Mark-recapture Estimates of Survival in Populations of the Asp Viper, *Vipera aspis aspis*

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Abstract.—We estimated the annual survivorship of two populations of the asp viper, *Vipera aspis aspis*, by recapturing known adult individuals in the field over six and nine years respectively. The snakes at the two study sites in the Jura mountains of northwestern Switzerland were active between mid-March and mid-October. *Vipera a. aspis* is easily captured by hand, has individually recognizable marks and is, therefore, well suited for long-term mark-recapture studies. The maximum likelihood estimates of annual survivorship are about 0.75 in both populations. The probability that a snake will be recaptured in any given year is about 0.4 (habitat A) and about 0.33 (habitat B). Sampling effort within a year had little effect on the probability of recapture. Our best estimate of annual survival of 0.75 for the two habitats combined compares well with other previous estimates in viperids and in *V. aspis* in particular. We found no detectable differences in the survival rates between sexes even when the two habitats were combined. We found weak evidence that there was a difference in the recapture probability between the sexes. The minimal adequate model for the combined data set suggested that there is a higher probability of recapturing surviving females (0.545) than males (0.331).

The study of animal populations and their dynamics frequently depends on analysis of life history parameters and differences in the life history traits among individuals. The understanding of patterns of survival and reproduction remains one of the fundamental challenges of ecology (Partridge and Harvey, 1988; Southwood, 1988; Caswell, 1989) and it is particularly important in biogeography, community ecology, and population regulation (e.g., Blondel, 1986; Crawley and May, 1987; Soulé, 1987).

However, when studying animal populations in the field it is usually impossible to follow individuals closely enough for long enough to know when they actually died (Lebreton et al., 1992) or if they have temporarily emigrated from the population (e.g., Nichols et al., 1987). The failure to find a marked animal might also be due to the probabilitic nature of sampling. Recently developed methods of analysis of mark-recapture data allow a separate estimation of survival and capture probabilities (Lebreton et al., 1992). The asp viper *Vipera aspis* (e.g., Saint Girons, 1947, 1952, 1957; Duguy, 1963; Naulleau, 1965; Monney, 1994) offer good opportunities for field studies, because they are easily captured by hand and individuals recognized by their unique markings.

Despite the increasing literature on snake

population ecology (see Parker and Plummer, 1987 for review), there are few dependable data (Shine and Charnov, 1992) on survival under natural conditions. This lack of information is one of the major constraints in snake conservation (Dodd, 1993). Low recapture rates (Turner, 1977) make it essential that recapture rates are accounted for in any dependable survival estimates.

The asp viper (*Vipera aspis*), is an ovoviviparous snake that reaches sexual maturity at 3 to 5.5 yr, and a maximum age under natural conditions of 18 yr (Saint Girons, 1952, 1957). Growth continues throughout life. Male vipers have an annual reproductive cycle, but females only reproduce every two to four years. Saint Girons (1952) and other authors estimated a sex ratio of 1:1, which implies equal survival rates for males and females. Population densities have been estimated at 6 animals ha⁻¹ (Moser et al., 1984) and 16.11 adults ha⁻¹ (Naulleau and Bonnet, 1995).

Between 1986 and 1995 we studied several populations of the asp viper (subspecies *Vipera aspis aspis*) in the Jura mountains of northern Switzerland. Local females reproduce every second or third year; gestation requires four to five months, and clutch sizes vary from five to fifteen. Activity lasts from mid-March until mid-October (Flatt and Dummermuth, 1993). *Vipera aspis* is a wide ranging species and is common in many parts of its range (e.g., large parts of France, Saint Girons, 1989), whereas populations in the northeastern part of its range

(northern Switzerland) are declining (e.g., Hotz and Broggi, 1982). Although the life history and ecology of this species has been well studied, there is little information about natural survivorship. Here we present survival estimates from our long-term capture-recapture data of two populations based on modern statistical methods (Lebreton et al., 1992). These estimates provide insight into the survival processes among snakes in general and are essential data in the determination of the status of threatened populations.

MATERIALS AND METHODS

We began studying the first of four populations in 1986, and additional populations were added in 1989, 1991, and 1992. Only two populations (A, B) have sufficient sample sizes for analysis (see Flatt and Dummermuth, 1993 for details about populations A and B). Over the course of six years, 50 different adult snakes (50 cm or longer) were found in habitat A, 18 of which were re-sighted in more than one year. During nine years, 22 different adult snakes were found in habitat B, nine of which were re-sighted in more than one year. The complete capture histories of the snakes can be obtained from the corresponding author (BA).

Our two study sites are located in the Jura mountains of Canton Solothurn, northwestern Switzerland. The study sites are isolated from each other and also isolated from other appropriate habitat. No snakes were ever seen in a different study site than in the one they were originally seen. Habitat A lies on a SSE facing slope 800 to 900 m above sea level. The most important area of this habitat covers a stretch approximately 600 m long and 100 m wide and includes areas covered with stones and small boulders as well as forested sections. It contains one of the biggest remaining populations of *V. aspis* in Canton Solothurn that we estimate at consisting of approximately 20 adults. For details about habitat A see Flatt and Dummermuth (1993). Habitat B lies on a SE facing rocky ridge, at an altitude of 800 to 920 m above sea level. The ridge is approximately 700 m long and 100 m wide. Whereas the ridge itself is mostly forested, there lies a steep, in parts almost vertical, rocky slope south-east of the ridge. This slope seems to be of great importance for gravid females and young snakes. As many of the asp vipers observed in this habitat were only found once or twice during the whole observation period, and large portions of the area are almost inaccessible due to their steepness, it is difficult to estimate the population size. For further details concerning habitat B see Flatt and Dummermuth (1993).

For each individual *V. aspis* we found in hab-

itats A and B, we recorded date and time of capture or resighting, sex, the exact location of the individual in its habitat, notes on weather conditions, approximate temperature, and overall condition of the snakes (ecdysis, digestion, reproductive status etc.), on every site visit. Observation dates were combined into yearly blocks of time. As far as possible we measured total body length and photographed each snake. In addition to these photographs, we made drawings showing the head and neck coloration of the different individuals. The most important criteria used for distinguishing individuals from each other were their coloration, dorsal pattern of spots, scars and other distinctive marks. Individuals were clearly identifiable without scale-clipping or branding scales (see Sauer, 1994 for the method of photographic identification). To avoid disturbance, we handled the vipers as little as possible, and located the snakes from a distance with tele-lenses, binoculars, or by sight while walking slowly through the terrain. After location we identified individuals from reasonable proximity or when identity was in doubt, by hand capture. Site visits took between one and a half to three hours depending on time of day and season. Field work was carried out by one or two persons during the entire yearly activity period of the asp vipers, from mid-March to mid-October. Because field work was restricted to warm and cloudy or sunny days, prevailing weather conditions during the different years of observation sometimes led to an irregular pattern of the site visits. Several visits could follow each other within a few days; sometimes several weeks might go by without any site visits when weather conditions were not favorable for observing the snakes (no surface activity). Habitat A was sampled an average of 18 times per year (range 6–30) from 1989 to 1995. Habitat B was sampled an average of 5.2 times per year (range 2–9) from 1986 to 1995.

The vast majority of sightings occured between the beginning of May and the end of August. This presents the possibility that some recapture events occurred only 8 mo apart while others occurred 16 mo apart. However, snakes that were seen in more than one year were usually sighted between 2 and 10 times in any one year. The few snakes that were only sighted once in a year had recapture intervals of between 11 and 13 mo.

We estimated survival and recapture rates from the Cormack-Jolly-Seber (CJS) model (Cormack, 1964; Jolly, 1965; Seber, 1986) using maximum-likelihood methods implemented in SURGE 4.2. (Lebreton et al., 1992; Pradel and Lebreton, 1993) after determining that the data did not show significant deviations from the CJS

model using the program RELEASE (Burnham et al., 1987). Within habitats we tested specifically for differences in survival and/or recapture rates between males and females, and among years. We also modelled the probability of recapture explicitly as a logistic function of effort (number of resighting attempts per year). Finally, we also compared the probabilities of survival and recapture between sites. In this analysis, zeros were entered as the capture histories of the animals in habitat A for the first three years of the study. Then we specified that the probability of recapture in habitat A was zero in the first three years when habitat A was not sampled (1986–1988). This subterfuge allows us to get unbiased estimates of survival in the two habitats even though they were not both sampled for all of the same years.

The statistical significance of individual variables in explaining the recapture of individuals was tested using likelihood ratios. We compared the deviance ($2 \times$ log-likelihood) of models without a variable with models that included the variable. Differences in deviance are asymptotically χ^2 distributed with degrees of freedom equal to the difference in the number of parameters. We also present 95% confidence intervals based on profile likelihoods. The minimal adequate model was chosen on the basis of minimizing Akaike's information criterion which is the deviance of the model plus two times the number of parameters in the model (Akaike, 1973; Lebreton et al., 1992; Burnham et al., 1995). The criterion often performs better than decisions based on statistical significance alone (Burnham et al., 1995).

RESULTS

Fit of the Data to the CJS Model.—Program RELEASE (Test2 + Test3) detected no significant deviations of the fit of the data to the assumptions of CJS model in habitat A ($\chi^2 = 18.1$; df = 14, $P = 0.20$), habitat B ($\chi^2 = 12.9$; df = 8, $P = 0.11$), or when the two habitats were combined ($\chi^2 = 13.4$; df = 14, $P = 0.49$). However, the data sets are relatively small so the power of the test to detect deviations is low.

Individual Habitats.—There were no detectable differences in the survival rates or probability of recapture between males and females in either habitat A or B (Tables 1 and 2). The best estimate of annual survival rate is about 0.75 in both habitats with 95% confidence limits extending from 0.55 to 0.9. Similarly, the probability that an animal will be recaptured in any given year is about 0.4 in habitat A and about 0.33 in habitat B even though sampling effort was more than twice as high in habitat A. Confidence limits were wide (Tables 1c, 2c). Although sampling effort varied considerably

among years, it had no detectable effect on the probability of recapture. Explicit modelling of the effort did not yield any predictive power for the probability of recapture in either habitat (Tables 1 and 2).

Habitats Combined.—The lack of a difference between sexes for either survival or recapture in both habitats prompted us to combine the two habitats for analysis to test for a habitat effect and increase our sample size to narrow the confidence limits on the estimates. There were no detectable differences in the probability of survival or recapture between the two habitats. (Table 3). Although the probability of recapture was not significantly higher for females than males ($P = 0.08$ to 0.15), the 95% confidence limits did not overlap the means and the effect of sex on recapture was included in the minimal adequate model (Table 3). When included in the model, there was only a one-half percent difference between males and females in the probability of surviving from year to year. The minimal adequate model, therefore, is one with constant survival and recapture probabilities with the same parameter values across habitats, no effect of sex on survival, but a slightly higher probability of recapture for females. The best estimate of annual survival rate is 74.9% (95% CL: 61.2–84.9%) and of probability of recapture is 54.5% (95% CL: 35.2–72.4%) for females and 33.1% (95% CL. 18.5–51.9) for males.

DISCUSSION

Demographic field studies on snakes often suffer from low recapture rates (often as low as 15%) and consequently survival estimates with wide confidence limits (Turner, 1977; Parker and Plummer, 1987). These low recapture rates might be due to the secretive behavior of most snakes and the use of hand capture rather than using traps (Fitch, 1987; Seigel, 1993). However *Vipera berus* and *V. aspis* are quite easily recaptured by hand (e.g., Monney, 1990; Madsen and Shine, 1992b; Flatt and Dummermuth, 1993; Forsman, 1995; pers. obs. on Swiss *V. berus* and *V. aspis*). Our best estimates of recapture probability for the two habitats combined were 54% for females and 33% for males (45% combined probability). These recapture probabilities can be interpreted in two opposing ways. Either the snakes are always there and we have only a 0.45 chance of seeing them, or the snakes are present in the study area 0.45 of the time and when present we always see them Clearly, neither of these extremes is likely to be the case, but several lines of evidence suggest that when present in the habitat, recapture rates are high. Snakes were usually seen several times in a year or not at all. If each snake has an equal probability of being in the sampled habitat or not, this is not

TABLE 1. SURGE 4.2 Analysis of deviance of mark-recapture data in Habitat A. **A** Maximum likelihood estimates of the deviance of models incorporating parameters for survival (ϕ) and recapture (P) probabilities as a function of sex (s), year (t), and recapture effort (e). The minimal model is chosen by minimizing Akaike's Information Criterion and is marked in boldface. **B** Likelihood ratio tests of the effect of sex, time, and effort on survival and recapture probabilities. **C** Maximum likelihood estimates and profile likelihood 95% confidence limits of parameters for the minimal adequate model.

A	Survival	Recapture	np	Deviance	AIC
(1)	$\phi_{s \cdot t}$	$P_{s \cdot t}$	22	116.7	160.7
(2)	ϕ_s	$P_{s \cdot t}$	14	121.9	149.9
(3)	ϕ	$P_{s \cdot t}$	13	123.4	149.4
(4)	$\phi_{s \cdot t}$	P_s	14	130.3	158.3
(5)	$\phi_{s \cdot t}$	P	13	130.3	156.3
(6)	ϕ_s	P_s	4	138.4	146.4
(7)	ϕ	P_s	3	138.5	144.5
(8)	ϕ	P	**2**	**138.7**	**142.7**
(9)	ϕ	P_e	3	138.7	144.7

B Effect	Comparison	df	χ^2	P-value
ϕ_t	1 v 2	8	5.2	0.74
	4 v 6	10	8.1	0.62
ϕ_s	2 v 3	1	1.5	0.22
	6 v 7	1	0.1	0.75
P_t	1 v 4	8	13.6	0.09
	2 v 6	10	16.5	0.09
	3 v 7	10	15.1	0.13
P_s	4 v 5	1	<0.1	0.85
	7 v 8	1	0.2	0.65
P_e	8 v 9	1	<0.1	0.81

C Parameter	Estimate	95% confidence limits	
Survival	0.754	0.561	0.880
Recapture	0.407	0.250	0.585

TABLE 2. SURGE 4.2 Analysis of deviance of mark-recapture data in Habitat B. **A** Maximum likelihood estimates of the deviance of models incorporating parameters for survival (ϕ) and recapture (P) probabilities as a function of sex (s), year (t), and recapture effort (e). The minimal model is chosen by minimizing Akaike's Information Criterion and is marked in boldface. **B** Likelihood ratio tests of the effect of sex, time, and effort on survival and recapture probabilities. **C** Maximum likelihood estimates and profile likelihood 95% confidence limits of parameters for the minimal adequate model.

A	Survival	Recapture	np	Deviance	AIC
(1)	$\phi_{s \cdot t}$	$P_{s \cdot t}$	34	52.7	120.7
(2)	$\phi_{s \cdot t}$	P_s	20	69.4	109.4
(3)	$\phi_{s \cdot t}$	P_t	27	57.9	111.9
(4)	$\phi_{s \cdot t}$	P	19	69.5	107.5
(5)	ϕ_s	P	3	84.2	90.2
(6)	ϕ_t	P	10	77.2	97.2
(7)	ϕ	P	**2**	**85.6**	**89.6**
(8)	ϕ	P_e	3	84.7	90.7

B Effect	Comparison	df	χ^2	P-value
ϕ_t	4 v 5	16	14.7	0.55
	6 v 7	8	8.4	0.40
ϕ_s	4 v 6	9	8.3	0.50
	5 v 7	1	1.4	0.24
P_t	1 v 2	14	16.7	0.27
	3 v 4	8	11.6	0.17
P_s	4 v 6	9	7.7	0.56
	5 v 7	1	1.4	0.24
P_e	7 v 8	1	0.9	0.34

C Parameter	Estimate	95% confidence limits	
Survival	0.786	0.599	0.900
Recapture	0.339	0.187	0.534

a violation of the assumptions of the CJS model. However, differential habitat use or movement of specific subunits of the population (e.g., females in different reproductive stages, hunting individuals, males in search of mates [Saint Girons, 1952; Viitanen, 1967; Monney, 1992; Flatt and Dummermuth, 1993; Reinert, 1993, Baron et al. 1996]) do violate the simple CJS model and should be accommodated with subunit specific parameters (in exactly the same way we can account for the effect of sex [Baron et al. 1996]). The probability of recapture may also depend on previous capture history. This deviation from the simple CJS model can be accommodated using multistate models where individuals move from one subunit of the population to another (Brownie et al., 1993). The lack of a significant Test 2 + Test 3 suggests that violations of the

assumptions are likely to be small. However we approach these estimates with caution. Sampling all snakes in the population with equal probability is difficult to achieve because snakes may appear more numerous where they exhibit less cryptic behavior (Reinert, 1993). For example, Baron et al. (1996) have found higher recapture probabilities for gravid females and fluctuating probabilities of recapture for males of *Vipera ursinii*.

Our best estimate of annual survival rates of 0.749 per year compares well with other estimates of survival in adult viperids ranging from 0.70 to 0.85 per year (Turner, 1977; Shine and Charnov, 1992; Baron et al., 1996). Previous estimates for annual survival in *V. aspis* are within our confidence limits at 0.78 per year (Shine and Charnov, 1992). Saint Girons (1957) estimated an adult mortality between 20 and 25% (=75–80% survival) for the same species. Among

TABLE 3. SURGE 4.2 Analysis of deviance of mark-recapture data for both habitats combined. **A** Maximum likelihood estimates of the deviance of models incorporating parameters for survival (ϕ) and recapture (P) probabilities as a function of habitat (h), year (t), and sex (s). The minimal model is marked in boldface. **B** Likelihood ratio tests of the effect of the factors habitat, time and sex on survival and recapture probabilities. **C** Maximum likelihood estimates and profile likelihood 95% confidence limits of parameters for the minimal adequate model. The minimal model is chosen by minimizing Akaike's Information Criterion.

A

	Survival	Recapture	np	Deviance	AIC
(1)	$\phi_{h \cdot t}$	$P_{h \cdot t}$	31	197.0	259.0
(2)	ϕ_{h}	$P_{h \cdot t}$	17	212.9	246.9
(3)	ϕ_{t}	$P_{h \cdot t}$	24	206.8	254.8
(4)	ϕ	$P_{h \cdot t}$	16	213.0	245.0
(5)	ϕ	P_{h}	3	226.6	232.6
(6)	ϕ	P_{t}	10	216.2	236.2
(7)	ϕ_{s}	P_{s}	4	223.6	231.6
(8)	ϕ_{s}	P	3	227.7	233.7
(9)	ϕ	P_{s}	**3**	**223.6**	**229.6**
(10)	ϕ	P	2	226.7	230.7

B

Effect	Comparison	df	χ^2	P-value
ϕ_t	1 v 2	14	15.9	0.32
	3 v 4	8	6.2	0.62
ϕ_h	1 v 3	7	9.8	0.20
	2 v 4	1	0.1	0.75
ϕ_s	7 v 9	1	0.1	0.95
	8 v 10	1	1.0	0.32
P_t	4 v 5	13	13.6	0.40
	6 v 7	8	10.5	0.23
P_h	4 v 6	6	3.2	0.78
	5 v 7	1	0.1	0.75
P_s	7 v 8	1	2.1	0.15
	9 v 10	1	3.1	0.08

C

Parameter	Estimate	95% confidence limits	
Survival (sexes combined)	0.749	0.612	0.849
Recapture—Females	0.545	0.352	0.724
Recapture—Males	0.331	0.185	0.519

these other studies, only Baron et al. (1996) explicitly accounted for the effect of recapture probability as we have here.

Some authors have found differences in survival between sexes among snake species (e.g., Feaver, 1977; Brown and Parker, 1984; Forsman, 1995; Baron et al., 1996) and between colour morphs (e.g., Forsman, 1995; *Vipera berus*). As Madsen and Shine (1992a) showed, survival of females in *Vipera berus* seems to be reduced after parturition, probably reflecting the high energy cost of reproduction. Although males in this species reproduce each year and may mate with more than one female, survival may be strongly

related with lifetime reproductive success (Madsen and Shine, 1992b; see Forsman, 1995 for further discussion). We were not able to detect differences in the survival rates or recapture probabilities between male and female *Vipera a. aspis* in either habitat by itself. Combining the two habitats allowed us to detect a slight difference in the probability of recapture but the probability of survival was almost identical between the sexes. The difference in recapture rate is not significant using likelihood ratios, however the 95% confidence limits do not overlap the means. We hope that increasing the data set to include more years and habitats will resolve this ambiguity. Including the effect of sex on the probability of recapture in the statistical model improves our estimate of the probability of survival.

We were unable to detect year or habitat effects in survival or recapture (Tables 1, 2 and 3). Although Baron et al. (1996) were also unable to detect temporal or spatial variation in survival and recapture, it seems unlikely that no such effects exist. A longer data set coupled with modelling of specific environmental variables (Lebreton et al., 1992) may reveal some effects. For example, Brown and Parker (1984) and Forsman (1995) have found considerable differences in survival among years.

Jayne and Bennett (1990) showed that larger body size positively affects survival in garter snakes, Forsman (1993) showed size-dependent differences in survival of *Vipera berus*, and Baron et al. (1996) showed variation in age-specific survival for *Vipera ursinii*. Generally, it appears that juvenile and first-year mortality is much higher than adult mortality among snakes (e.g., Saint Girons, 1957; Brown and Parker, 1984). Saint Girons (1957) estimated a mortality of over 50% in *V. aspis* juveniles during their first months of their life. Unfortunately, we have insufficient data on neonate and juvenile asp vipers due to the difficulties of sampling these small secretive snakes.

With a larger data set, the probabilities of recapture and survival as a function of body size can be readily estimated using multi-state models following the methodology of Nichols et al. (1992). Similarly, the effect of reproduction on survival and recapture success can also be estimated using multi-state models (Nichols et al., 1994).

Many populations of *V. aspis* are dramatically declining at their northernmost limits in Switzerland (Hotz and Broggi, 1982; Dusej and Billing, 1991; Hofer, 1991), with some populations going extinct (Moser, 1984). During the course of our 9 yr study the two populations appeared to be stable, as is the northernmost relict population of *V. aspis* in the Black Forest (Germany)

(Fritz and Lehnert, 1993). Whether the difference between declining and stable populations is due to mortality or a failure of recruitment will only be determined by additional long-term studies such as this one.

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