

Winter weather affects asp viper *Vipera aspis* population dynamics through susceptible juveniles

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Altwegg, R., Dummermuth, S., Anholt, B. R. and Flatt, T. 2005. Winter weather affects asp viper *Vipera aspis* population dynamics through susceptible juveniles. – Oikos 110: 55–66.

Detailed studies on mammals and birds have shown that the effects of climate variation on population dynamics often depend on population composition, because weather affects different subsets of a population differently. It is presently unknown whether this is also true for ectothermic animals such as reptiles. Here we show such an interaction between weather and demography for an ectothermic vertebrate by examining patterns of survival and reproduction in six populations of a threatened European snake, the asp viper (*Vipera aspis*), over six to 17 years. Survival was lowest among juvenile and highest among adult snakes. The estimated annual probability for females to become gravid ranged from 26% to 60%, and was independent of whether females had reproduced in the year before or not. Variation in juvenile survival was strongly affected by winter temperature, whereas adult survival was unaffected by winter harshness. A matrix population model showed that winter weather affected population dynamics predominantly through variation in juvenile survival, although the sensitivity of the population growth rate to juvenile survival was lower than to adult survival. This study on ectothermic vipers revealed very similar patterns to those found in long-lived endothermic birds and mammals. Our results thus show that climate and life history can interact in similar ways across biologically very different vertebrate species, and suggest that these patterns may be very general.

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Stochastic variation in weather and climate increases the temporal variation in fitness components, thereby affecting the dynamics and extinction risk of a population (Andrewartha and Birch 1954, Lande 1993). Recent studies have revealed that weather does not affect all age classes and both sexes in the same way (Leirs et al. 1997, Coulson et al. 2001). For example, temperature fluctuations explained a large proportion of the variance in juvenile but not adult survival in barn owls (Altwegg et al. 2003). The effect of environmental variability on fluctuations in population numbers therefore critically

depends on the demographic composition of the population and the life history of the species (Sæther et al. 2002).

The effect of variation in a particular fitness component on variation in population numbers depends on how sensitive the population growth rate is to changes in that component (Caswell 2001). In large herbivores and long-lived birds, for example, the population growth rate is least sensitive to variation in reproduction and survival of young individuals (Sæther 1997, Gaillard et al. 2000). Yet, those fitness components that have the least effect

Accepted 12 December 2004

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ISSN 0030-1299

on population growth rate tend to be the most variable ones (Gaillard et al. 2000), whereas traits more closely linked to population dynamics tend to be less variable (Sæther and Bakke 2000). This pattern may be due to selection for reduced variance, acting most strongly on those traits that are closely linked to fitness (Gillespie 1977, Stearns and Kawecki 1994, Pfister 1998).

Stochastic environmental factors may thus affect populations through complex interactions with demography. However, only detailed individual-based studies of natural populations can unravel such processes. Although such data sets have begun to accumulate for large mammals and birds, where individuals can be followed relatively easily throughout their lives (Gaillard et al. 1998, Sæther and Bakke 2000), there is almost no information on the interplay between demography and environmental stochasticity in ectothermic vertebrates. Yet, the insights gained from endothermic mammals and birds may not be readily applicable to ectothermic vertebrates for two reasons. First, the activity patterns of ectotherms such as reptiles and amphibians depend more on ambient temperature than those of mammals and birds. Second, the low energy requirements make ectotherms less susceptible in terms of survivorship to long periods of weather-caused food shortage (Pough 1980, Peterson et al. 1993). Thus, to understand how weather affects fitness and population dynamics of ectothermic vertebrates, we need longterm individual-based studies.

Here we illustrate the interaction between weather and demography in a threatened ectothermic vertebrate, the asp viper (*Vipera aspis* L.). We monitored 415 individuals in six populations located in the Jura mountains in northern Switzerland for 6 to 17 years (Flatt and Dummermuth 1993, Flatt et al. 1997). First, we estimated age- and sex-specific survival rates and the reproductive rate of females using capture-mark-recapture models (Lebreton et al. 1992). Second, we used the same methods to relate temporal variation in these fitness components to active-season and winter weather. Finally, we estimated the sensitivity of the population growth rate to changes in each of the fitness components using matrix population models and calculated the effects of weather-caused variation on population growth (Caswell 2001). Several studies estimated survival rates in snakes (Saint Girons 1957, Viitanen 1967, Gregory 1977, Brown and Parker 1984), and examined the effect of weather or climatic conditions on various aspects of reptile ecology (Moser et al. 1984, Peterson et al. 1993, Daltry et al. 1998, Flatt et al. 2001, Sun et al. 2001, Lourdais et al. 2004). Our study extends these findings in two important ways. First, we account for variation in detection probability, which is likely to be lower for juvenile than for adult snakes, and may depend on the weather during the surveys. Second, we explicitly model the life cycle of our study organism, and thus

estimate the impact of external factors (such as weather) on population dynamics through variation in a particular fitness component. An explicit representation of the life cycle is necessary because similar changes in two different fitness components will not necessarily have similar effects on overall fitness and population dynamics (Ehrlén 2003).

Methods

Field methods

Between 1986 and 2002, we monitored six isolated populations of asp vipers. Flatt and Dummermuth (1993) and Flatt et al. (1997) provide a description of the natural history of the asp viper and methodological details of fieldwork. Sample sizes and short descriptions of the study sites are given in Appendix I. We visited each site between one and 35 times per year during the entire activity period, from mid-March to mid-October, but 74% of the observations were made between May and September. Snakes were located from a distance with telephoto lenses, binoculars or by sight while walking slowly through the terrain. Identification of known individuals was based on photographs and detailed drawings of the head and neck coloration made at first encounter. We used overall coloration, dorsal colour pattern, scars and other distinctive marks for identification. In most cases, individuals were clearly identifiable from close distance and were only hand-captured if their identity was in doubt (10–20% of the cases). For each individual we recorded at every encounter the age class, sex, sight-estimated size, and reproductive status for females. Gravid female asp vipers recognisably change their body proportions within a few weeks after copulation. In doubtful cases, the snake was captured and its reproductive status verified by hand-scanning the body. We avoided capture whenever possible in order to minimise the disturbance of these threatened animals. Comparisons using captive animals showed that our estimates of body size are within 10% of the measured size (S. Dummermuth, unpubl.).

Age determination of individuals at first encounter was based on approximate body size. We classified individuals smaller than 30 cm as juvenile, individuals between 30 and 50 cm as subadult, and larger individuals as adult. In our populations, female vipers generally start reproducing at 50 cm and in their 4th or 5th year (S. Dummermuth, pers. obs.). Males may start reproducing earlier, but their reproductive status could not be assessed in the field. Since the subadult stage usually takes three years to complete, we assigned individuals to yearly age classes based on their size at first encounter, assuming similar growth rates among individuals over the first four years of life (first year subadult: <37 cm, second year: between 37 and 44 cm,

third year: >44 cm). Growth may vary with food abundance, and our size estimates may be less accurate than if we had been able to hand-measure each individual. We therefore estimated the impact of potential errors in age determination on our survival estimates for population B, which is the smallest population with age effects, and thus potentially most affected by errors. We generated ten data sets that were equal to the original one, except that we added a substantial amount of random error to the estimates of body size. The errors were drawn from a normal distribution with standard deviation equal to 10% of the estimated body size. The ten data sets with artificially increased error yielded survival rates that were almost identical to the ones obtained from the original data set. The most extreme value for any survival rate was within 70% of the standard error of the original estimate, and our estimates are therefore robust to errors in age and size determination.

Statistical methods

We used basic capture–mark–recapture (CMR) methods (Lebreton et al. 1992) to estimate recapture and survival rates. CMR methods allow modelling of the recapture rate (probability that an individual was recaptured or resighted at time i , given that it was alive and in the study area at that time) independently of the survival rate. We can therefore examine factors affecting the recapture rate (e.g. effort in the field) and the survival rate separately, and CMR gives unbiased estimates of survival even if a proportion of the individuals was not observed at every recapture occasion. Mortality here includes both death and permanent emigration. In terms of the population ecology of vipers in our area, death and emigration are essentially equivalent, since we only observed two adult males who successfully moved between populations and there are no other populations nearby where emigrants could establish. Second, we used multi-state extensions of CMR models to calculate reproductive probabilities of females (Nichols et al. 1994). CMR models assume that all individuals within one group have the same probability of survival and recapture in each time step, and that all individuals are identified correctly (Lebreton et al. 1992). We verified that our data met these assumptions using a goodness-of-fit test provided by the program RELEASE (Test 2+3, Burnham et al. 1987) and found that a general time dependent model described the data well (each population tested separately: A: $\chi^2 = 33.30$, $df = 29$, $P = 0.27$; B: $\chi^2 = 25.72$, $df = 23$, $P = 0.22$; C: $\chi^2 = 9.07$, $df = 6$, $P = 0.17$; D: $\chi^2 = 15.51$, $df = 18$, $P = 0.63$; E: $\chi^2 = 15.70$, $df = 12$, $P = 0.21$; F: $\chi^2 = 19.23$, $df = 17$, $P = 0.32$). The other models are generalisations or simplifications of these models and do therefore also meet the assump-

tions. We are, however, violating the additional assumption that recaptures are instantaneous in time, and this may lead to overestimating survival. Hargrove and Borland (1994) estimated this bias to be <5% in situations comparable to ours.

Because the sample sizes precluded fitting large numbers of models or overly complex models, we limited our analyses to a few factors that seemed most likely on biological grounds, and a minimal number of models. These models form our set of candidate models. Additional models, coming up as interesting alternatives during analysis, were fitted a posteriori and are marked in the tables accordingly. All models were fitted using maximum-likelihood methods implemented in the program MARK (White and Burnham 1999). To compare models we used the sample-size adjusted Akaike's information criterion (AIC_c ; Burnham and Anderson 2002). The model with the lowest AIC_c value is best supported by the data. For each model, we also calculated Akaike weights (w) to assess the relative support from the data for a particular model as compared to the other models in the set (Burnham and Anderson 2002). Model selection identifies the model that best describes the structure in a data set, and favours the model that provides the best balance between overfitting (hence loss of precision) and underfitting (hence bias, Burnham and Anderson 2002). Like with any statistical method, smaller effects need larger sample sizes to be detected, and smaller data sets therefore tend to select simpler models than large data sets.

Modelling and estimation of recapture and survival probabilities

We proceeded in three steps. First, we investigated sex- and age-differences, and temporal variation in survival and recapture rates for each of the six populations separately. Second, we analysed differences between populations in age-specific survival and recapture in a single analysis. It turned out that sex effects were always weaker than age effects, with opposite trends across populations. In order to simplify the modelling procedure, we therefore did not examine sex differences at this second step. Third, we related age-specific survival to weather variation, using data provided by MeteoSwiss meteorological stations. An initial analysis with the largest data set (population F) showed that variation in survival and recapture was best represented by positive linear relationships with age, and we used this relationship for the rest of the analysis. As a consequence, estimates for subadults always lay between the estimates for adults and juveniles, and we do not always report the former separately. We also investigated whether recapture effort, i.e. the number of visits to a field site, affected the recapture rate in all populations. If a population was not visited at all in a particular year, the recapture rate was set to zero for that year. Daily mean temperatures

were measured at Wynau (UTM coordinates: 626400/233860, 422 m above sea level, for populations A to E) and Neuchâtel (563110/205600, 487 m a.s.l., for population F) and monthly precipitation was measured at Balsthal (619250/240860, 502 m a.s.l., for populations A to E) and Yverdon (539840/181450, 433 m a.s.l., for population F). We considered separate models for the effect of winter and active-season weather. The winter effect consisted of the mean temperature measured on the coldest day and the number of days with mean temperature below 0°C. The active-season effect consisted of the linear and quadratic effects of mean daily temperature and mean monthly precipitation between 1 April and 31 October. Quadratic effects were included in the active-season effect because snakes may be sensitive to extreme weather conditions at both ends of the scale (Saint Girons 1952, 1981). Each of the climate effects entered the models either as a main effect or as an interaction with the age effect. As none of the weather variables were significantly correlated with each other, we did not attempt to reduce their number by principal components analysis.

Analysis of probability of reproduction

We estimated the probabilities for females to reproduce in a given year using multi-state models (Nichols et al. 1994). We defined two states that sexually mature females could assume: gravid versus non-gravid. The transition probabilities between these states were then 1) the probability of becoming gravid in the following year for a currently non-gravid female (ψ_{nr}); 2) the probability for a non-gravid female to remain in this condition ($1-\psi_{nr}$); 3) the probability of not being gravid in the following year for a currently gravid female (ψ_{rn}); and 4) the probability for a gravid female to be gravid again in the following year ($1-\psi_{rn}$). These transitions are conditional on survival, i.e. an individual has to survive the time interval before it can change its state. We further make the presently untestable assumption that all individuals with a particular state are equally likely to change from one state into the other. The analysis of reproductive probability included only adult individuals, even though some of the individuals classified as 3rd year subadult may have reproduced in rare cases. Due to the large data requirements of multi-state models, we pooled the data of the populations in close proximity to each other (A to E) and only considered the period between 1994 and 1999 during which all these populations were studied simultaneously. Population F yielded enough data to be analysed separately. We examined the effects of temporal variation and active-season weather on both transition probabilities. We did not consider quadratic effects of active-season weather as in the survival analysis because the smaller sample size and the shorter time span did not warrant more complex effects.

Matrix population modelling

We used Leslie matrices to estimate the sensitivity of the population growth rate (λ) to variation in vital rates. Methods exist to estimate sensitivity from CMR data directly (Nichols et al. 2000). However, with strongly age-dependent survival as in our data set, these methods are not applicable. The matrix entries were the age-specific survival rates taken from the CMR models and reproductive rates (Appendix II). The latter are the product of the probability for females to reproduce, litter size, the sex ratio within the litter, and the survival probability of new-born from birth in late fall until next spring. Whereas the probability of reproducing was also obtained from the CMR models (above), data on the other components of recruitment could not be estimated from the data directly. We therefore used data obtained from the literature, supported by occasional observations in our study populations. We used a mean litter size of ten, a 1:1 sex ratio (Saint Girons 1952, Flatt and Dummermuth 1993), and set the survival of new-born equal to the survival of juvenile individuals. Due to the uncertainty in the estimate of reproductive rates, we did not further examine variation in this trait. First, we assessed the effects of variation in fitness components on population growth using sensitivity and elasticity analyses (Stearns 1992, Caswell 2001). We calculated 95% confidence limits by generating 1000 matrices with elements drawn from a normal distribution with mean and variance obtained from the logit transformed CMR estimates. After being sorted by their magnitude, the 25th and 975th bootstrap replicates represent the lower and the upper confidence limits. Second, in a retrospective analysis (Caswell 2000), we asked how much of the weather-caused variance in survival during the different life stages contributed to variation in λ . To do this, we used survival rates obtained from the weather-dependent CMR model and multiplied the variances in stage specific survival with the square of the corresponding sensitivities (Caswell 2001). All matrix analyses were performed for the pooled populations A to E and for population F using the S-plus-2000 software package (Insightful Corp., Seattle USA).

Results

Recapture rates

Model selection showed that the recapture probabilities were lower for juvenile than for adult snakes in populations A, C, D and F and varied with recapture effort or time for all populations but D. In no population did the recapture rate differ between the sexes. The estimates ranged from 0.05 to 0.74 in A, 0.25 to 0.90 in B, 0.002 to 0.91 in C, 0.29 to 0.79 in D, 0.27 to 1 in E, and from 0 to 0.89 in F.

Patterns of survival

Model selection showed similar demographic patterns in all populations. AIC_c favoured the model incorporating age-dependent survival in populations A, B, E, and F (Table 1). Survival was lowest for juveniles, higher for subadults, and highest for adults (Fig. 1). Population C showed a similar pattern, but the confidence intervals for the estimates were large. The best estimate of the relationship in population D was very near zero (Fig. 1). The AIC_c -selected best models did not include differences between the sexes in any population except F. Population F included the effect of sex and the interaction between age and sex, suggesting higher survival for adult females compared to adult males, but equal survival of the

juveniles of both sexes (Fig. 1). Survival stayed fairly constant throughout the duration of our study in all populations, and the models accounting for potential time effects were always poorly supported by the data.

Comparison between populations

We quantitatively compared all populations, A through F, in a single analysis. We used all data collected between 1986 and 2002 while setting the corresponding recapture rate to zero if a population was not sampled in a particular year. The best-supported models accounted for the effects of sampling effort and age on recapture

Table 1. Model selection for survival of asp vipers in six populations (A to F) in northern Switzerland. The selected models for the recapture probability included the effects of sampling effort (A, B, C), age (A, C, D), time (E), and simultaneous effects of age, time and their interaction (F) (model selection for recapture not shown). The fit of the models is assessed by Akaike's information criterion (AIC_c); lower values indicate better fit. ΔAIC_c gives the difference in AIC_c between each 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. K is the number of estimated parameters of a given model. The deviance is the difference in $-2 \log$ likelihood between each model and the saturated model, the saturated model being the one with the number of parameters equal to the sample size.

Population (recapture)	Factors in survival model	K	Deviance	AIC_c	ΔAIC_c	w
A (age, effort)	constant	4	216.276	258.957	1.192	0.244
	time	14	209.912	276.430	18.665	0.000
	age	5	212.897	257.765	0.000	0.443
	sex	5	216.260	261.128	3.363	0.082
	sex, age	6	212.532	259.628	1.863	0.174
	sex, age, interaction	7	212.517	261.881	4.116	0.057
						$\Sigma = 1$
B (effort)	constant	3	166.067	199.409	6.154	0.025
	time	13	149.595	207.768	14.513	0.000
	age	4	157.709	193.255	0.000	0.535
	sex	4	164.448	199.994	6.739	0.018
	sex, age	5	156.539	194.345	1.090	0.310
	sex, age, interaction	6	156.272	196.395	3.140	0.111
					$\Sigma = 1$	
C (age, effort)	constant	4	76.158	103.687	0.000	0.493
	time	14	74.952	132.181	28.494	0.000
	age	5	75.105	105.058	1.371	0.248
	sex	5	76.030	105.983	2.296	0.156
	sex, age	6	75.087	107.565	3.878	0.071
	sex, age, interaction	7	74.056	109.168	5.481	0.032
						$\Sigma = 1$
D (age)	constant	3	128.738	215.877	0.000	0.477
	time	10	122.418	225.574	9.697	0.004
	age	4	128.737	218.032	2.155	0.162
	sex	4	128.026	217.321	1.444	0.232
	sex, age	5	127.995	219.488	3.611	0.078
	sex, age, interaction	6	126.766	220.500	4.623	0.047
						$\Sigma = 1$
E (time)	constant	8	121.764	264.84	10.160	0.004
	time	13	119.01	273.741	19.061	0.000
	age	6	116.039	254.68	0.000	0.646
	sex	7	121.659	262.502	7.822	0.013
	sex, age	7	115.736	256.579	1.899	0.250
	sex, age, interaction	8	115.612	258.687	4.007	0.087
						$\Sigma = 1$
F (age, time, interaction)	constant	11	216.600	523.450	13.505	0.001
	time	14	213.171	526.599	16.654	0.000
	age	12	206.225	515.252	5.307	0.043
	sex	12	208.488	517.515	7.570	0.014
	sex, age	13	199.942	511.162	1.217	0.332
	sex, age, interaction	14	196.517	509.945	0.000	0.610
						$\Sigma = 1$

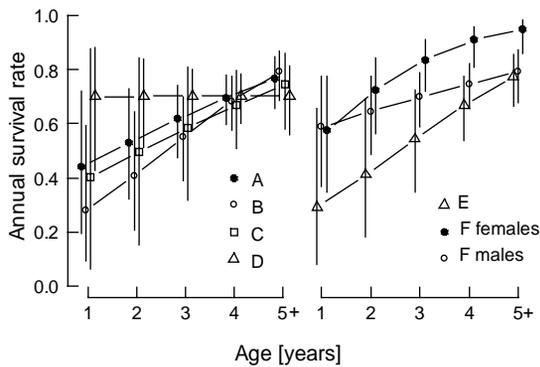


Fig. 1. Age specific survival in six populations of asp vipers in northern Switzerland. The estimates are taken from the age specific model for populations A to E, and from the model with interacting age and sex effects for population F. The error bars show the 95% confidence interval, which is derived from the linear predictors, on the logit scale. The symbols are slightly offset for ease of interpretation.

rates (models 2 to 11, Table 2). AIC_c further showed that recapture rates differed between populations (models 4 to 11, Table 2). Among the a priori models (models 1 to 10, Table 2), AIC_c selected the one allowing for survival differences between populations and accounting for interactions between age and winter weather (model 8). A close competitor of model 8 was model 2, excluding the effect of winter weather, while the other models were poorly supported. A posteriori, we investigated the role of winter harshness by fitting a reduced winter-weather model including only the effect of the number of days with temperatures below zero. The AIC_c value of this model was 3.26 units lower and thus considerably better supported by the data than the best a priori model, suggesting that juvenile survival was strongly dependent on winter harshness whereas adult survival was unaffected (Fig. 2).

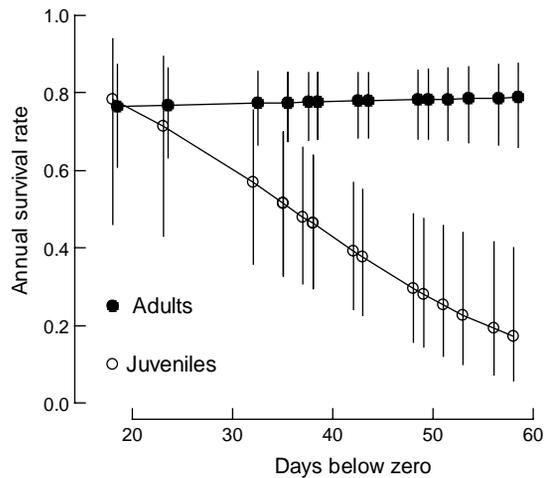


Fig. 2. Interaction between winter harshness, expressed as the number of days with average temperatures below zero, and age on survival of asp vipers for population B, which has been studied over the longest time. Estimates for the other populations differ from those shown by a constant value. The vertical lines show the 95% confidence interval, which is derived from the linear predictors, on the logit scale. Estimates from model 11, Table 2.

Probabilities of reproduction

The multi-state models required pooling populations A to E for calculating the probability for females to become gravid, but we were able to examine population F separately. Model selection suggested constant reproductive probabilities over time except that reproducers in population F were more likely to reproduce again after relatively warm and wet summers (model 1 and model 5, Table 3). Model 1, suggesting constant reproductive probabilities, was a close competitor to the best model in population F. In populations A to E the probabilities of reproducing in the following year were 0.27 (95%

Table 2. Model selection for the comparison between six populations of the asp viper in northern Switzerland. Effort = number of visits to a site per season. Models 7 to 11 examine the effects of weather on survival: winter = minimum temperature and number of days below zero, active season = mean daily temperature between 1 April and 31 October and mean precipitation over the same period (both effects linear and quadratic). Only the a priori models were included in the calculation of w , and ΔAIC_c is the difference in AIC_c to the best a priori model. \times between two effects symbolises interactive effects; \ddagger post hoc model including the number of days below zero only. See also legend to Table 1.

Factors in survival model	Factors in recapture model	K	Deviance	AIC_c	ΔAIC_c	w
1 population, age	population, age, time	29	757.040	1557.423	8.190	0.007
2 population, age	population, age, effort	15	778.667	1549.485	0.252	0.346
3 population, age	age, effort	10	795.751	1556.252	7.019	0.012
4 age	population, age, effort	10	794.074	1554.575	5.342	0.027
5 population	population, age, effort	14	804.809	1573.554	24.321	0.000
6 population \times age	population, age, effort	20	774.124	1555.386	6.153	0.018
7 population, age, winter	population, age, effort	17	775.896	1550.876	1.643	0.173
8 population, age \times winter	population, age, effort	19	770.070	1549.233	0.000	0.393
9 population, age, active season	population, age, effort	19	776.126	1555.288	6.055	0.019
10 population, age \times active season	population, age, effort	23	769.912	1557.501	8.268	0.006
11 \ddagger population, age \times days below zero	population, age, effort	17	770.997	1545.977	-3.256	
						$\Sigma = 1$

Table 3. Model selection for multi-state models examining the probability of asp vipers to reproduce in populations A to E (a, n = 51 females), and F (b, n = 34 females). We included data collected between 1994 and 1999 for populations A to E, and data collected between 1987 and 1992 for population F. For both data sets the most parsimonious model included constant survival and recapture rates, except that reproducers survived better than non-reproducers in populations A to E (model selection for these components not shown). K is the number of structural parameters, which were all estimable for the best-supported models. See also legend to Table 1.

Currently not reproducing (ψ_{nr})	Currently reproducing (ψ_{rn})	K	Deviance	AIC _c	Δ AIC _c	w
a) Populations A to E						
1 constant	constant	5	127.977	238.638	0.000	0.522
2 time	constant	9	119.854	240.225	1.587	0.236
3 constant	time	9	124.127	244.498	5.860	0.028
4 active-season	constant	7	125.880	241.265	2.627	0.140
5 constant	active season	7	127.192	242.576	3.938	0.073
						$\Sigma = 1$
b) Population F						
1 constant	constant	4	156.853	277.373	0.734	0.249
2 time	constant	8	153.440	283.096	6.457	0.014
3 constant	time	8	151.249	280.904	4.265	0.043
4 active season	constant	6	156.739	281.730	5.091	0.028
5 constant	active season	6	151.648	276.639	0.000	0.360
						$\Sigma = 1$

CI: 0.14/0.45) for currently non-reproductive females and 0.26 (CI: 0.09/0.57) for currently reproducing females. In population F the probabilities of reproducing were 0.40 (95% CI: 0.13/0.75) for currently non-reproductive females and 0.60 (CI: 0.36/0.80) for currently reproducing females.

For populations A to F, reproducing females survived better than non-reproducing ones. Omitting this factor from the best model (model 1, Table 3a) resulted in a poorly fitting model (K = 4, deviance = 132.608, AIC_c = 240.999, Δ AIC_c = 2.361). For population F, we found no evidence for differential survival between the two types of females (adding this factor to model 5, Table 3b, resulted in a poorly fitting model: K = 7, deviance = 151.503, AIC_c = 278.802, Δ AIC_c = 2.163).

Sensitivity of λ to variation in survival and recruitment

The matrix model (Appendix II) yielded an asymptotic population growth rate (λ), i.e. the growth rate once the population has reached a stable age distribution (Caswell 2001), of 0.873 (95% confidence interval: 0.811/0.936) for the pooled populations A to E and 1.057 (0.943/1.152) for population F. These estimates show that populations A to E are projected to decrease given the estimated fitness components, whereas population F is projected to stay constant. For all populations, the sensitivity and elasticity analyses consistently showed that population growth was most affected by variation in adult survival and least affected by variation in reproduction (Table 4). However, the retrospective analysis showed that weather affected λ most strongly through the survival of juveniles as weather caused the largest variation in this life stage (Table 4).

Discussion

This study examined the interactive effects of demography and weather on fitness components, and their effect on the growth rate of six populations of a threatened European snake, the asp viper. Despite the large biological differences of the study species, our results reveal the same patterns reported for mammals and birds (Gaillard et al. 1998, Sæther and Bakke 2000), suggesting that these patterns may be general for terrestrial vertebrates. Our main finding is that variation in juvenile survival, but not adult survival, was strongly affected by winter temperature. Winter temperature affected population growth rate predominantly through variation in juvenile survival, even though the sensitivity of the population growth rate to juvenile survival was lower than to adult survival.

Climatic variation often affects subsets of a population differently, and in such cases its effect on population dynamics depends on the current demographic composition of the population (Leirs et al. 1997, Coulson et al. 2001, Stenseth et al. 2002). For instance, different responses of the sexes and age classes to climatic variation is one of the factors leading to different population dynamics in the otherwise ecologically similar red deer and Soay sheep on Scottish islands (Clutton-Brock and Coulson 2002). If such patterns are common, detailed knowledge of the demography and differential susceptibility of demographic components of a population to climatic variation is crucial for a mechanistic understanding of population dynamics. Despite the extensive literature on snake population ecology (Parker and Plummer 1987), there are few data on survival under natural conditions (Turner 1977, Shine and Charnov 1992, Flatt et al. 1997). This lack of information is one of the major constraints in snake conservation (Dodd Jr. 1993).

Table 4. Sensitivity (with 95% confidence limits) and elasticity of the population growth rate (λ) of asp vipers in northern Switzerland to variation in fitness components. Both analyses ask by how much growth rate is changed by a certain change in a fitness component. The former considers absolute changes, whereas the latter considers proportional changes and is thus better suited to compare traits that are measured at different scales. The elasticities sum to one over the whole life cycle. The retrospective analysis (RA) asks how much the observed variance in survival, caused by winter weather, contributed to variance in λ , and is given in % relative to the other survival rates. Sample sizes for the retrospective analysis were 16 years for the pooled populations A-E and five years for population F.

	Populations A-E			Population F		
	Sensitivity	Elasticity	RA	Sensitivity	Elasticity	RA
Juvenile survival	0.193 (0.128/0.266)	0.094	61.3	0.206 (0.128/0.273)	0.114	44.0
1st year subadult survival	0.159 (0.107/0.210)	0.094	28.3	0.180 (0.112/0.233)	0.114	24.0
2nd year subadult survival	0.136 (0.093/0.179)	0.094	9.4	0.162 (0.101/0.206)	0.114	12.0
3rd year subadult survival	0.120 (0.080/0.155)	0.094	<1	0.148 (0.093/0.187)	0.114	4.0
Adult survival	0.629 (0.548/0.728)	0.531	<1	0.558 (0.477/0.695)	0.430	16.0
Reproduction*	0.092 (0.063/0.138)	0.094		0.100 (0.061/0.181)	0.114	

*reproduction is the product of the probability of reproducing, litter size, sex ratio within litter, and survival of new-born until the spring after birth.

The results presented here suggest that survival of juvenile asp vipers is more susceptible to harsh winter conditions than are other fitness components. Several factors could lead to these results: differences between age classes could arise because young individuals are less experienced in finding suitable winter quarters than adults. Alternatively, juveniles may be more likely to run out of fat reserves during hibernation than adults. Our results are unlikely to be affected by differential emigration, as our results would imply greater mobility of young snakes in colder winters, which seems unlikely for these ectothermic organisms. Substantial winter losses have also been found in adult garter snakes (*Thamnophis sirtalis*; winter mortality: 34 to 48%; Gregory 1977), and in the European adder (*Vipera berus*; juvenile mortality: 47.2%, and adult mortality: 18.1%; Viitanen 1967). These estimates are probably biased high, however, as these studies could not account for detection probabilities.

In accordance with the general patterns found in long-lived turtles, birds and mammals (Crouse et al. 1987, Pfister 1998, Gaillard et al. 2000, Sæther and Bakke 2000), population growth in our asp viper populations was less sensitive to changes in the more variable juvenile survival than the less variable adult survival. Yet, winter weather affected population growth predominantly through juvenile survival because it caused most variation in this trait. This is consistent with the finding that ungulate population dynamics are mostly driven through variation in juvenile survival despite the relatively low impact of this fitness component on population growth (Gaillard et al. 2000).

Our age-specific estimates of survival compare well with earlier estimates on this or similar species (Parker and Plummer 1987, Flatt et al. 1997). For example, Flatt et al. (1997) found an average adult survival rate of 0.75 for populations A and B over the first six and nine years of the study. Our corresponding estimates are 0.74 for populations A to E, and 0.84 for population F. However,

as in our previous study (Flatt et al. 1997), we were unable to detect temporal variation in survival of adult vipers. In contrast, the studies by Brown and Parker (1984) and Forsman (1995) have found substantial variation in survival among years. This result potentially is affected by variable recapture success, for which these studies did not correct.

While it generally appears that juvenile and first-year mortality is higher than adult mortality among snakes (Saint Girons 1957, Brown and Parker 1984), there is little data on survival of young age classes, and to our knowledge only one study accounted for the possibly lower detection probabilities of young snakes (Stanford 2002). Viitanen (1967) found lower survival in juveniles as compared to adult *V. berus*, and Saint Girons (1957) estimated a mortality of over 50% in *V. aspis* during their first months of life. Consistent with this, Jayne and Bennett (1990) and Stanford (2002) found that larger body size positively affects survival in garter snakes, Forsman (1993) demonstrated size-dependent differences in survival of *V. berus*, and Baron et al. (1996) showed variation in age-specific survival for *Vipera ursinii*. In our study, we used body size at first encounter as a measure of age and assumed similar growth rates for all snakes during the first four years of their life. We can therefore not strictly distinguish between age effects and size effects. However, our results are mainly based on contrasts between juveniles and adults, the two life stages least sensitive to these assumptions. If anything, inaccuracies in age determination and variation in growth rate would have led to underestimated age effects, and our results are thus conservative. We further found that potential errors in size determination had a negligible effect on our results.

Based on observations that did not take into account variation in detection probabilities, Saint Girons (1952, 1957) argued that female vipers reproduce every two to four years. Using the multi-state model, we could quantify the breeding probability and found that the

estimated annual probability for females to become gravid ranged from 26% to 60% in our study populations. This result suggests that females reproduced on average every second to fourth year (Flatt and Dummermuth 1993), even though the confidence intervals around these estimates were relatively large. Interestingly, the probability of reproducing did not depend on whether a female had reproduced in the year before or not. This result contrasts with estimates from an asp viper population in western France, where females reproduce only after having reached a certain threshold in body condition, and most of the females were found to reproduce only once in their life-time (Naulleau and Bonnet 1996, Bonnet et al. 2002, Lourdais et al. 2002). We found at least two females that were gravid in four consecutive years. Furthermore, we found no evidence for reduced survival of reproductive females. If anything, they had higher survival than non-reproducers. The difference between these studies suggests that there is considerable geographic variation in life history of *Vipera aspis* (Moser et al. 1984).

The effects of weather and microclimatic conditions on many aspects of the ecology of terrestrial ectothermic vertebrates such as reptiles is well studied (Moser et al. 1984, Peterson et al. 1993, Daltry et al. 1998, Flatt et al. 2001, Sun et al. 2001, Lourdais et al. 2004), yet linking this knowledge to population dynamics requires detailed demographic models. So far, the precise demographic data required to parameterise such models are rare for reptiles and amphibians (Flatt et al. 1997, Anholt et al. 2003). This is partly due to the difficulty of observing these mostly secretive and less active ectotherms. Here we present such a demographic model for the asp viper. While our data permitted us to model age-specific survival, we could not observe reproduction frequently enough to analyse the effects of weather on variation in reproductive output. Nevertheless, our study is a step towards a better understanding of the factors driving the population dynamics of ectothermic vertebrates. For instance, many Swiss populations of the asp viper have been declining, with some populations going extinct (Moser et al. 1984, Monney 2001). Except for habitat destruction, the factors driving the decline or extinction are typically unknown. Only longterm ecological field studies based on large numbers of populations and individuals can unravel the underlying causes of such changes in population dynamics. Our study suggests that a complex interplay between climatic variation and demography may be important for the population dynamics of ectothermic vertebrates.

Acknowledgements – We thank M. T. Miller for advice with the matrix models, S. J. Downes and R. Shine for useful references and discussion, and B. Erni, P. Govindarajulu, P. T. Gregory, M. Kéry, B. Schmidt and M. Voordouw for valuable comments on a previous version of the manuscript. Weather data were kindly provided by the Swiss Federal Office of Meteorology and Climatology (MeteoSwiss). TF was supported by the Swiss

Study Foundation and the Roche Research Foundation, and TF and RA were supported by the Swiss Nationalfonds (grants no. 81ZH-68483 to RA and no. 3100-053601.98 to T.J. Kawecki).

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Subject Editor: Tim Benton

Appendix I. Number of captures/resightings (number of newly encountered individuals in parenthesis) in six populations (A to F) of *Vipera aspis* over the years of the study. Total number of captures/resightings is given for each population and year (number of new individuals for each year, and total numbers of individuals per population in parenthesis).

	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	Total
A				5 (5)	8 (6)	5 (3)	16 (13)	21 (11)	16 (7)	10 (5)	10 (1)	7 (2)	3 (1)	4 (2)	6 (4)	4 (2)	1 (0)	116 (62)
B	3 (3)	8 (6)	7 (2)	1 (0)	4 (1)	5 (4)	3 (1)	8 (7)	6 (4)	5 (0)	5 (0)	3 (0)	7 (3)	10 (5)	5 (0)	5 (4)	5 (1)	90 (41)
C						3 (3)	5 (4)	5 (2)	6 (2)	6 (5)	6 (2)	5 (1)	6 (3)	5 (1)	7 (4)	1 (0)	2 (1)	57 (28)
D									9 (9)	17 (12)	13 (6)	8 (2)	6 (2)	18 (13)	13 (4)	25 (16)	13 (2)	122 (66)
E							2 (2)	22 (20)	20 (5)	35 (19)	36 (16)	21 (6)	14 (7)	17 (7)				167 (82)
F		49 (49)	81 (50)	64 (16)	55 (11)	41 (7)	33 (3)											323 (136)
	3 (3)	57 (55)	88 (52)	70 (21)	67 (18)	54 (17)	59 (23)	56 (40)	57 (27)	73 (41)	70 (25)	44 (11)	36 (16)	54 (28)	31 (12)	35 (22)	21 (4)	875 (415)

Notes: populations A-E are located near Solothurn (coordinates: 607067/229174) and F is in Vaud, near Neuchâtel (coordinates: 563110/205600). Because the asp viper is a threatened and protected species, we do not give here the exact coordinates and locations of our study sites. Site A (approx. 4.6 km from Solothurn) lies on a SSE facing slope 800 to 900 m above sea level. The most important area of this site is a stretch approximately 600 m long and 100 m wide that includes areas covered with stones and small boulders as well as forested sections (Flatt and Dummermuth 1993). Site B (approx. 4.9 km from Solothurn) lies on a SE facing rocky forested ridge, approximately 700 m long and 100 m wide, at an altitude of 800 to 920 m above sea level. The ridge runs out into a steep rocky slope at the south-eastern end. Site C (approx. 5 km from Solothurn) consists of a S to SSE-facing rocky ridge and adjacent boulder and talus strewn areas between two quarries at an altitude of 710 to 740 m above sea level and measures approximately 100 × 60 m. Site D (approx. 8 km from Solothurn) is a stretch approximately 500 m long and 150 to 200 m wide on a rocky ridge facing S to SE. Forested areas intersect talus and rocky areas. With an altitude of 860 to 1060 m above sea level site D is one of the most elevated viper habitats in northern Switzerland. Site E (approx. 18.5 km from Solothurn) lies on an altitude of 519 to 686 m above sea level and covers a S to SSE facing forested slope interspersed with rock walls and talus areas. The site covers a surface of approximately 1000 × 150 m. Site F (approx. 22 km from Neuchâtel) covers an area of about 6 ha, is mainly SSE facing and lies at an altitude of 429 to 475 m above sea level. Half of the surface of this site is covered by oak groves. Most vipers live in an old abandoned quarry in the centre of the site and on adjacent talus slopes.

Appendix II.

Population projection matrix (with 95% confidence limits) for populations A to E:

$$\begin{bmatrix} 0 & 0 & 0 & 0 & 0.923 \\ & & & & (0.423/1.560) \\ 0.420 & 0 & 0 & 0 & 0 \\ (0.308/0.544) & & & & \\ 0 & 0.506 & 0 & 0 & 0 \\ & (0.418/0.587) & & & \\ 0 & 0 & 0.591 & 0 & 0 \\ & & (0.534/0.645) & & \\ 0 & 0 & 0 & 0.671 & 0.744 \\ & & & (0.628/0.710) & (0.703/0.782) \end{bmatrix}$$

Population projection matrix (with 95% confidence limits) for population F:

$$\begin{bmatrix} 0 & 0 & 0 & 0 & 1.323 \\ & & & & (0.412/2.331) \\ 0.574 & 0 & 0 & 0 & 0 \\ (0.457/0.681) & & & & \\ 0 & 0.655 & 0 & 0 & 0 \\ & (0.564/0.738) & & & \\ 0 & 0 & 0.727 & 0 & 0 \\ & & (0.660/0.839) & & \\ 0 & 0 & 0 & 0.792 & 0.841 \\ & & & (0.735/0.839) & (0.784/0.885) \end{bmatrix}$$