the number and quality of metamorphosing larvae leaving a pond and thus the number recruiting into the terrestrial adult population. A number of recent population models, however, suggest that the juvenile and adult terrestrial stages (i.e., variation in losses) are the most important determinants of population growth (Taylor & Scott 1997; Biek et al. 2002; Hels & Nachman 2002; Vonesh & De la Cruz 2002). These models suggest that negative effects on eggs and larvae may not translate into population declines. Indeed, such a link between individual-level effects and population declines has not yet been empirically demonstrated (Biek et al. 2002; Vonesh & De la Cruz 2002; Blaustein et al. 2003).

Confirmation or rejection of the predictions of the mathematical population models and analyses of the demographic processes underlying the population dynamics of natural populations are needed. Reliable demographic data for all stages of the complex life cycle of amphibians are difficult to collect and therefore are rarely available (e.g., Biek et al. 2002; Vonesh & De la Cruz 2002) and often of unknown quality (Schmidt et al. 2002). With modern mark-recapture methods it is possible to estimate contributions to population growth rate based on data from adults only. Nichols et al. (2000) pointed out that population growth rate (λ_i) can be expressed as the sum of local adult survival (ϕ_i) and recruitment (f_i):

$$\lambda_i = \phi_i + f_i. \tag{1}$$

Thus, estimation of survival and recruitment probabilities allows one to determine which process is the most important determinant of the observed population growth rates (Nichols et al. 2000), and one can empirically answer the question of which of the two demographic components (gains or losses) is responsible for the observed change in population growth rate. Therefore, the mark-recapture models of Nichols et al. (2000) are a powerful approach to address important questions in conservation biology because these models can be used to better understand the demography of natural populations and to confirm or reject predictions of population models.

Based on data from long-term mark-recapture studies of two natural populations of the fire salamander (*Salamandra salamandra terrestris*), we empirically estimated the relative contributions of recruitment (i.e., gains that include in situ reproduction and immigration) and local adult survival (i.e., losses that could result from mortality or emigration) to amphibian population growth rate.

Methods

The Species and Data Collection

S. salamandra is a terrestrial salamander. During spring, females migrate to small forest streams where they give birth to larvae. After about 2 months, larvae undergo

metamorphosis. Juveniles and adults live in montane beech (*Fagus sylvatica* L.) forest near the streams (Thiesmeier & Günther 1996; Thiesmeier & Grossenbacher 2004). *S. salamandra* has been declining in parts of Europe (Homolka & Kokes 1994; Martínez-Solano et al. 2003; B.R.S., unpublished data) and is on the red list of several European countries (e.g., Spain, Switzerland).

We sampled two populations of the fire salamander annually during their hibernation near Fredeburg and Littfeld, Germany, from 1965 to 1985 and from 1965 to 1982, respectively (Feldmann 1967, 1987). Their hibernation sites were two abandoned mine tunnels situated within the beech forest and were used by juveniles and adults. Salamanders were captured, photographed, and released immediately. Each salamander has a unique pattern of yellow spots that allows individual identification, so no marking is necessary (Feldmann 1967). Salamanders were all postmetamorphic but not necessarily adult. In total, we captured and photographed 376 different individuals in the Fredeburg population and 181 individuals in the Littfeld population (Feldmann 1987).

Testing for a Trend in Population Size

We tested for temporal trends in population size by regressing $\log_e$-transformed population counts against year of observation. Thus, the slope of the regression estimates an annual proportional change (rather than absolute numbers) in population size. We used information-theoretic model selection (Burnham & Anderson 2002) to assess whether a model that includes a trend is better supported by the data than a model that assumes no change (i.e., we compared the models ln[population count] = intercept + slope $*$ year and ln[population size count] = intercept). Standard errors of regression parameters were estimated with a bootstrap procedure (Meyer et al. 1998). We used Akaike weights (a posterior model probability; Burnham & Anderson 2002) to calculate model-averaged slopes and standard errors that account for model selection uncertainty (Burnham & Anderson 2002; Wintle et al. 2003).

Estimating Demographic Rates

We estimated three demographic parameters: local survival (ϕ_i), recruitment (f_i), and seniority probabilities (γ_{i+1}). In this salamander species, f_i refers to the aquatic larval stage (it is a summary statistic of litter size, larval survival, and other such parameters) and immigration, whereas ϕ_i refers to terrestrial juveniles and adults. Because we had no data on size at first capture, we could not differentiate between juveniles and adults. They were therefore both combined into the "losses" (ϕ_i) component of population growth.

Survival probabilities can be estimated using standard mark-recapture methodology (Lebreton et al. 1992). Local survival is affected by both mortality and permanent emigration. The estimation of recruitment and seniority

is based on reverse-time mark-recapture methods (Pradel 1996; Nichols et al. 2000). Local recruitment is defined as the number of new animals in the population at time *i* per animal in the population at time *i*-1 (Pradel 1996), and it includes in situ reproduction and immigration. The seniority probability γ_{i+1} is the probability that an individual present in the population at time $i+1$ was present in the population already at time *i*. Additionally, γ_{i+1} measures retrospectively the elasticity of population growth rate (λ_i) to changes in ϕ_i (Nichols et al. 2000; Nichols & Hines 2002). If $\gamma > 0.5$, adult survival contributes more to population growth than recruitment (Nichols et al. 2000). Survival, recruitment, seniority probabilities, and population growth rate are linked through the equality $\lambda_i = \phi_i + f_i = \phi_i/\gamma_{i+1}$ (Nichols & Hines 2002).

The first step in the process leading to parameter estimation was to perform goodness-of-fit tests to check which model should be used for parameter estimation. We used the program U-Care (Choquet et al. 2003) to perform goodness-of-fit tests of the Cormack-Jolly-Seber (CJS) model (Lebreton et al. 1992). The goodness-of-fit tests indicated significant lack of fit only for the Fredeburg population ($\chi^2_{72} = 152.1$, $p < 0.001$; Littfeld: $\chi^2_{54} = 60.8$, $p = 0.24$). Inspection of the goodness-of-fit test for the Fredeburg population suggested the presence of transients and nonrandom temporary emigration. Both transients and temporary emigration may be common in amphibian populations (Schmidt et al. 2002). Temporary emigration suggests that salamanders show only partial fidelity to the hibernation site (where we sampled the population). That is, they may hibernate somewhere else in some years.

To get unbiased survival estimates, we built a novel multistate model with unobservable states. The model combines the transients-only model (Pradel et al. 1997; Schaub et al. 2004a) and the temporary-emigration-only model (Kendall & Nichols 2002; Schaub et al. 2004b) and can be described by a transition matrix and vectors of state-specific survival and recapture probabilities

$$
\begin{array}{c}
\text{initial} \\
\text{transient} \\
\text{nontransient, present} \\
\text{nontransient, absent}
\end{array}
\begin{bmatrix}
0 & \tau & (1-\tau)(1-e) & (1-\tau)e \\
0 & 1 & 0 & 0 \\
0 & 0 & (1-e) & e \\
0 & 0 & i & (1-i)
\end{bmatrix}_i
$$

$$
\begin{bmatrix} \phi \\ 0 \\ \phi \\ \phi \end{bmatrix}_i
\begin{bmatrix} 0 \\ 0 \\ p \\ 0 \end{bmatrix}_i, \qquad (2)
$$

where τ_i is the probability that a salamander caught for the first time at *i* is a transient; e_i is the probability that a nontransient salamander at the study site at *i* emigrates temporarily from the study site shortly before $i+1$; i_i is the probability that a nontransient salamander not at the study site at *i* returns to the study site shortly before $i+1$ (*e* and *i* describe emigration from and immigration to, respectively, the hibernation site [where salamanders were

sampled] and not dispersal to and from other populations); ϕ_i is the probability that a nontransient salamander survives from i to $i+1$; and p_i is the probability that a nontransient salamander alive and at the study site at i is recaptured at i.

The capture histories were adjusted to fit the model to the data. Occasions when an individual was not seen were coded with a 0, the occasion when the individual was first encountered was coded with a 1 ("initial" state), and the occasions when the individual was reencountered were coded with a 3 ("nontransient, present" state) in the individual capture history vector. The states "transient" and "nontransient, absent" do not occur in the capture histories but need to be specified when setting up the model in the program MARK (White & Burnham 1999).

For the Littfeld population, where the goodness-of-fit test was not significant, we used standard and reverse-time mark-recapture models to estimate survival, seniority, and recruitment probabilities (Pradel 1996; Nichols et al. 2000). We used MARK (White & Burnham 1999) for model selection and parameter estimation. Parameters (survival, capture, seniority, recruitment, and transition probabilities) in candidate models were allowed to vary over time (denoted by subscript t), to show a linear trend (T), or to be constant (the subscript is a dot in that case). Model selection was based on the small-sample Akaike's information criterion (AIC_c; Burnham & Anderson 2002). To account for model selection uncertainty (Wintle et al. 2003), parameter estimates were averaged across all candidate models, whereby each parameter of each model was weighed by the Akaike weight of the corresponding model (Burnham & Anderson 2002).

Results

Based on population counts, one population remained stable through the 20 years of the study, whereas the other declined to local extinction (Fig. 1). The Littfeld population declined annually by 12.9% (SE 1.1%). A model with a trend had an Akaike weight of 1.0, whereas a model assuming no trend was not supported by the data at all. The Fredeburg population showed strong fluctuations but remained stable (−0.6% [SE 0.2%] per year). A model with no trend was better supported by the data than a model with a trend (Akaike weights were 0.63 and 0.37, respectively).

Model-averaged parameter estimates showed a weak increasing trend of adult survival probabilities in the stable Fredeburg population (from 0.87 [SE 0.02] to 0.89 [0.02]; Fig. 2, Table 1). In that population, we could not estimate seniority and recruitment probabilities because the goodness-of-fit tests suggested there were both transients and temporary emigrants. Consequently, the elasticity of population growth rate with respect to adult survival could not be assessed (Nichols & Hines 2002).
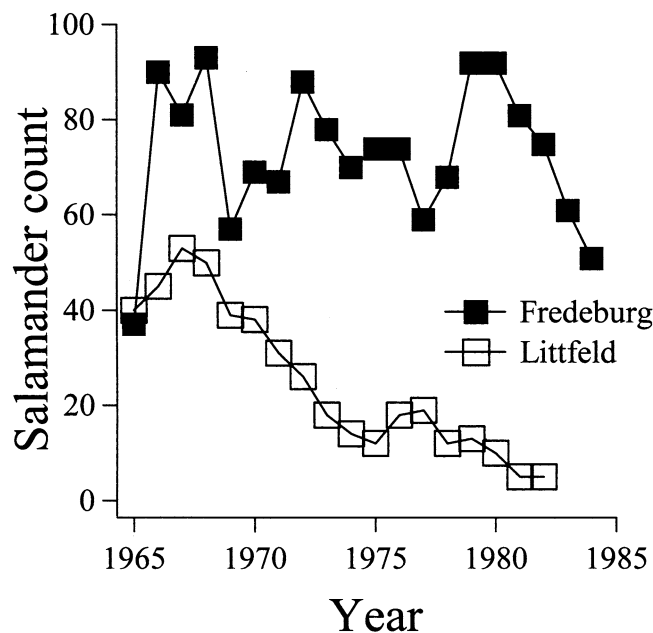

Figure 1. Time series of two populations of the salamander Salamandra salamandra. *Data points are salamander counts at the hibernation sites. Population surveys were halted earlier in the Littfeld population.*

The declining Littfeld population was characterized by a strong negative trend in survival probabilities (from 0.78 [SE 0.03] to 0.57 [0.05]) and a weak increasing trend in recruitment probabilities (from 0.20 [0.03] to 0.22 [0.04], Fig. 2, Table 1). The slight increase in recruitment probabilities did not halt the population decline. To balance the observed relative decline in survival of 26%, a relative increase of recruitment by 104% would have been necessary. This is because the elasticity of population growth rate with respect to adult survival was high (γ_i slightly declined over the years of the study from 0.79 [0.03] to 0.74 [0.06]). Therefore, a relative change in the loss component resulted in a 3-4 (calculated as $\gamma/(1-\gamma)$; Nichols et al. 2000) times stronger change in population growth rate than an equal relative change in the gain component. Population growth was negative in all years, albeit close to 1 in the early years of the study. Because survival probabilities decreased, the decline in the Littfeld population accelerated.

Discussion

The results of our demographic analyses showed that variation in local adult survival was most important for salamander population trends. In the stable (i.e., stationary) Fredeburg population adult local survival was constant over time, but survival decreased strongly in the declining Littfeld population. Moreover, a relative change in
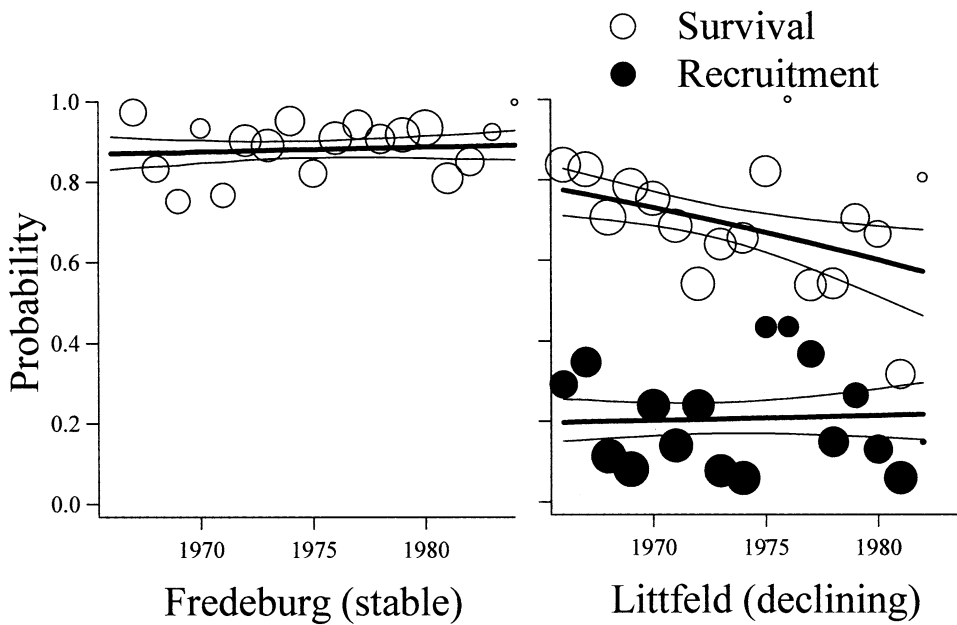
Figure 2. Demography of two populations (Fredeburg and Littfeld) of the salamander Salamandra salamandra. *Symbols represent parameter estimates from models in which parameters were allowed to vary with time (Fredeburg: ϕ_t, τ., e., d., p_t, Littfeld: ϕ_t, p., f_t) even if the models had little support from the data (Fredeburg: Akaike weight w = 0.01; Littfeld w < 0.01). The thick line represents model-averaged parameter estimates (thin lines are 95% unconditional CI). The size of the symbols is inversely proportional to the standard error.*

local adult survival resulted in a much stronger change in population growth than a similar relative change in local recruitment. Thus, the importance of losses in the adult stage, and local adult survival in particular, for population growth rate in this relatively long-lived salamander appears to be similar to other "classic" long-lived vertebrates such as turtles, ungulates, and whales (Crouse et al. 1987; Gaillard et al. 1998; Fujiwara & Caswell 2001).

Table 1. Selection of models for the estimation of survival, seniority, and recruitment probabilities of salamanders and testing hypotheses on the demographic parameters.*

Model description and parameters estimated	Parameters	ΔAIC_c	Akaike weight
Fredeburg population survival			
ϕ., τ., e., i., p_t	24	0.00	0.53
ϕ_T, τ., e., i., p_t	25	0.32	0.45
ϕ_t, τ., e., i., p_t	42	8.36	0.01
Littfeld population seniority			
γ., p.	2	0.00	0.53
γ_T, p.	3	0.24	0.47
Littfeld survival and recruitment			
ϕ_T, f., p.	4	0.00	0.65
ϕ_T, f_T, p.	5	1.40	0.32
ϕ., f., p.	3	7.26	0.02
ϕ., f., p_T	4	8.52	0.01

**The table shows the candidate models, as selected by AIC_c, that have an Akaike weight (a posterior model probability) ≥ 0.01. The ΔAIC_c is the difference between the AIC_c-selected best model and the given model. Parameters in the models are ϕ, survival; τ, transients; e, emigration; i, immigration; p, capture; γ, seniority; and f, recruitment probabilities. Subscripts: t, time-variant parameters and T, linear trend in the parameter; a dot (.), time-invariant parameters.*

The importance of the adult stage contradicts, at least for this species, the popular and often tacit assumption of ecologists and conservationists that amphibian population dynamics are governed by the larval stage (e.g., Wilbur & Collins 1973; Kiesecker et al. 2001; Semlitsch 2003) and supports increasing awareness of the crucial importance of the terrestrial juvenile and adult terrestrial stages (Denton et al. 1997; Biek et al. 2002; Vonesh & De la Cruz 2002).

The decline in the Littfeld population may be the result of a change in forest management that lowered the quality of the terrestrial environment (Feldmann 1987). The deciduous forest (mainly beech, *Fagus sylvatica* L.) surrounding the hibernation site was clearcut in the late 1960s and was replaced by conifers (spruce, *Picea abies* [L.] Karst; Feldmann 1987). Thus, the quality of the terrestrial habitat used by the adult salamander was lowered gradually, and this may have caused the decline in adult survival probabilities. Such a response of the salamander population would be in line with the results of several studies that show negative effects of forest management practices such as clearcutting and conversion of natural deciduous forest to conifer plantations on the abundance of salamanders and other amphibians (e.g., deMaynadier & Hunter 1995; Sattler & Reichenbach 1998; Waldick et al. 1999; Bartman et al. 2001).

Salamanders may have emigrated from the study area rather than died. Bartman et al. (2001) found no emigration of salamanders from plots after timber harvest, whereas Sattler and Reichenbach (1998) argue that in their study salamanders may have emigrated after plots were clearcut. Given our study design, we could not tease apart mortality from permanent emigration. This does

not, however, affect our main conclusion: Because local survival of adult salamanders decreased, either because they died or because they emigrated, increasing recruitment (in situ reproduction or immigration of juveniles or adults) could not halt a decline, as occurred in the Littfeld population. Density dependence in adult survival might buffer population growth rate against reductions in adult survival. A model with the Fredeburg population count as a covariate, however, did not fit the data well ($\{\phi_{\ln(count)}$, $\tau., e., i., p_{t.}\}$, $\Delta AIC_c = 8.21$), suggesting that adult survival is independent of density.

The important roles of terrestrial stage and terrestrial habitat contrast with the common assumption that the success of amphibian populations is determined primarily by the number and quality of metamorphosing larvae (see Introduction). Because recruitment is often intermittent, it is argued that populations are characterized by short periods of increases and long periods of decline (Pechmann & Wilbur 1994; Alford & Richards 1999). Although this pattern of amphibian population dynamics may be observed in some populations of some species (Meyer et al. 1998), it is unlikely to be general (Green 2003).

Recruitment may be responsible for most of the variance in population growth rates of many amphibian populations (Pechmann & Wilbur 1994; Pfister 1998; Biek et al. 2002). Recruitment is often highly variable in amphibian populations (e.g., Shoop 1974), whereas adult survival may fluctuate little, as it does in many other vertebrate species (Gaillard et al. 1998). Hence, variability in recruitment determines variability in population growth, whereas adult survival determines minimum population growth (recall that $\lambda_i = \phi_i + f_i$ and we assumed that ϕ_i is roughly constant and f_i is zero in some years). As long as environmental variation is within the range normally experienced by the population, the larval stage may determine the magnitude of population fluctuations.

If a reduction in habitat quality lowers adult survival, however, even a small reduction in adult survival could change the population trajectory from stable to declining. Recruitment is, as observed in the Littfeld population (Fig. 2), unlikely to halt a population decline (Biek et al. 2002; Hels & Nachman 2002; Vonesh & De la Cruz 2002). Generally, adult survival is likely to be more important for population persistence than recruitment because adult survival determines how long a population can persist without recruitment. This is why bet-hedging theory predicts that adults are selected for high survival when recruitment is highly variable (Seger & Brockmann 1987). This does not mean the larval stage is unimportant. For example, if introduced predatory fish kill all tadpoles, populations will decline. An introduced predator that kills adults, however, would cause a more rapid population decline.

The relative importance of adult survival versus recruitment for population growth is likely to be proportional to adult survival (Sæther & Bakke 2000). Amphibians that reproduce in temporary ponds where variation in larval survival is high are selected for high adult survival (Seger & Brockmann 1987). In these species, adult survival is likely to be more important for population growth than recruitment. In contrast, one may expect lower adult survival in species that breed in permanent ponds where recruitment is probably less variable. In these species, recruitment rather than adult survival is likely to be more important for population growth. Comparative analyses of amphibian life histories and the importance of environmental stochasticity and density dependence could give important insights (e.g., Sæther et al. 2002). Mark-recapture analyses of the available amphibian population data sets may help in such a comparative analysis (Schmidt 2004).

Our understanding of amphibian population dynamics is still limited. In the future, the focus of amphibian population studies should be on all life-history stages and population growth rate rather than single vital rates (Hellriegel 2000; Biek et al. 2002; Forbes & Calow 2002; Vonesh & De la Cruz 2002). Our observational study cannot establish causation in the experimental sense but confirms the predictions of population models. Ultimately, population-level experiments in which the different life-history stages are manipulated are required to fully understand amphibian population dynamics. Such experiments will be a challenging task, but equally difficult experiments have been done with mammals and birds (Krebs et al. 1995; Hudson et al. 1998). Only if we combine the insights from experimental and observational studies and population models will we achieve a better understanding of amphibian demography and population dynamics, which is necessary if we are to understand, halt, and reverse local and global amphibian population declines (Blaustein et al. 1994, 2003). We suggest expanding the focus in conservation practice from aquatic habitats and larval amphibians to a management strategy in which the terrestrial habitat and survival of adults is considered as well (Denton et al. 1997; Gibbons 2003; Semlitsch 2003).

Acknowledgments

Literature Cited

Alford, R. A., and S. J. Richards. 1999. Global amphibian declines: a problem in applied ecology. Annual Reviews of Ecology and Systematics **30:**133–165.

Bartman, C. E., K. C. Parker, J. Laerm, and T. S. McCay. 2001. Short-term response of Jordan's salamander to a shelterwood timber harvest in western North Carolina. Physical Geography **22:**154–166.

Biek, R., W. C. Funk, B. A. Maxell, and L. S. Mills. 2002. What is missing

in amphibian decline research: insights from ecological sensitivity analysis. Conservation Biology **16:**728–734.

Blaustein, A. R., D. B. Wake, and W. P. Sousa. 1994. Amphibian declines: judging stability, persistence, and susceptibility to local and global extinctions. Conservation Biology **8:**60–71.

Blaustein, A. R., J. M. Romansic, J. M. Kiesecker, and A. C. Hatch. 2003. Ultraviolet radiation, toxic chemicals and amphibian population declines. Diversity and Distributions **9:**123–140.

Boone, M. D., and C. M. Bridges. 2003. Effects of pesticides on amphibian populations. Pages 152–167 in R. D. Semlitsch, editor. Amphibian conservation. Smithsonian Institution Press, Washington, D.C.

Burnham, K. P., and D. R. Anderson. 1984. Tests of compensatory vs. additive hypotheses of mortality in mallards. Ecology **65:**105–112.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference. Springer-Verlag, Berlin.

Choquet, R., A. M. Reboulet, R. Pradel, O. Gimenez, and J.-D. Lebreton. 2003. U-CARE version 2.0. CEFE/CNRS, Montpellier, France. Available from ftp.cefe.cnrs.mop.fr/biom/Soft-CR (accessed July 2004).

Collins, J. P., and A. Storfer. 2003. Global amphibian declines: sorting the hypotheses. Diversity and Distributions **9:**89–98.

Crouse, D. T., L. B. Crowder, and H. Caswell. 1987. A stage-based population model for loggerhead sea turtles and implications for conservation. Ecology **68:**1412–1423.

deMaynadier, P. G., and M. L. Hunter. 1995. The relationship between forest management and amphibian ecology: a review of the North American literature. Environmental Reviews **3:**230–261.

Denton, J. S., S. P. Hitchings, T. J. C. Beebee, and A. Gent. 1997. A recovery program for the natterjack toad (*Bufo calamita*) in Britain. Conservation Biology **11:**1329–1338.

Feldmann, R. 1967. Nachweis der Ortstreue des Feuersalamanders, *Salamandra salamandra terrestris* Lacépède, 1788, gegenüber seinem Winterquartier. Zoologischer Anzeiger **178:**42–48 (in German).

Feldmann, R. 1987. Überwinterung, Ortstreue und Lebensalter des Feuersalamanders, *Salamandra salamandra terrestris*. Schlussbericht einer Langzeituntersuchung. Jahrbuch für Feldherpetologie **1:**33–44 (in German).

Forbes, V. E., and P. Calow. 2002. Population growth rate as a basis for ecological risk assessment of toxic chemicals. Philosophical Transactions of the Royal Society of London, Biological Sciences **357:**1299–1306.

Fujiwara, M., and H. Caswell. 2001. Demography of the endangered north Atlantic right whale. Nature **414:**537–541.

Gaillard, J.-M., M. Festa-Bianchet, and N. G. Yoccoz. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends Ecology & Evolution **13:**58–63.

Gibbons, J. W. 2003. Terrestrial habitat: a vital component for herpetofauna of isolated wetlands. Wetlands **23:**630–635.

Green, D. M. 2003. The ecology of extinction: population fluctuation and decline in amphibians. Biological Conservation **111:**331–343.

Hellriegel, B. 2000. Single- or multistage regulation in complex life cycles: does it make a difference? Oikos **88:**239–249.

Hels, T., and G. Nachman. 2002. Simulating viability of a spadefoot toad *Pelobates fuscus* metapopulation in a landscape fragmented by a road. Ecography **25:**730–744.

Homolka, M., and J. Kokes. 1994. Effect of air pollution and forestry practice on the range and abundance of *Salamandra salamandra*. Folia Zoologica **43:**49–56.

Houlahan, J. E., C. S. Findlay, B. R. Schmidt, A. H. Meyer, and S. L. Kuzmin. 2000. Quantitative evidence for global amphibian population declines. Nature **404:**752–755.

Hudson, P. J., A. P. Dobson, and D. Newborn. 1998. Prevention of population cycles by parasite removal. Science **282:**2256–2258.

Kendall, W. L., and J. D. Nichols. 2002. Estimating state-transition probabilities for unobservable states using capture-recapture/resighting data. Ecology **83:**3276–3284.

Kiesecker, J. M., A. R. Blaustein, and L. K. Belden. 2001. Complex causes of amphibian declines. Nature **410:**681–684.

Krebs, C. J., S. Boutin, R. Boonstra, A. R. E. Sinclair, J. N. M. Smith, M. R. T. Dale, K. Martin, and R. Turkington. 1995. Impact of food and predation on the snowshoe hare cycle. Science **269:**1112–1115.

Lebreton, J.-D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs **62:**67–118.

Martínez-Solano, I., J. Bosch, and M. García-París. 2003. Demographic trends and community stability in a montane amphibian assemblage. Conservation Biology **17:**238–244.

McPeek, M. A., and B. L. Peckarsky. 1998. Life histories and the strengths of species interactions: combining mortality, growth, and fecundity effects. Ecology **79:**867–879.

Meyer, A. H., B. R. Schmidt, and K. Grossenbacher. 1998. Analysis of three amphibian populations with quarter-century long time-series. Proceedings of the Royal Society of London, Series B **265:**523–528.

Nichols, J. D., J. E. Hines, J.-D. Lebreton, and R. Pradel. 2000. Estimation of contributions to population growth: a reverse-time capture-recapture approach. Ecology **81:**3362–3376.

Nichols, J. D., and J. E. Hines. 2002. Approaches for the direct estimation of λ, and demographic contributions to λ, using capture-recapture data. Journal of Applied Statistics **29:**539–568.

Pechmann, J. H. K., and H. M. Wilbur. 1994. Putting declining amphibian populations in perspective: natural fluctuations and human impacts. Herpetologica **50:**65–84.

Pfister, C. A. 1998. Patterns of variance in stage-structured populations: evolutionary predictions and ecological implications. Proceedings of the National Academy of Sciences of the U.S.A. **95:** 213–218.

Pradel, R. 1996. Utilization of capture-mark-recapture for the study of recruitment and population growth rate. Biometrics **52:** 703–709.

Pradel, R., J. E. Hines, J.-D. Lebreton, and J. D. Nichols. 1997. Capture-recapture models taking account of transients. Biometrics **53:**60–72.

Sattler, P., and N. Reichenbach. 1998. The effects of timbering on *Plethodon hubrichti*: short-term effects. Journal of Herpetology **32:**399–404.

Sæther, B.-E., and Ø. Bakke. 2000. Avian life history variation and contribution of demographic traits to the population growth rate. Ecology **81:**642–653.

Sæther, B.-E., S. Engen, and E. Matthysen. 2002. Demographic characteristics and population dynamical patterns of solitary birds. Science **295:**2070–2073.

Schaub, M., F. Liechti, and L. Jenni. 2004*a*. Departure of migrating European robins, *Erithacus rubecula*, from a stopover site in relation to wind and rain. Animal Behaviour **67:**229–237.

Schaub, M., O. Gimenez, B. R. Schmidt, and R. Pradel. 2004*b*. Estimating survival and temporary emigration in the multistate capture-recapture framework. Ecology **85:**2107–2113.

Schmidt, B. R. 2004. Declining amphibian populations: the pitfalls of count data in the study of diversity, distributions, dynamics, and demography. Herpetological Journal **14:**167–174.

Schmidt, B. R., M. Schaub, and B. R. Anholt. 2002. Why you should use capture-recapture methods when estimating survival and breeding probabilities: on bias, temporary emigration, overdispersion, and common toads. Amphibia-Reptilia **23:**375–388.

Seger, J., and H. J. Brockmann. 1987. What is bet-hedging? Oxford Surveys in Evolutionary Biology **4:**182–211.

Semlitsch, R. D. 2003. Conservation of pond-breeding amphibians. Pages 8–23 in R. D. Semlitsch, editor. Amphibian conservation. Smithsonian Institution Press, Washington, D.C.

Shoop, C. R. 1974. Yearly variation in larval survival of *Ambystoma maculatum*. Ecology **55:**440–444.

Sutherland, W. J., and K. Norris. 2002. Behavioural models of population growth rates: implications for conservation and prediction. Philosophical Transactions of the Royal Society of London, Biological Sciences **357:**1273–1284.

Taylor, B. E., and D. E. Scott. 1997. Effects of larval density dependence on population dynamics of *Ambystoma opacum*. Herpetologica **53:**132–145.

Thiesmeier, B., and K. Grossenbacher. 2004. *Salamandra salamandra* (Linnaeus, 1758)—Feuersalamander. Pages 1059–1132 in B. Thiesmeier and K. Grossenbacher, editors. Handbuch der Reptilien und Amphibien Europas: Schwanzlurche IIB. Aula Verlag, Wiesbaden, Germany (in German).

Thiesmeier, B., and R. Günther. 1996. Feuersalamander—*Salamandra salamandra* (Linnaeus, 1758). Pages 82–104 in R. Günther, editor. Die Amphibien und Reptilien Deutschlands. Gustav Fischer Verlag, Jena, Germany (in German).

Vonesh, J. R., and O. De la Cruz. 2002. Complex life cycles and density dependence: assessing the contribution of egg mortality to amphibian declines. Oecologia **133:**325–333.

Waldick, R. C., B. Freedman, and R. J. Wassersug. 1999. The consequences for amphibians of the conversion of natural, mixed-species forests to conifer plantations in southern New Brunswick. Canadian Field Naturalist **113:**408–418.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study **46** (suppl.):120–139.

Wilbur, H. M. 1980. Complex life cycles. Annual Reviews of Ecology and Systematics **11:**67–93.

Wilbur, H. M., and J. P. Collins. 1973. Ecological aspects of amphibian metamorphosis. Science **182:**1305–1314.

Wintle, B.A., M. A. McCarthy, C. T. Volinsky, and R. P. Kavanagh. 2003. The use of Bayesian model averaging to better represent uncertainty in ecological models. Conservation Biology **17:** 1579–1590.