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

Res Altwegg[1]

Department of Biology, University of Victoria, Victoria, British Columbia, V8W 3N5 Canada

Stefan Dummermuth

Weissensteinstrasse 111, CH-4515 Oberdorf, Switzerland

Bradley R. Anholt

Department of Biology, University of Victoria, Victoria, British Columbia, V8W 3N5 Canada

Thomas Flatt[2]

Department of Biology, Unit of Ecology and Evolution, University of Fribourg, Chemin du Musée 10, CH-1700 Fribourg, Switzerland

[1]Corresponding author. E-mail: altwegg@uvic.ca

[2] Present address: Department of Ecology and Evolutionary Biology, Brown University, Box G-W, Providence, Rhode Island 02912, USA

1 **Abstract**

2   Detailed studies on mammals and birds have shown that the effects of climate variation

3 on population dynamics often depend on population composition, because weather affects

4 different subsets of a population differently. It is presently unknown whether this is also true for

5 ectothermic animals such as reptiles. Here we show such an interaction between weather and

6 demography for an ectothermic vertebrate by examining patterns of survival and reproduction in

7 six populations of a threatened European snake, the asp viper (*Vipera aspis*), over six to 17 years.

8 Survival was lowest among juvenile and highest among adult snakes. The estimated annual

9 probability for females to become gravid ranged from 26% to 60%, and was independent of

10 whether females had reproduced in the year before or not. Variation in juvenile survival was

11 strongly affected by winter temperature, whereas adult survival was unaffected by winter

12 harshness. A matrix population model showed that winter weather affected population dynamics

13 predominantly through variation in juvenile survival, although the sensitivity of the population

14 growth rate to juvenile survival was lower than to adult survival. This study on ectothermic

15 vipers revealed very similar patterns to those found in long-lived endothermic birds and

16 mammals. Our results thus show that climate and life history can interact in similar ways across

17 biologically very different vertebrate species, and suggest that these patterns may be very general.

18

Introduction

18

19   Stochastic variation in weather and climate increases the temporal variation in fitness

20   components, thereby affecting the dynamics and extinction risk of a population (Andrewartha and

21   Birch 1954, Lande 1993). Recent studies have revealed that weather does not affect all age

22   classes and both sexes in the same way (Leirs et al. 1997, Coulson et al. 2001). For example,

23   temperature fluctuations explained a large proportion of the variance in juvenile but not adult

24   survival in barn owls (Altwegg et al. 2003). The effect of environmental variability on

25   fluctuations in population numbers therefore critically depends on the demographic composition

26   of the population and the life history of the species (Sæther et al. 2002).

27   The effect of variation in a particular fitness component on variation in population

28   numbers depends on how sensitive the population growth rate is to changes in that component

29   (Caswell 2001). In large herbivores and long-lived birds, for example, the population growth rate

30   is least sensitive to variation in reproduction and survival of young individuals (Sæther 1997,

31   Gaillard et al. 2000). Yet, those fitness components that have the least effect on population

32   growth rate tend to be the most variable ones (Gaillard et al. 2000), whereas traits more closely

33   linked to population dynamics tend to be less variable (Sæther and Bakke 2000). This pattern

34   may be due to selection for reduced variance, acting most strongly on those traits that are closely

35   linked to fitness (Gillespie 1977, Stearns and Kawecki 1994, Pfister 1998).

36   Stochastic environmental factors may thus affect populations through complex

37   interactions with demography. However, only detailed individual-based studies of natural

38   populations can unravel such processes. Although such data sets have begun to accumulate for

39   large mammals and birds, where individuals can be followed relatively easily throughout their

40   lives (Gaillard et al. 1998, Sæther and Bakke 2000), there is almost no information on the

41   interplay between demography and environmental stochasticity in ectothermic vertebrates. Yet,

42   the insights gained from endothermic mammals and birds may not be readily applicable to

43   ectothermic vertebrates for two reasons. First, the activity patterns of ectotherms such as reptiles

44   and amphibians depend more on ambient temperature than those of mammals and birds. Second,

45   the low energy requirements make ectotherms less susceptible in terms of survivorship to long

46   periods of weather-caused food shortage (Pough 1980, Peterson et al. 1993). Thus, to understand

47   how weather affects fitness and population dynamics of ectothermic vertebrates, we need long-

48   term individual-based studies.

49   Here we illustrate the interaction between weather and demography in a threatened

50   ectothermic vertebrate, the asp viper (*Vipera aspis* L.). We monitored 415 individuals in six

51   populations located in the Jura mountains in northern Switzerland for 6 to 17 years (see also Flatt

52   and Dummermuth 1993, Flatt et al. 1997). First, we estimated age- and sex-specific survival rates

53   and the reproductive rate of females using capture-mark-recapture models (Lebreton et al. 1992).

54   Second, we used the same methods to relate temporal variation in these fitness components to

55   active-season and winter weather. Finally, we estimated the sensitivity of the population growth

56   rate to changes in each of the fitness components using matrix population models and calculated

57   the effects of weather-caused variation on population growth (Caswell 2001). Several studies

58   estimated survival rates in snakes (e.g. Saint Girons 1957, Viitanen 1967, Gregory 1977, Brown

59   and Parker 1984), and examined the effect of weather or climatic conditions on various aspects of

60   reptile ecology (e.g., Moser et al. 1984, Peterson et al. 1993, Daltry et al. 1998, Flatt et al. 2001,

61   Sun et al. 2001, Lourdais et al. 2004, and references therein). Our study extends these findings in

62   two important ways. First, we account for variation in detection probability, which is likely to be

63   lower for juvenile than for adult snakes, and may depend on the weather during the surveys.

64   Second, we explicitly model the life cycle of our study organism, and thus estimate the impact of

65 external factors (such as weather) on population dynamics through variation in a particular fitness

66 component. An explicit representation of the life cycle is necessary because similar changes in

67 two different fitness components will not necessarily have similar effects on overall fitness and

68 population dynamics (Ehrlén 2003).

69 **Methods**

70 **Field methods**

71   Between 1986 and 2002, we monitored six isolated populations of asp vipers. Flatt and

72 Dummermuth (1993) and Flatt et al. (1997) provide a description of the natural history of the asp

73 viper and methodological details of fieldwork. Sample sizes and short descriptions of the study

74 sites are given in Appendix I. We visited each site between one and 35 times per year during the

75 entire activity period, from mid-March to mid-October, but 74% of the observations were made

76 between Mai and September. Snakes were located from a distance with telephoto lenses,

77 binoculars or by sight while walking slowly through the terrain. Identification of known

78 individuals was based on photographs and detailed drawings of the head and neck coloration

79 made at first encounter. We used overall coloration, dorsal colour pattern, scars and other

80 distinctive marks for identification. In most cases, individuals were clearly identifiable from close

81 distance and were only hand-captured if their identity was in doubt (10-20% of the cases). For

82 each individual we recorded at every encounter the age class, sex, sight-estimated size, and

83 reproductive status for females. Gravid female asp vipers recognisably change their body

84 proportions within a few weeks after copulation. In doubtful cases, the snake was captured and its

85 reproductive status verified by hand-scanning the body. We avoided capture whenever possible in

86 order to minimise the disturbance of these threatened animals. Comparisons using captive

87   animals showed that our estimates of body size are within 10% of the measured size (SD,

88   unpublished data).

89   Age determination of individuals at first encounter was based on approximate body size.

90   We classified individuals smaller than 30 cm as juvenile, individuals between 30 and 50 cm as

91   subadult, and larger individuals as adult. In our populations, female vipers generally start

92   reproducing at 50 cm and in their 4th or 5th year (SD, personal observation). Males may start

93   reproducing earlier, but their reproductive status could not be assessed in the field. Since the

94   subadult stage usually takes three years to complete, we assigned individuals to yearly age classes

95   based on their size at first encounter, assuming similar growth rates among individuals over the

96   first four years of life (first year subadult: < 37 cm, second year: between 37 and 44 cm, third

97   year: > 44 cm). Growth may vary with food abundance, and our size estimates may be less

98   accurate than if we had been able to hand-measure each individual. We therefore estimated the

99   impact of potential errors in age determination on our survival estimates for population B, which

100   is the smallest population with age effects, and thus potentially most affected by errors. We

101   generated ten data sets that were equal to the original one, except that we added a substantial

102   amount of random error to the estimates of body size. The errors were drawn from a normal

103   distribution with standard deviation equal to 10% of the estimated body size. The ten data sets

104   with artificially increased error yielded survival rates that were almost identical to the ones

105   obtained from the original data set. The most extreme value for any survival rate was within 70%

106   of the standard error of the original estimate, and our estimates are therefore robust to errors in

107   age and size determination.

108   **Statistical methods**

109   We used basic capture-mark-recapture (CMR) methods (Lebreton et al. 1992) to estimate

110   recapture and survival rates. CMR methods allow modelling of the recapture rate (probability that

111   an individual was recaptured or resighted at time *i*, given that it was alive and in the study area at

112   that time) independently of the survival rate. We can therefore examine factors affecting the

113   recapture rate (e.g. effort in the field) and the survival rate separately, and CMR gives unbiased

114   estimates of survival even if a proportion of the individuals was not observed at every recapture

115   occasion. Mortality here includes both death and permanent emigration. In terms of the

116   population ecology of vipers in our area, death and emigration are essentially equivalent, since

117   we only observed two adult males who successfully moved between populations and there are no

118   other populations nearby where emigrants could establish. Second, we used multi-state

119   extensions of CMR models to calculate reproductive probabilities of females (Nichols et al.

120   1994). CMR models assume that all individuals within one group have the same probability of

121   survival and recapture in each time step, and that all individuals are identified correctly (Lebreton

122   et al. 1992). We verified that our data met these assumptions using a goodness-of-fit test provided

123   by the program RELEASE (Test 2+3, Burnham et al. 1987) and found that a general time

124   dependent model described the data well (each population tested separately: A: $\chi^2 = 33.30$, df=

125   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,

126    $P = 0.63$; E: $\chi^2 = 15.70$, df= 12, $P = 0.21$; F: $\chi^2 = 19.23$, df= 17, $P = 0.32$). The other models are

127   generalisations or simplifications of these models and do therefore also meet the assumptions.

128   We are, however, violating the additional assumption that recaptures are instantaneous in time,

129   and this may lead to overestimating survival. Hargrove and Borland (1994) estimated this bias to

130   be <5% in situations comparable to ours.

131   Because the sample sizes precluded fitting large numbers of models or overly complex

132   models, we limited our analyses to a few factors that seemed most likely on biological grounds,

133   and a minimal number of models. These models form our set of candidate models. Additional

134   models, coming up as interesting alternatives during analysis, were fitted a posteriori and are

135   marked in the tables accordingly. All models were fitted using maximum-likelihood methods

136   implemented in the program MARK (White and Burnham 1999). To compare models we used

137   the sample-size adjusted Akaike's Information Criterion (AIC_c; Burnham and Anderson 2002).

138   The model with the lowest AIC_c value is best supported by the data. For each model, we also

139   calculated Akaike weights (*w*) to assess the relative support from the data for a particular model

140   as compared to the other models in the set (Burnham and Anderson 2002). Model selection

141   identifies the model that best describes the structure in a data set, and favours the model that

142   provides the best balance between overfitting (hence loss of precision) and underfitting (hence

143   bias, see Burnham and Anderson 2002). Like with any statistical method, smaller effects need

144   larger sample sizes to be detected, and smaller data sets therefore tend to select simpler models

145   than large data sets.

146   *Modelling and estimation of recapture and survival probabilities*. —— We proceeded in

147   three steps. First, we investigated sex- and age-differences, and temporal variation in survival and

148   recapture rates for each of the six populations separately. Second, we analysed differences

149   between populations in age-specific survival and recapture in a single analysis. It turned out that

150   sex effects were always weaker than age effects, with opposite trends across populations. In order

151   to simplify the modelling procedure, we therefore did not examine sex differences at this second

152   step. Third, we related age-specific survival to weather variation, using data provided by

153   MeteoSwiss meteorological stations. An initial analysis with the largest data set (population F)

154   showed that variation in survival and recapture was best represented by positive linear

155   relationships with age, and we used this relationship for the rest of the analysis. As a

156   consequence, estimates for subadults always lay between the estimates for adults and juveniles,

157   and we do not always report the former separately. We also investigated whether recapture effort,

158   i.e. the number of visits to a field site, affected the recapture rate in all populations. If a

159   population was not visited at all in a particular year, the recapture rate was set to zero for that

160   year. Daily mean temperatures were measured at Wynau (UTM coordinates: 626400/233860, 422

161   m above sea level, for populations A to E) and Neuchâtel (563110/205600, 487 m a.s.l., for

162   population F) and monthly precipitation was measured at Balsthal (619250/240860, 502 m a.s.l.,

163   for populations A to E) and Yverdon (539840/181450, 433 m a.s.l., for population F). We

164   considered separate models for the effect of winter and active-season weather. The winter effect

165   consisted of the mean temperature measured on the coldest day and the number of days with

166   mean temperature below 0°C. The active-season effect consisted of the linear and quadratic

167   effects of mean daily temperature and mean monthly precipitation between 1 April and 31

168   October. Quadratic effects were included in the active-season effect because snakes may be

169   sensitive to extreme weather conditions at both ends of the scale (e.g., Saint Girons 1952, 1981).

170   Each of the climate effects entered the models either as a main effect or as an interaction with the

171   age effect. As none of the weather variables were significantly correlated with each other, we did

172   not attempt to reduce their number by principal components analysis.

173   *Analysis of probability of reproduction.* —— We estimated the probabilities for females to

174   reproduce in a given year using multi-state models (Nichols et al. 1994). We defined two states

175   that sexually mature females could assume: gravid versus non-gravid. The transition probabilities

176   between these states were then 1) the probability of becoming gravid in the following year for a

177   currently non-gravid female (ψ_{nr}); 2) the probability for a non-gravid female to remain in this

178   condition ($1-\psi_{nr}$); 3) the probability of not being gravid in the following year for a currently

179   gravid female (ψ_{rn}); and 4) the probability for a gravid female to be gravid again in the following

180   year ($1-\psi_{rn}$). These transitions are conditional on survival, i.e. an individual has to survive the

181   time interval before it can change its state. We further make the presently untestable assumption

182   that all individuals with a particular state are equally likely to change from one state into the

183   other. The analysis of reproductive probability included only adult individuals, even though some

184   of the individuals classified as 3rd year subadult may have reproduced in rare cases. Due to the

185   large data requirements of multi-state models, we pooled the data of the populations in close

186   proximity to each other (A to E) and only considered the period between 1994 and 1999 during

187   which all these populations were studied simultaneously. Population F yielded enough data to be

188   analysed separately. We examined the effects of temporal variation and active-season weather on

189   both transition probabilities. We did not consider quadratic effects of active-season weather as in

190   the survival analysis because the smaller sample size and the shorter time span did not warrant

191   more complex effects.

192   **Matrix population modelling**

193   We used Leslie matrices to estimate the sensitivity of the population growth rate (λ) to

194   variation in vital rates. Methods exist to estimate sensitivity from CMR data directly (Nichols et

195   al. 2000). However, with strongly age-dependent survival as in our data set, these methods are

196   not applicable. The matrix entries were the age-specific survival rates taken from the CMR

197   models and reproductive rates (Appendix II). The latter are the product of the probability for

198   females to reproduce, litter size, the sex ratio within the litter, and the survival probability of

199   new-born from birth in late fall until next spring. Whereas the probability of reproducing was

200   also obtained from the CMR models (see above), data on the other components of recruitment

201   could not be estimated from the data directly. We therefore used data obtained from the literature,

202   supported by occasional observations in our study populations. We used a mean litter size of ten,

203   a 1:1 sex ratio (Saint Girons 1952, Flatt and Dummermuth 1993), and set the survival of new-

204   born equal to the survival of juvenile individuals. Due to the uncertainty in the estimate of

205   reproductive rates, we did not further examine variation in this trait. First, we assessed the effects

206   of variation in fitness components on population growth using sensitivity and elasticity analyses

207   (Stearns 1992, Caswell 2001). We calculated 95% confidence limits by generating 1000 matrices

208   with elements drawn from a normal distribution with mean and variance obtained from the logit

209   transformed CMR estimates. After being sorted by their magnitude, the 25th and 975th bootstrap

210   replicates represent the lower and the upper confidence limits. Second, in a retrospective analysis

211   (Caswell 2000), we asked how much of the weather-caused variance in survival during the

212   different life stages contributed to variation in λ. To do this, we used survival rates obtained from

213   the weather-dependent CMR model and multiplied the variances in stage specific survival with

214   the square of the corresponding sensitivities (Caswell 2001). All matrix analyses were performed

215   for the pooled populations A to E and for population F using the S-plus-2000 software package

216   (Insightful Corp., Seattle USA).

217   **Results**

218   **Recapture rates**

219   Model selection showed that the recapture probabilities were lower for juvenile than for

220   adult snakes in populations A, C, D and F and varied with recapture effort or time for all

221   populations but D. In no population did the recapture rate differ between the sexes. The estimates

222   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

223   in E, and from 0 to 0.89 in F.

224   **Patterns of survival**

225   Model selection showed similar demographic patterns in all populations. AICc favoured

226   the model incorporating age-dependent survival in populations A, B, E, and F (Table 1). Survival

227   was lowest for juveniles, higher for subadults, and highest for adults (Fig. 1). Population C

228   showed a similar pattern, but the confidence intervals for the estimates were large. The best

229   estimate of the relationship in population D was very near zero (Fig. 1). The AICc-selected best

230   models did not include differences between sexes in any population except F. Population F

231   included the effect of sex and the interaction between age and sex, suggesting higher survival for

232   adult females compared to adult males, but equal survival of the juveniles of both sexes (Fig. 1).

233   Survival stayed fairly constant throughout the duration of our study in all populations, and the

234   models accounting for potential time effects were always poorly supported by the data.

235   **Comparison between populations**

236   We quantitatively compared all populations, A through F, in a single analysis. We used all

237   data collected between 1986 and 2002 while setting the corresponding recapture rate to zero if a

238   population was not sampled in a particular year. The best-supported models accounted for the

239   effects of sampling effort and age on recapture rates (models 2 to 11, Table 2). AICc further

240   showed that recapture rates differed between populations (models 3 to 11, Table 2). Among the a

241   priori models (models 1 to 10, Table 2), AICc selected the one allowing for survival differences

242   between populations and accounting for interactions between age and winter weather (model 8).

243   A close competitor of model 8 was model 2, excluding the effect of winter weather, while the

244   other models were poorly supported. A posteriori, we investigated the role of winter harshness by

245   fitting a reduced winter-weather model including only the effect of the number of days with

246   temperatures below zero. The AICc value of this model was 3.26 units lower and thus

247   considerably better supported by the data than the best a priori model, suggesting that juvenile

248   survival was strongly dependent on winter harshness whereas adult survival was unaffected (Fig.

249   2).

250   **Probabilities of reproduction**

251   The multi-state models required pooling populations A to E for calculating the probability

252   for females to became gravid, but we were able to examine population F separately. Model

253   selection suggested constant reproductive probabilities over time except that reproducers in

254   population F were more likely to reproduce again after relatively warm and wet summers (model

255   1 and model 5, Table 3). Model 1, suggesting constant reproductive probabilities, was a close

256   competitor to the best model in population F. In populations A to E the probabilities of

257   reproducing in the following year were 0.27 (95% CI: 0.14 / 0.45) for currently non-reproductive

258   females and 0.26 (CI: 0.09 / 0.57) for currently reproducing females. In population F the

259   probabilities of reproducing were 0.40 (95% CI: 0.13 / 0.75) for currently non-reproductive

260   females and 0.60 (CI: 0.36 / 0.80) for currently reproducing females.

261   For populations A to F, reproducing females survived better than non-reproducing ones.

262   Omitting this factor from the best model (model 1, Table 3a) resulted in a poorly fitting model

263   (K= 4, Deviance = 132.608, AICc= 240.999, Δ AICc= 2.361). For population F, we found no

264   evidence for differential survival between the two types of females (adding this factor to model 5,

265   Table 3b, resulted in a poorly fitting model: K= 7, Deviance = 151.503, AICc= 278.802, Δ

266   AICc= 2.163).

267   **Sensitivity of λ to variation in survival and recruitment**

268   The matrix model (Appendix II) yielded an asymptotic population growth rate (λ), i.e. the

269   growth rate once the population has reached a stable age distribution (Caswell 2001), of 0.873

270   (95% confidence interval: 0.811 / 0.936) for the pooled populations A to E and 1.057 (0.943 /

271   1.152) for population F. These estimates show that populations A to E are projected to decrease

272   given the estimated fitness components, whereas population F is projected to stay constant. For

273   all populations, the sensitivity and elasticity analyses consistently showed that population growth

274   was most affected by variation in adult survival and least affected by variation in reproduction

275   (Table 4). However, the retrospective analysis showed that weather affected λ most strongly

276   through the survival of juveniles as weather caused the largest variation in this life stage (Table

277   4).

Discussion

279   This study examined the interactive effects of demography and weather on fitness

280   components, and their effect on the growth rate of six populations of a threatened European

281   snake, the asp viper. Despite the large biological differences of the study species, our results

282   reveal the same patterns reported for mammals and birds (Gaillard et al. 1998, Sæther and Bakke

283   2000), suggesting that these patterns may be general for terrestrial vertebrates. Our main finding

284   is that variation in juvenile survival, but not adult survival, was strongly affected by winter

285   temperature. Winter temperature affected population growth rate predominantly through variation

286   in juvenile survival, even though the sensitivity of the population growth rate to juvenile survival

287   was lower than to adult survival.

288   Climatic variation often affects subsets of a population differently, and in such cases its

289   effect on population dynamics depends on the current demographic composition of the

290   population (Leirs et al. 1997, Coulson et al. 2001, Stenseth et al. 2002). For instance, different

291   responses of the sexes and age classes to climatic variation is one of the factors leading to

292   different population dynamics in the otherwise ecologically similar red deer and Soay sheep on

293   Scottish islands (Clutton-Brock and Coulson 2002). If such patterns are common, detailed

294   knowledge of the demography and differential susceptibility of demographic components of a

295   population to climatic variation is crucial for a mechanistic understanding of population

296   dynamics. Despite the extensive literature on snake population ecology (Parker and Plummer

297   1987), there are few data on survival under natural conditions (e.g. Turner 1977, Shine and

298   Charnov 1992, Flatt et al. 1997). This lack of information is one of the major constraints in snake

299   conservation (Dodd Jr. 1993).

300   The results presented here suggest that survival of juvenile asp vipers is more susceptible

301   to harsh winter conditions than are other fitness components. Several factors could lead to these

302   results: differences between age classes could arise because young individuals are less

303   experienced in finding suitable winter quarters than adults. Alternatively, juveniles may be more

304   likely to run out of fat reserves during hibernation than adults. Our results are unlikely to be

305   affected by differential emigration, as our results would imply greater mobility of young snakes

306   in colder winters, which seems unlikely for these ectothermic organisms. Substantial winter

307   losses have also been found in adult garter snakes (*Thamnophis sirtalis*; winter mortality: 34 to

308   48%; Gregory 1977), and in the European adder (*Vipera berus*; juvenile mortality: 47.2%, and

309   adult mortality: 18.1%; Viitanen 1967). These estimates are probably biased high, however, as

310   these studies could not account for detection probabilities.

311   In accordance with the general patterns found in long-lived turtles, birds and mammals

312   (Crouse et al. 1987, Pfister 1998, Sæther and Bakke 2000, Gaillard et al. 2000), population

313   growth in our asp viper populations was less sensitive to changes in the more variable juvenile

314   survival than the less variable adult survival. Yet, winter weather affected population growth

315   predominantly through juvenile survival because it caused most of the variation in this trait. This

316   is consistent with the finding that ungulate population dynamics are mostly driven through

317   variation in juvenile survival despite the relatively low impact of this fitness component on

318   population growth (Gaillard et al. 2000).

319   Our age-specific estimates of survival compare well with earlier estimates on this or

320   similar species (Parker and Plummer 1987; see also discussion in Flatt et al. 1997). For example,

321   Flatt et al. (1997) found an average adult survival rate of 0.75 for populations A and B over the

322   first six and nine years of the study. Our corresponding estimates are 0.74 for populations A to E,

323   and 0.84 for population F. However, as in our previous study (Flatt et al. 1997), we were unable

324   to detect temporal variation in survival of adult vipers. In contrast, the studies by Brown and

325   Parker (1984) and Forsman (1995) have found substantial variation in survival among years. This

326   result potentially is affected by variable recapture success, for which these studies did not correct.

327   While it generally appears that juvenile and first-year mortality is higher than adult

328   mortality among snakes (Saint Girons 1957, Brown and Parker 1984), there is little data on

329   survival of young age classes, and to our knowledge only one study accounted for the possibly

330   lower detection probabilities of young snakes (Stanford 2002). Viitanen (1967) found lower

331   survival in juveniles as compared to adult *V. berus*, and Saint Girons (1957) estimated a mortality

332   of over 50% in *V. aspis* during their first months of life. Consistent with this, Jayne and Bennett

333   (1990) and Stanford (2002) found that larger body size positively affects survival in garter

334   snakes, Forsman (1993) demonstrated size-dependent differences in survival of *V. berus*, and

335   Baron et al. (1996) showed variation in age-specific survival for *Vipera ursinii*. In our study, we

336   used body size at first encounter as a measure of age and assumed similar growth rates for all

337   snakes during the first four years of their life. We can therefore not strictly distinguish between

338   age effects and size effects. However, our results are mainly based on contrasts between juveniles

339   and adults, the two life stages least sensitive to these assumptions. If anything, inaccuracies in

340   age determination and variation in growth rate would have led to underestimated age effects, and

341   our results are thus conservative. We further found that potential errors in size determination had

342   a negligible effect on our results.

343   Based on observations that did not take into account variation in detection probabilities,

344   Saint Girons (1952, 1957) argued that female vipers reproduce every two to four years. Using the

345   multi-state model, we could quantify the breeding probability and found that the estimated annual

346   probability for females to become gravid ranged from 26% to 60% in our study populations. This

347   result suggests that females reproduced on average every second to fourth year (see also Flatt and

348   Dummermuth 1993), even though the confidence intervals around these estimates were relatively

349   large. Interestingly, the probability of reproducing did not depend on whether a female had

350   reproduced in the year before or not. This result contrasts with estimates from an asp viper

351   population in western France, where females reproduce only after having reached a certain

352   threshold in body condition, and most of the females were found to reproduce only once in their

353   life-time (Naulleau and Bonnet 1996, Lourdais et al. 2002, Bonnet et al. 2002). We found at least

354   two females that were gravid in four consecutive years. Furthermore, we found no evidence for

355   reduced survival of reproductive females. If anything, they had higher survival than non-

356   reproducers. The difference between these studies suggests that there is considerable geographic

357   variation in life history of *Vipera aspis* (see also discussion in Moser et al. 1984).

358   The effects of weather and microclimatic conditions on many aspects of the ecology of

359   terrestrial ectothermic vertebrates such as reptiles is well studied (e.g., Moser et al. 1984,

360   Peterson et al. 1993, Daltry et al. 1998, Flatt et al. 2001, Sun et al. 2001, Lourdais et al. 2004, and

361   references therein), yet linking this knowledge to population dynamics requires detailed

362   demographic models. So far, the precise demographic data required to parameterise such models

363   are rare for reptiles and amphibians (but see Flatt et al. 1997, Anholt et al. 2003). This is partly

364   due to the difficulty of observing these mostly secretive and less active ectotherms. Here we

365   present such a demographic model for the asp viper**.** While our data permitted us to model age-

366   specific survival, we could not observe reproduction frequently enough to analyse the effects of

367   weather on variation in reproductive output. Nevertheless, our study is a step towards a better

368   understanding of the factors driving the population dynamics of ectothermic vertebrates. For

369   instance, many Swiss populations of the asp viper have been declining, with some populations

370   going extinct (Moser et al. 1984, Monney 2001). Except for habitat destruction, the factors

371   driving the decline or extinction are typically unknown. Only long-term ecological field studies

372   based on large numbers of populations and individuals can unravel the underlying causes of such

373   changes in population dynamics. Our study suggests that a complex interplay between climatic

374   variation and demography may be important for the population dynamics of ectothermic

375   vertebrates.

References

385   Altwegg, R., Roulin, A., Kestenholz, M., and Jenni, L. 2003. Variation and covariation in

386   survival, dispersal, and population size in barn owls *Tyto alba*. - J. Anim. Ecol. 72: 391-

387   399.

388   Andrewartha, H. G. and Birch, L. C. 1954. The distribution and abundance of animals. -

389   University of Chicago Press, Chicago.

390   Anholt, B. R., Hotz, H., Guex, G.-D., and Semlitsch, R. D. 2003. Over winter survival of *Rana*

391   *lessonae* and its hemiclonal associate *Rana esculenta*. - Ecology 84: 391-397.

392   Baron, J. P., Ferrière, R., Clobert, J., and Saint Girons, H. 1996. Stratégie démographique de

393   *Vipera ursinii* au Mont Ventoux (France). - CR Acad Sci III Vie 319: 57-69.

394   Bonnet, X., Lourdais, O., Shine, R., and Naulleau, G. 2002. Reproduction in a typical capital

395   breeder: costs, currencies, and complications in the aspic viper. - Ecology 83: 2124-2135.

396   Brown, W. S. and Parker, W. S. 1984. Growth, reproduction and demography of the racer,

397   *Coluber constrictor mormon*, in Northern Utah. - In: Seigel, R. A., Hunt, L. F., Knight, J.

398   L., Malaret, L., and Zuschlag, N. L. (eds), Vertebrate Ecology and Systematics - A

399   Tribute to Henry S. Fitch. University of Kansas Museum of Natural History, Special

400   Publications, No. 10, pp. 13-40.

401   Burnham, K. P. and Anderson, D. R. 2002. Model selection and multimodel inference: a practical

402   information-theoretic approach. - 2nd edition. Springer, New York.

403   Burnham, K. P., Anderson, D. R., White, G. C., Brownie, C., and Pollock, K. H. 1987. Design

404   and analysis methods for fish survival experiments based on release-recapture. -

405   American Fishing Society, Monograph 5. Bethesda, MD.

406   Caswell, H. 2000. Prospective and retrospective perturbation analyses: their roles in conservation

407   biology. - Ecology 81: 619-627.

408   Caswell, H. 2001. Matrix population models. - 2nd edition. Sinauer, Sunderland, MA.

409   Clutton-Brock, T. H. and Coulson, T. 2002. Comparative ungulate dynamics: the devil is in the

410   detail. - Phil. Trans. Roy. Soc. B 357: 1285-1298.

411   Coulson, T., Catchpole, E. A., Albon, S. D., Morgan, B. J. T., Pemberton, J. M., Clutton-Brock,

412   T. H., Crawley, M. J., and Grenfell, B. T. 2001. Age, sex, density, winter weather, and

413   population crashes in Soay sheep. - Science 292: 1528-1531.

414   Crouse, D. T., Crowder, L. B., and Caswell, H. 1987. A stage-based population model for

415   loggerhead sea turtles and implications for conservation. - Ecology 68: 1412-1423.

416   Daltry, J.C., Ross, T., Thorpe, R.S., and Wuester, W. 1998. Evidence that humidity influences

417   snake activity patterns: a field study of the Malayan pit viper *Calloselasma rhodostoma*. –

418   Ecography 21: 25-34.

419   Dodd Jr., C. K. 1993. Strategies for snake conservation. - In: Seigel, R. A. and Collins, J. T.

420   (eds), Snakes - Ecology and Behavior. McGraw-Hill, New York., pp. 363-393.

421   Ehrlén, J. 2003. Fitness components versus total demographic effects: Evaluating herbivore

422   impacts on a perennial herb. - Am. Nat. 162: 796-810.

423   Flatt, T. and Dummermuth, S. 1993. Zur Kenntnis der Aspis- oder Juraviper *Vipera a aspis* (L.,

424   1758) im Kanton Solothurn. - Mittl. Nat. Ges. Kanton Solothurn 36: 75-102.

425   Flatt, T., Dummermuth, S., and Anholt, B. R. 1997. Mark-recapture estimates of survival in

426   populations of the asp viper *Vipera aspis aspis*. - J. Herpetol 31: 558-564.

427   Flatt, T., Shine, R., Borges-Landaez, P.A., and Downes, S.J.. 2001. Phenotypic variation in an

428   oviparous montane lizard: effects of thermal and hydric incubation environments. - Biol.

429   J. Linn. Soc. 74: 339-350.

430   Forsman, A. 1993. Survival in relation to body size and growth rate in the adder, *Vipera berus*. -

431   J. Anim. Ecol. 62: 647-655.

432   Forsman, A. 1995. Opposing fitness consequences of colour pattern in male and female snakes. -

433   J. Evol. Biol. 8: 53-70.

434   Gaillard, J.-M., Festa-Bianchet, M., and Yoccoz, N. G. 1998. Population dynamics of large

435   herbivores: variable recruitment with constant adult survival. - Trends Ecol. Evol. 13: 58-

436   63.

437   Gaillard, J.-M., Festa-Bianchet, M., Yoccoz, N. G., Loison, A., and Toigo, C. 2000. Temporal

438   variation in fitness components and population dynamics of large herbivores. - Annu.

439   Rev. Ecol. Syst. 31: 367-393.

440 Gillespie, J. H. 1977. Natural selection for variances in offspring numbers: a new evolutionary

441   principle. - Am. Nat. 111: 1011-1014.

442 Gregory, P. T. 1977. Life-history parameters of the red-sided garter snake (*Thamnophis sirtalis*)

443   in an extreme environment, the Interlake region of Manitoba. - Nat. Mus. Can. Publ. Zool.

444   13: 1-44.

445 Hargrove, J. W. and Borland, C. H. 1994. Pooled population parameter estimates from mark-

446   recapture data. - Biometrics 50: 1129-1141.

447 Jayne, B. C. and Bennett, A. F. 1990. Selection on locomotor performance capacity in a natural

448   population of garter snakes. - Evolution 44: 1204-1229.

449 Lande, R. 1993. Risks of population extinction from demographic and environmental

450   stochasticity and random catastrophes. - Am. Nat. 142: 911-927.

451 Lebreton, J. D., Burnham, K. P., Clobert, J., and Anderson, D. R. 1992. Modeling survival and

452   testing biological hypotheses using marked animals: a unified approach with case studies.

453   - Ecol. Monogr. 62: 67-118.

454 Leirs, H., Stenseth, N. C., Nichols, J. D., Hines, J. E., Verhagen, R., and Verheyen, W. 1997.

455   Stochastic seasonality and nonlinear density-dependent factors regulate population size in

456   an African rodent. - Nature 389: 176-180.

457 Lourdais, O., Bonnet, X., Shine, R., Denardo, D., Naulleau, G., and Guillon, M. 2002. Capital-

458   breeding and reproductive effort in a variable environment: a longitudinal study of a

459   viviparous snake. - J. Anim. Ecol. 71: 470-479.

460 Lourdais, O., Shine, R., Bonnet, X., Guillon, M., and Naulleau, G. 2004. Climate affects

461   embryonic development in a viviparous snake, *Vipera aspis*. – Oikos 104: 551-560.

462   Monney, J.-C. 2001. *Vipera aspis* (Linnaeus, 1758) - Aspisviper. - In: Hofer, U., Monney, J.-C.,

463   and Dušej (eds), Die Reptilien der Schweiz - Verbreitung, Lebensräume, und Schutz.

464   Birkhäuser, Basel, Boston, Berlin., pp. 107-114.

465   Moser, A., Graber, C., and Freyvogel, T. A. 1984. Observations sur l'éthologie et l'évolution

466   d'une population de *Vipera aspis* (L.) au nord du Jura Suisse. - Amphibia-Reptilia 5: 373-

467   393.

468   Naulleau, G. and Bonnet, X. 1996. Body condition threshold for breeding in a viviparous snake. -

469   Oecologia 107: 301-306.

470   Nichols, J. D., Hines, J. E., Lebreton, J.-D., and Pradel, R. 2000. Estimation of contributions to

471   population growth: a reverse-time capture-recapture approach. - Ecology 81: 3362-3376.

472   Nichols, J. D., Hines, J. E., Pollock, K. H., Hinz, R. L., and Link, W. A. 1994. Estimating

473   breeding proportions and testing hypotheses about costs of reproduction with capture-

474   recapture data. - Ecology 75: 2052-2065.

475   Parker, W. S. and Plummer, M. V. 1987. Population ecology. - In: Seigel, R. A., Collins, J. T.,

476   and Novak, S. S. (eds), Snakes: Ecology and Evolutionary Biology. McGraw-Hill, New

477   York., pp. 253-301.

478   Peterson, C. R., Gibson, A. R., and Dorcas, M. E. 1993. Snake thermal ecology: the causes and

479   consequences of body-temperature variation. - In: Seigel, R. A., Collins, J. T., and

480   Nowak, S. S. (eds), Snakes: Ecology and Evolutionary Biology. McGraw-Hill, New

481   York., pp. 241-314.

482   Pfister, C. A. 1998. Patterns of variance in stage-structured populations: evolutionary predictions

483   and ecological implications. - Proc. Natl. Acad. Sci. USA 95: 213-218.

484   Pough, F. H. 1980. The advantages of ectothermy for tetrapods. - Am. Nat. 115: 92-112.

485   Sæther, B.-E. 1997. Environmental stochasticity and population dynamics of large herbivores: a

486   search for mechanisms. - Trends Ecol. Evol. 12: 143-149.

487   Sæther, B.-E. and Bakke, Ø. 2000. Avian life history variation and contribution of demographic

488   traits to the population growth rate. - Ecology 81: 642-653.

489   Sæther, B.-E., Engen, S., and Matthysen, E. 2002. Demographic characteristics and population

490   dynamical patterns of solitary birds. - Science 295: 2070-2073.

491   Saint Girons, H. 1952. Ecologie et éthologie des vipères de France. - Ann. Sci. Nat., Zool., Paris

492   14: 263-343.

493   Saint Girons, H. 1957. Croissance et fécondité de *Vipera aspis* (L.). - Vie et Milieu 31: 59-64.

494   Saint Girons, H. 1981. Cycle annuel et survie de quelques vipères d'Europe. Influence des

495   températures exceptionellement élevées de l'année 1976. - Vie et Milieu 31: 59-64.

496   Shine, R. and Charnov, E. L. 1992. Patterns of survival, growth, and maturation in snakes and

497   lizards. - Am. Nat. 139: 1257-1269.

498   Stanford, K. M. 2002. Demography and life history of an urban population of plains garter

499   snakes, *Thamnophis radix*. - Northern Illinois University, Illinois, Masters thesis.

500   Stearns, S. C. 1992. The evolution of life histories. - Oxford University Press, Oxford.

501   Stearns, S. C. and Kawecki, T. J. 1994. Fitness sensitivity and the canalization of life-history

502   traits. - Evolution 48: 1438-1450.

503   Stenseth, N. C., Mysterud, A., Ottersen, G., Hurrell, J. W., Chan, K.-S., and Lima, M. 2002.

504   Ecological effects of climate fluctuations. - Science 297: 1292-1296.

505   Sun, L.-X., Shine R., Debi, Z., and T. Zhengren. 2001. Biotic and abiotic influences on activity

506   patterns of insular pit-vipers (*Gloydius shedaoensis*, Viperidae) from north-eastern China.

507   – Biol. Conserv. 97: 387-398.

508   Turner, F. B. 1977. The dynamics of populations of squamates, crocodilians, and

509   rhynchocephalians. - In: Gans, C. and Tinkle, D. W. (eds), Biology of the Reptilia.

510   Academic Press, New York., pp. 157-264.

511   Viitanen, P. 1967. Hibernation and seasonal movements of the viper, *Vipera berus berus* (L.), in

512   southern Finland. - Ann. Zool. Fenn. 4: 472-546.

513   White, G. C. and Burnham, K. P. 1999. Program MARK: Survival estimation from populations

514   of marked animals. - Bird Study 46: S120-139.

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 (AICc); lower values indicate better fit. ΔAICc gives the difference in AICc 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	AICc	Δ AICc	w
A	constant	4	216.276	258.957	1.192	0.244
(age, effort)	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
						Σ= 1
B	constant	3	166.067	199.409	6.154	0.025
(effort)	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
						Σ= 1
C	**constant**	**4**	**76.158**	**103.687**	**0.000**	**0.493**
(age, effort)	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
						Σ= 1
D	**constant**	**3**	**128.738**	**215.877**	**0.000**	**0.477**
(age)	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
						Σ= 1

Table 1, continued.

Population	Factors in survival model	K	Deviance	AICc	Δ AICc	w
E	constant	8	121.764	264.84	10.160	0.004
(time)	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
						Σ= 1
F	constant	11	216.600	523.450	13.505	0.001
(age, time, interaction)	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**
						Σ= 1

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 Δ AICc is the difference in AICc to the best a priori model. * between two effects symbolises interactive effects; ‡ 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	AICc	Δ AICc	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 * 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 * 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 * active season	population, age, effort	23	769.912	1557.501	8.268	0.006
11 ‡	population, age * days below zero	population, age, effort	17	770.997	1545.977	-3.256	

Σ= 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	AICc	Δ AICc	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
						Σ= 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**
						Σ= 1

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.

Figure 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.

Figure 2. Interaction between winter harshness, expressed as the number of days with average temperatures below zero, and age on survival of asp vipers. The figure shows estimates 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.
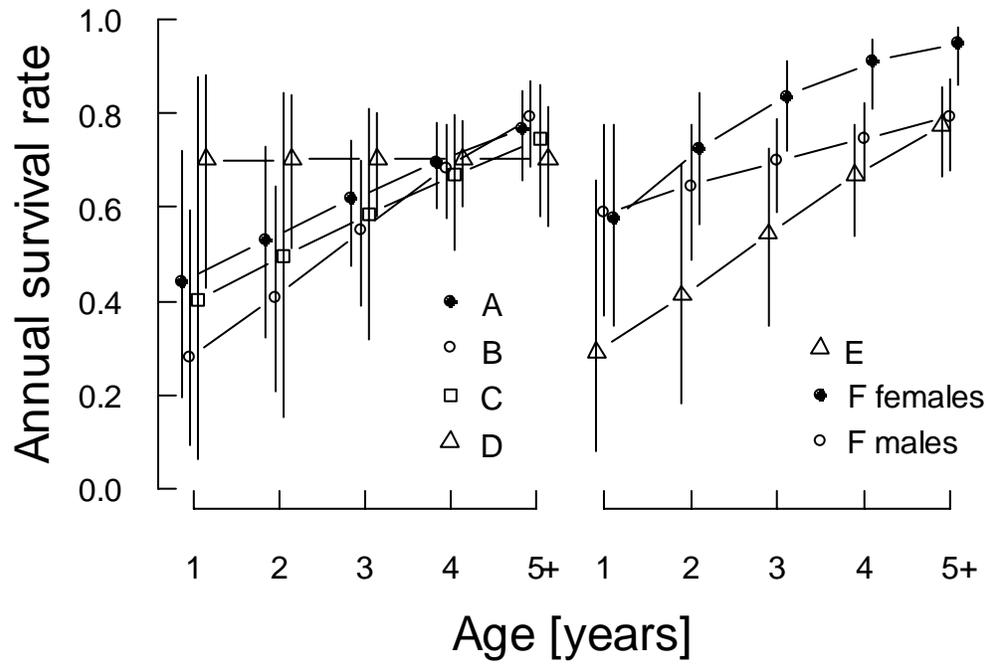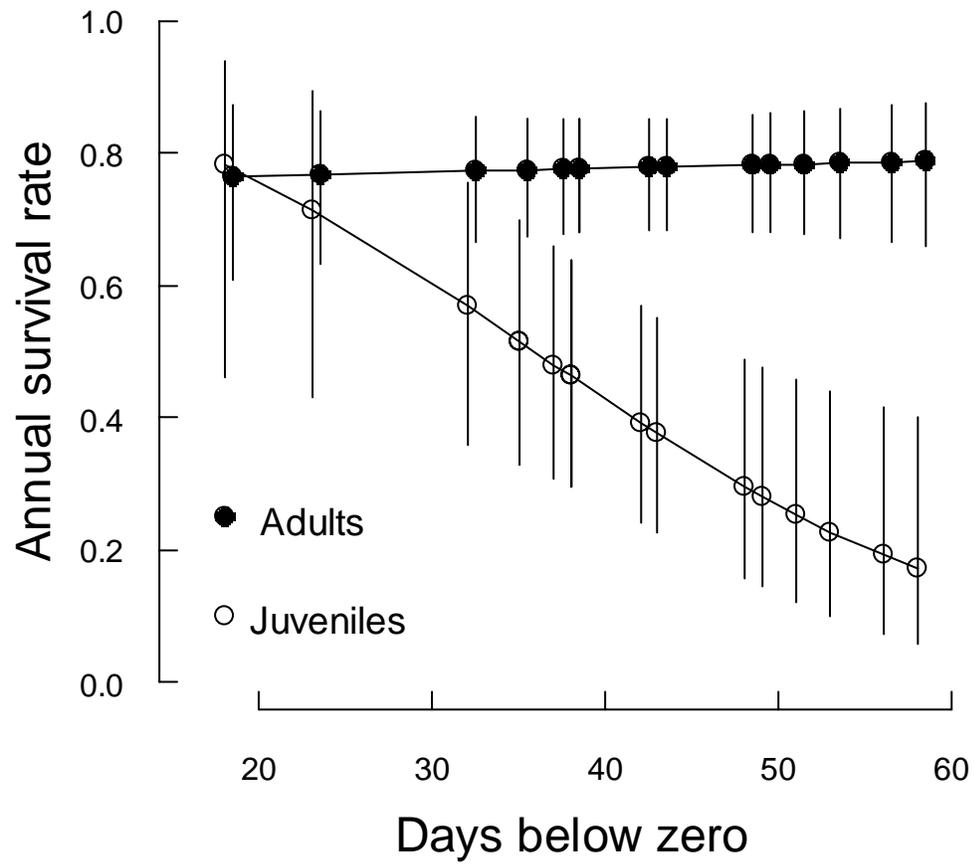
Figure 1.

Figure 2

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	8	5	16	21	16	10	10	7	3	4	6	4	1	116
				(5)	(6)	(3)	(13)	(11)	(7)	(5)	(1)	(2)	(1)	(2)	(4)	(2)	(0)	(62)
B	3	8	7	1	4	5	3	8	6	5	5	3	7	10	5	5	5	90
	(3)	(6)	(2)	(0)	(1)	(4)	(1)	(7)	(4)	(0)	(0)	(0)	(3)	(5)	(0)	(4)	(1)	(41)
C						3	5	5	6	6	6	5	6	5	7	1	2	57
						(3)	(4)	(2)	(2)	(5)	(2)	(1)	(3)	(1)	(4)	(0)	(1)	(28)
D									9	17	13	8	6	18	13	25	13	122
									(9)	(12)	(6)	(2)	(2)	(13)	(4)	(16)	(2)	(66)
E							2	22	20	35	36	21	14	17				167
							(2)	(20)	(5)	(19)	(16)	(6)	(7)	(7)				(82)
F		49	81	64	55	41	33											323
		(49)	(50)	(16)	(11)	(7)	(3)											(136)
	3	57	88	70	67	54	59	56	57	73	70	44	36	54	31	35	21	875
	(3)	(55)	(52)	(21)	(18)	(17)	(23)	(40)	(27)	(41)	(25)	(11)	(16)	(28)	(12)	(22)	(4)	(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 (see Flatt and Dummermuth 1993). **Site B** (approx. 4.9 km from Solohthurn) lies on a SE facing rocky forested ridge, approximately 700 ml 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 x 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 1'060 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 x 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:

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

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

$$
\begin{bmatrix}
0 & 0 & 0 & 0 & \begin{matrix} 1.323 \\ (0.412/2.331) \end{matrix} \\
\begin{matrix} 0.574 \\ (0.457/0.681) \end{matrix} & 0 & 0 & 0 & 0 \\
0 & \begin{matrix} 0.655 \\ (0.564/0.738) \end{matrix} & 0 & 0 & 0 \\
0 & 0 & \begin{matrix} 0.727 \\ (0.660/0.787) \end{matrix} & 0 & 0 \\
0 & 0 & 0 & \begin{matrix} 0.792 \\ (0.735/0.839) \end{matrix} & \begin{matrix} 0.841 \\ (0.784/0.885) \end{matrix}
\end{bmatrix}
$$