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Do sex divergences in reproductive ecophysiology translate into dimorphic demographic patterns?

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Abstract We examined the influence of sex divergences in reproductive role and physiology on catchability and demographic patterns in a closed population of aspic viper (*Vipera aspis* Linné). During 8 years, there were 4800 captures of 988 adults. In both sexes, captures were more frequent in spring when climatic conditions and reproductive activities impose extended basking periods that make animals more detectable. On average, males were captured more than females, reflecting intense sexual activity (i.e., mate searching) in spring. Reproductive females were more catchable than nonreproductive females, illustrating a major increase in basking behavior associated with reproduction. Estimates of population size revealed a sexually dimorphic demographic system with marked year-to-year fluctuations in females contrasting with a more stable male population. This sex difference in population dynamic reflects sex divergences in the acquisition and allocation of energy for reproduction. In both sexes, reproduction is fueled by body reserves. Females, however, need to accumulate substantial body reserves to reach a high body condition threshold before reproduction, whereas the male pattern of energy allocation is more gradual (i.e., no fixed threshold). In addition, reproduction entails major survival cost in females (i.e., most females reproduce just once), whereas males are generally annual breeders. As a consequence of this sex divergence, food abundance, through its

direct effect on body store dynamics, influenced major demographic parameters of females (e.g., proportion of reproducing individuals, annual changes in population size) but not males.

Key words Catchability · Population size · Capital breeding · Snake

Introduction

Descriptions of variations in life history traits and their causes constitute a fundamental theme in the study of evolution and adaptation (Stearns 1992). Accurate quantification of variation expressed in wild populations often requires capture and recapture of marked individuals over periods that are biologically relevant to the species generation time. Therefore, estimates of population parameters such as growth rate, survival, and population size necessitate long-term mark-recapture techniques (Southwood 1988). Although requiring extensive effort and time commitment, longitudinal approaches provide a multitude of benefits that have been extensively illustrated in different fields of ecology (Tinkle 1979). Data gathered in long-term studies permit the examination of individual reproductive success, survival, and possibly lifetime reproductive success (e.g., the basic raw material for natural selection; Clutton-Brock 1988). Additionally, longitudinal work provides an opportunity to correlate population characteristics with environmental factors such as food availability, predator abundance, or climatic fluctuation that affect life history traits (Ballinger 1977; Seigel and Fitch 1985).

Unfortunately, for logistical reasons, long-term mark-recapture studies are usually not feasible. Individuals of some species are too small to permit marking or too secretive to catch a reasonably large subset of a population. Similarly, recapture avoidance and long-distance displacement invalidate or at least seriously complicate any estimate of population size or mortality (Nichols et al. 1987; Brodie 1989; Cooper et al. 1990; Lebreton et al. 1992; Shine and

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Schwarzkopf 1992; Houston and Shine 1994). Due to their cryptic behavior, snakes are superficially poor models for recapture studies (Seigel 1993; Saint Girons 1996). This impression, however, is not necessarily valid as some species fit within the requirements already outlined. Temperate viperid snakes, for example, are typical sit-and-wait predators that can be locally abundant, and a number of field studies have been successfully conducted on these animals (Saint Girons 1949, 1952, 1957a,b, 1975; Fitch 1960; Klauber 1972; Brown 1991; Madsen and Shine 1993; Martin 1993). Snakes from temperate climates may be especially conducive to studies based on recaptures. Although snakes in general are extremely secretive animals and frequently go undetected, species in cooler climates often must bask in the sun to meet the thermal requirements of major physiological processes such as digestion, ecdysis, and particularly reproduction (Huey 1982; Peterson et al. 1993). In males and females, reproduction entails alterations in activity pattern (e.g., mate searching, increased basking activities), which may render the snakes more visible (Bonnet et al. 1999b). Therefore, we hypothesize that any shift observed in catchability is directly linked to underlying physiological changes imposed by reproduction and foraging activities. That is, capture rates not only provide raw data for estimating demographic parameters such as population size but also provide information on the thermal and reproductive biology of the species under study.

Another interesting feature of studying temperate viperid snakes is that they offer extreme examples of capital breeding systems in that body reserves often constitute the primary fuel for reproductive activities (Seigel and Ford 1987; Naulleau and Bonnet 1996). Although fat stores are probably important for both males and females (Saint Girons 1957a,b; Olsson et al. 1997), proximate divergences exist in term of patterns of energy allocation toward reproduction. Most notable is the length of the reproductive cycle, females are generally pluriannual and males annual breeders (Saint Girons 1957b; Andren and Nilson 1983; Seigel and Ford 1987; Naulleau et al. 1999). Such a situation is particularly well described for the aspic viper (*Vipera aspis* Linné), probably the most intensively studied European snake (Saint Girons 1952, 1996; Naulleau 1997; Zuffi et al. 1999).

Marked sexual divergences in reproductive biology are likely to entail major ecological repercussions in term of sex-specific catchability and possibly demographic patterns. We tested for sex differences in catchability patterns and population dynamics of the aspic vipers using a data set from an 8-year mark–recapture study of a closed population in west-central France that is characterized by strong annual fluctuation in prey abundance (Bonnet et al. 2001; Loudais et al. 2002). We also examined whether any detected differences were congruent with pre-existing knowledge of the ecophysiology of this species.

Material and methods

Study species

The aspic viper is a small viviparous snake of the western Palearctic region and locally abundant in west-central France at the northern limit of its distribution. Females mature at 40 cm snout–vent length (SVL), which is attained in 2.5–3.5 years (Bonnet et al. 1999a). Females are typical capital breeders that delay reproduction until they have amassed enough energy reserves to reach a high body condition threshold (Naulleau and Bonnet 1996). In this area, the female reproductive cycle is longer than annual (Saint Girons 1957a,b; Bonnet and Naulleau 1996; Naulleau et al. 1999), leading to the coexistence of subpopulations of reproducing and non-reproducing females. Reproductive activity in females imposes marked behavioral changes that distinguish them from males and nonreproducing females. Notably, females spend more time basking from the onset of follicle production (March) through parturition (late August) to meet the metabolic requirements of vitellogenesis and gestation. In addition, females are more sedentary during gestation (Naulleau et al. 1996). These changes infer substantial survival costs of reproduction, and therefore most (>75%) female vipers reproduce no more than once in their lifetime (Bonnet et al. 2000, 2002b).

Male aspic vipers are also capital breeders in that fat stores are the sole source of energy during the sexual vernal anorexia. In contrast with females, reproductive investment is temporally reduced (broadly, 6–8 weeks in spring) and mainly concentrated on mate-searching activities. Males do not have to reach a fixed body condition to engage in reproductive activities, as reproductive effort is adjusted to their body reserves (Aubret et al. 2002). As a consequence, the reproductive cycle is generally annual in this sex (Vacher-Vallas et al. 1999). Because the smallest male found copulating (with sperm transmission) was 36.5 cm SVL, all individuals longer than this were considered adults.

Study site and methods

The study site, in west-central France near the village of Les Moutiers en Retz (47°03' N; 02°00' W), is a 33-ha grove with a mosaic of meadows and regenerating scrubland. The site is characterized by a temperate oceanic climate. From 1992 to 1999, one to four people patrolled on almost every favorable day (sunny and partially cloudy, or cloudy with air temperature above 15°C) encompassing the vipers' annual activity period, late February to late October. Although variations in searching effort occurred between years because of climatic fluctuations, effectiveness in locating vipers and the searching method were largely homogeneous throughout the study period (except in 1992, when searching effort was biased toward females and large males), because of the extended searching period. As a result, the catchability pattern observed by pooling all the years is highly consistent with the catchability pattern observed within each year (unpublished data). Total searching effort

exceeded 4000h and represented more than 670 “searching-days.” Snakes were caught by hand, sexed by eversion of the hemipenes, weighed to the nearest gram with an electronic scale, and measured (SVL and total length) to the nearest 5mm. More than 1000 adult and subadult vipers have been marked using passive integrated transponder (PIT) tags (sterile transponder TX1400L; Rhônes Mérieux, Lyon, France; product of Destron/IDI Inc.). On capture, each snake was color-marked on the back to avoid short-term recaptures and thus minimize disturbance. All snakes were released at their point of capture.

Female reproductive status was determined using two methods. First, at the beginning of vitellogenesis, a female with a body condition (mass scaled by size) greater than a predetermined threshold was considered reproductive (see Bonnet et al. 1994; Naulleau and Bonnet 1996, for validity of the method). Second, from mid-vitellogenesis (May) to the end of gestation (late August), reproductive status was easily determined either by palpation of follicles or embryos or by records of parturition (Fitch 1987; Naulleau and Bonnet 1996).

Catchability and population size

Different measurements of catchability were used in this study. First, for individuals marked at the onset of the study (1992 and 1993), we estimated long-term catchability by determining the number of consecutive years that an individual was observed. Second, we examined intraannual catchability by defining 18 successive 2-week capture–recapture sessions from March to November. These sessions were equally divided into three consecutive periods (broadly, the spring, summer, and fall seasons) that match with major events in the reproductive cycle (Table 1). For each individual, we calculated the mean number of captures per session for each season (seasonal capture rate) and for the entire year (annual capture rate).

Because capture occurrence typically follows a Poisson distribution, we tested the effect of different explanatory variables (body size, sex, and reproductive status) using multiple Poisson regression. For descriptive purposes, the effect of body size was also examined using three size classes. The variable of interest was standardized [$Z = (X - \text{mean value})/\text{SD}$] so that the distribution had a mean of 0 and a SD of 1. The three size classes were small ($Z \leq -0.43$), medium ($-0.43 < Z < 0.43$), and large ($Z > 0.43$) (Marti 1990). All tests were carried out using a single indi-

vidual contribution randomly sampled to avoid pseudoreplication. Estimates were based on the Wald statistic (Statistica 6.0). This statistic is a test of significance of the regression coefficient based on the asymptotic normality property of maximum-likelihood estimates and is computed as $W = b^2/\text{Var}(b)$. In this formula, b stands for the parameter estimates and $\text{Var}(b)$ stands for the asymptotic variance of the parameter estimates. The Wald statistic is tested against the chi-square distribution.

Population estimates were calculated using CAPTURE (Otis et al. 1978). Data from 1992 were excluded from the analysis because of low searching effort. The model used assumes a closed population (e.g., no birth, death, or migration) and is appropriate for use in a study covering a short time (Otis et al. 1978). Each 2-week period was considered a capture session. The analysis was restricted to spring (March–May) because the survival rate is high (>0.8 ; unpublished data). We found no evidence of emigration, and any snake not captured over a long period (>2 years) was considered dead (Naulleau et al. 1996; Vacher-Vallas et al. 1999). Birth did not influence our analysis because only adults were considered and neonates require at least 2.5 years to reach maturity (Bonnet et al. 1999a). Finally, CAPTURE provides the opportunity to test different models including heterogeneity of capture probabilities in populations (Mh), time-specific variation in probabilities of recapture (Mt), behavioral response after initial capture (Mb), and combinations of these models. In every case, the first model suggested by goodness-of-fit tests was adopted (Chao et al. 1992). Annual changes in population size (year n) were calculated from spring population size estimate in year $n + 1$ minus spring population size estimate in year n . Estimates were performed in spring, just after hibernation. Because mortality during hibernation is extremely low in our population (unpublished data), the difference between “year $n + 1$ ” and “year n ” estimates corresponds to the changes that occur over the active season (spring to hibernation) of the year n .

We analyzed the influences of demographic changes occurring in a year n on the operational sex ratio of the population in the following year. In the aspic vipers, sex is genetically determined, and analysis was not confounded by the effects of environmental variables on primary sex ratio. Estimates of sex ratio (SR) and operational sex ratio (OSR) were calculated as follows: SR = total number of adult males/(total number of adult males + total number of adult females); OSR = total number of adult males/(total number of adult males + total number of reproducing females). All

Table 1. Biological cycle of the aspic viper and organization of the 18 capture sessions

Period	1, Spring						2, Summer						3, Fall					
RF	Vitellogenesis						Ovulation, gestation						Parturition					
NRF	Fat store recovery						Fat store recovery						Fat store recovery					
M	Sexual anorexia						Fat store recovery						Fat store recovery					
Capture sessions	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Month	Mar	Apr	May				June	July	Aug				Sept	Oct	Nov			

RF, reproducing females; NRF, nonreproducing females; M, males
Source: From Bonnet (1996)

Table 2. Annual variation in captures, proportion of reproducing females, and the operational sex ratio

Year	Initial captures	Total captures	Proportion of reproducing females	Sex ratio	Operational sex ratio
1993	284	640	0.38	0.40	0.64
1994	385	1079	0.41	0.41	0.63
1995	273	649	0.20	0.53	0.85
1996	297	732	0.64	0.54	0.65
1997	341	834	0.59	0.40	0.53
1998	192	321	0.33	0.53	0.77
1999	167	279	0.53	0.57	0.80
Mean	277	565	0.44	0.48	0.69

Calculations were made as follows: Initial captures = number of different individuals captured each year; Total captures = initial captures + recaptures; Proportion of reproducing females = estimate of reproductive females number/estimate of total female population size; Sex ratio = estimate of adult male population size/(estimate of adult males population size + estimate of adult female population size); Operational sex ratio = estimate of adult male population size/(estimate of adult male population size + estimate of reproductive female number)

statistics were performed using Statistica 6.0 software (Statsoft, Tulsa, OK, USA).

Results

Recapture rates and long-term catchability

During the course of the study, 988 adult snakes were marked (463 females and 525 males). The recapture rate (i.e., the percentage of snakes contacted at least once after the initial capture) was 76.6%, and the cumulative number of captures and recaptures was 4723. The number of individuals captured varied from year to year (Table 2), with the highest number of animals observed in 1994. Considering only snakes marked at the onset of the study (1992–1993), most individuals (70.4%) were observed during a single year or 2 consecutive years and only a limited number (<7%) were recaptured over 5 or more years.

Determinants of catchability patterns

Our data enable us to examine the influence of the factors most likely to influence catchability in snakes from temperate zones: body size, sex, season, and reproductive status.

Annual capture rate

We used a multiple Poisson regression to test the influence of sex and body size on annual capture rate (using season and body size, respectively, as categorical and continuous predictor variables). Body size influenced positively capture rate (Wald $\chi^2 = 41.75$, $df = 1$, $P < 0.0001$), with larger individuals being more catchable than smaller ones (mean values obtained were 1.70, 2.03, and 2.75 for small, medium, and large individuals, respectively; Marti 1990). This effect held true when sex was taken into account (interaction between sex and body size: Wald $\chi^2 = 3.2$; $df = 2$; $P = 0.21$).

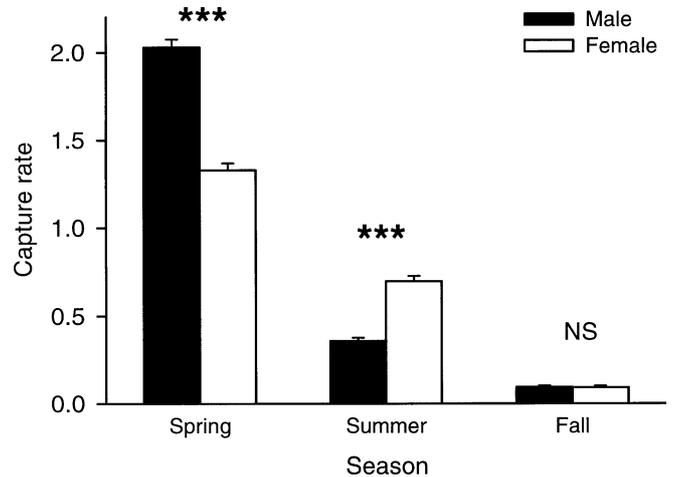


Fig. 1. Sex divergence in capture rate over the three seasons. Data for seasonal capture rate (e.g., mean number of capture per individual) are pooled from all years; error bars represent the standard error (SE). Statistical analyses compared males versus females during the same season. NS, nonsignificant; *** $P < 0.0001$

Annual capture rates were significantly higher in males than females (2.51 versus 2.16; Wald $\chi^2 = 5.79$; $df = 1$; $P < 0.01$).

Seasonal capture rate

Season had a major influence on captures rate (Wald $\chi^2 = 378.32$; $df = 2$; $P < 0.00001$). Snakes were more catchable in spring than in summer and autumn (mean capture rates were 1.55, 0.53, and 0.09 respectively). Further analysis revealed significant differences in such a seasonal shift between males and females (interaction between season and sex: Wald $\chi^2 = 42.68$; $df = 2$; $P < 0.0001$; Fig. 1). In spring, males were more catchable than females (Wald $\chi^2 = 56.23$; $df = 1$; $P < 0.0001$). During summer, however, the opposite was observed with females being captured more frequently (Wald $\chi^2 = 55.31$; $df = 1$; $P < 0.0001$). The two sexes

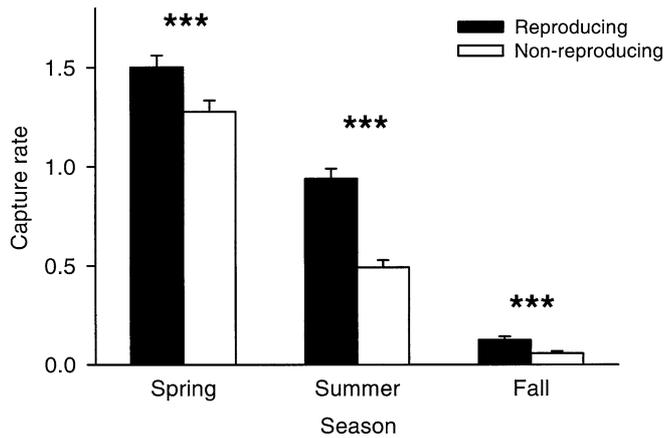


Fig. 2. Effect of reproductive status on female capture rate over the three seasons. Data for seasonal capture rate (e.g., mean number of captures per individual) are pooled from all years; error bars represent the standard error (SE). Statistical analyses compared reproductive and nonreproductive females during the same season. *** $P < 0.0001$

were equally catchable in fall (Wald $\chi^2 = 0.01$; $df = 1$; $P = 0.92$).

Among females, reproductive status strongly affected the seasonal catchability pattern. A multiple Poisson regression using reproductive status and seasons as independent factors revealed a significant shift in capture rate over time (Wald $\chi^2 = 535.65$; $df = 2$; $P < 0.0001$; Fig. 2) and showed that reproducing females were systematically more catchable than nonreproducing ones (Wald $\chi^2 = 26.58$; $df = 1$; $P < 0.0001$; Fig. 2).

Demographic patterns

In the spring, from 1993 to 1999, high recapture rates enabled us to estimate male, female, and total population size. In all cases, goodness-of-fit tests indicated that a time variation and individual heterogeneity in capture probabilities model was the best fit for our data (Mth) (Chao et al. 1992). Population size estimates are illustrated in Fig. 3.

Over the 7 years, the average estimated adult population size in spring was 365 ± 65 individuals (coefficient of variation, 0.17) with a mean density of 11 snakes/ha (total, 33 ha) and a biomass of 1.1 kg/ha (given a mean adult body mass of 100 g). Females exhibited greater fluctuation in population size than did males (coefficient of variation, 0.31 versus 0.08; see Fig. 3). Fluctuation in population size was greatest when reproducing females were considered alone (coefficient of variation, 0.45). Using a proportion of 44% of the total female population (the long-term mean proportion in the population; see Table 2), the proportion of reproducing females to nonreproducing females was significantly greater in 1996 and 1997 and lower in 1995 ($\chi^2 = 60.90$; $df = 6$; $P < 0.0001$; Table 2; Fig. 4).

Prey availability at the site varied annually, with 1996 having high rodent abundance, 1994 having low abundance, and all other years being intermediate (Bonnet et al. 2001; Lourdais et al. 2002). Food abundance in a given year was

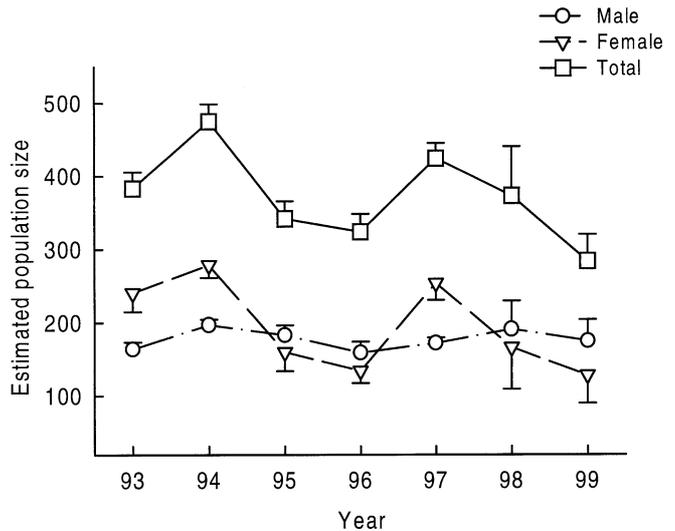


Fig. 3. Annual fluctuation in total number of adult snakes (squares, continuous line), males (circles, dash-dot line), and females (triangles, dashed line) in spring. Population estimates (\pm SE) were performed using the program CAPTURE (see text for statistics)

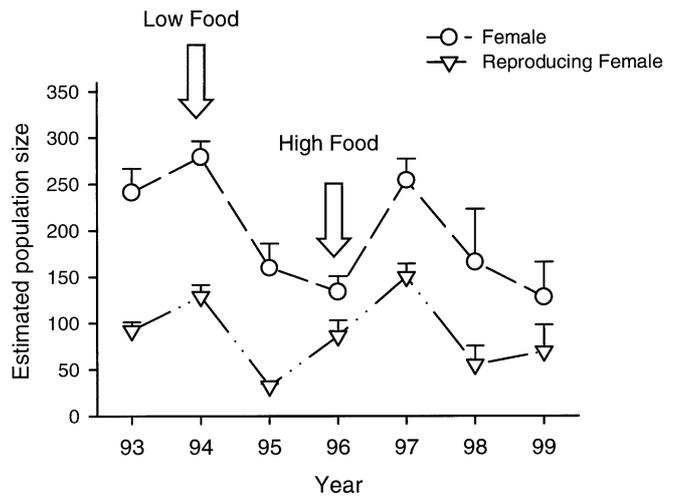


Fig. 4. Annual fluctuation in total number of adult females (circles, dashed line) and reproductive females (triangles, dash-dot-dot line) in spring. Population estimates (\pm SE) were performed using the program CAPTURE (see text for statistics)

independent of food abundance in the preceding year ($r = 0.16$; $F = 0.14$; $df = 1, 5$; $n = 7$; $P < 0.72$). Incorporating these existing rodent abundance data with our data, we discovered that rodent abundance was significantly correlated with the number of females reproducing the following year ($r = 0.87$; $F = 16.59$; $df = 1, 5$; $n = 7$; $P < 0.009$; Fig. 4), but not in the current year ($r = 0.07$; $F = 0.02$; $df = 1, 5$; $n = 7$; $P = 0.88$). Considering the proportion of reproducing females rather than their absolute number, 88% of that variance was explained by a multiple regression analysis with food abundance in a given year and food abundance in the preceding year as the independent variables ($r = 0.93$; $F = 14.5$; $df = 2, 4$; $n = 6$; $P < 0.014$; Table 3).

Table 3. Combined influences of food levels in year n (Food n) and food levels in year $n - 1$ (Food $n - 1$) on the proportion of reproducing females (RF)

	Beta \pm SE	Partial correlation	Semipartial	P value
Food n	0.74 \pm 0.17	0.90	0.73	0.013
Food $n - 1$	0.71 \pm 0.17	0.89	0.70	0.015

Multiple regression: $r^2 = 0.88$; $F = 14.51$; $df = 2, 4$; $n = 7$; $P < 0.014$

Table 4. Examination of annual changes in female population size

	Beta \pm SE	Partial correlation	Semipartial	P value
Model 1: $r^2 = 0.98$; $F = 112.92$; $df = 2, 3$; $n = 6$; $P < 0.001$				
Food n	0.85 \pm 0.13	0.99	0.83	0.001
Food $n - 1$	-0.37 \pm 0.13	-0.95	-0.36	0.01
Model 2: $r^2 = 0.97$; $F = 45.73$; $df = 2, 3$; $n = 6$; $P < 0.005$				
Food n	1.18 \pm 0.07	0.98	0.93	0.002
%RF n	-0.42 \pm 0.07	-0.88	-0.33	0.04

Population changes (during a year n) were calculated from spring population size in year $n + 1$ minus spring population size in year n

Model 1 was obtained by combining food levels in year n (Food n) and food levels in year $n - 1$ (Food $n - 1$) in the multiple regression

Model 2 was obtained by replacing food levels in year $n - 1$ by the proportion of reproducing females in year n (%RF n)

Table 5. Contribution of male and female annual changes in population size on overall changes observed in total adult population

	Beta \pm SE	Partial correlation	Semipartial	P value
Female	0.77 \pm 0.23	0.93	0.69	0.02
Male	0.34 \pm 0.23	0.75	0.30	0.14

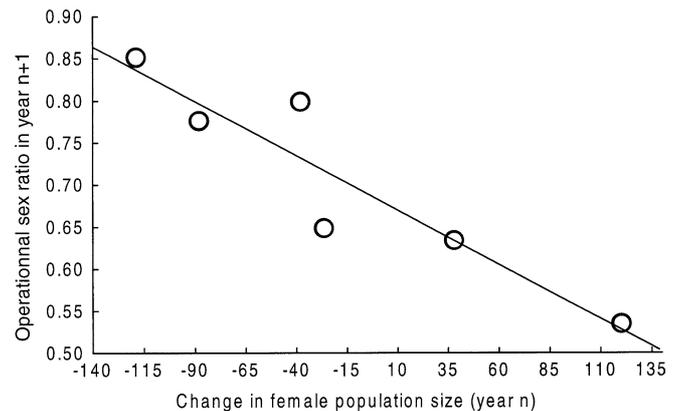
Calculated as spring population size in year $n + 1$ minus spring population size in year n

Multiple regression: $r^2 = 0.92$; $F = 19.1$; $df = 2, 3$; $n = 6$; $P < 0.019$

Annual changes in total female population size appeared closely related to current food levels ($r = 0.92$; $F = 23.57$; $df = 1, 4$; $n = 6$; $P < 0.008$). However, changes in female population size were better explained in a multiple regression combining current food abundance with food abundance in the preceding year (model 1; Table 4). Although food level in year n positively influenced changes in female population size during this year, a negative influence was detected for food level in year $n - 1$.

A similar influence was detected when replacing food level in year $n - 1$ by the proportion of reproducing females in year n (model 2; Table 4). Hence, the annual proportion of reproducing females (year n) negatively influenced the change in female population size over this year n . For males, variations in population size were limited, and no relationship was found between changes in population size and food level in year n , year $n - 1$, or a combination of both (respective P values: 0.17, 0.29, and 0.27).

When pooling data from males and females, changes in total adult population size were significantly explained by changes in female, not male, population size (Table 5). Finally, annual changes in female population size negatively influenced operational sex ratio in the following year ($r = -0.93$; $F = 25.94$; $df = 1, 4$; $n = 6$; $P < 0.007$; Fig. 5).

**Fig. 5.** Relationship between annual changes in female population size (calculated as spring population size in year $n + 1$ minus spring population size in year n) and operational sex ratio in year $n + 1$ (see text for statistics)

Discussion

Recently, it has been experimentally shown that female asp viper need to reach a high and precise body condition threshold to initiate reproduction and sexual behaviors, whereas males exhibit a more gradual relationship between body reserves and reproduction (Aubret et al. 2002). It has also been shown that this dichotomy is underlain by an “all-or-nothing” versus a “gradual” hormonal regulation of reproduction in females and males, respectively (Aubret et al. 2002). The present field study showed that such sex differences in the energy budget and regulation of reproduction translate into marked sex divergences of demographic characteristics. Sex differences in annual catchability patterns reflecting differences in reproductive activities are a some-

what classical result (Saint Girons 1949, 1952, 1957b). However, the juxtaposition of our extensive data set (>4500 captures) with published ecophysiological data provides for the first time a sequence of functional links between sex-specific reproductive roles, energy investment in reproduction, catchability characteristics, and resulting demographics patterns. The possibility to reveal the interdependence between these various traits (usually considered separately) results from the major significance attributable to the marked shifts in catchability of ectotherms.

In both sexes, capture rate was influenced by a combination of environmental and biological factors. Body size affected catchability, with smaller-sized adults being less catchable than large adults. Body size positively affects catchability in the asp viper (Naulleau and Bonnet 1996; this study) as well as other snakes (Bonnet et al. 2002c). Perhaps small snakes adopt a more secretive behavior in response to a size-dependent vulnerability to predators (Lima and Dill 1990; Houston and Shine 1994). Additionally, smaller-sized snakes may be less catchable because their higher body surface to volume ratio shortens heating times and thus reduces basking time. Alternately, the thermal requirements of small snakes may be lower than those of larger individuals. Whatever the case, in snakes, the major effect of body size on catchability is associated with sexual maturity. After birth, snakes remain extremely secretive until they reach maturity (unpublished data on more than 600 marked neonates; Madsen et al. 1999). The dramatic increase in catchability with maturity provides strong support to the notion that temperate snakes provide the opportunity to connect reproduction to survival costs associated with vulnerability and consequently to demographic patterns (Bonnet et al. 1999b).

Although snakes from all size and sex categories were caught throughout the active season, most of the captures occurred in spring when cool ambient temperatures make it necessary for the animals to bask in the sun to achieve and maintain optimal temperatures. Additionally, mate searching and male–male combat lead to a strong increase in the catchability of males at that time. After the relatively short mating season (March–April), males adopt more secretive behaviors and were observed only occasionally, usually during shedding episodes or digestion (unpublished observations). In females, reproduction also strongly and positively influenced catchability, with increased exposure of reproducing females over prolonged time periods (March–September). The higher catchability rates of reproducing females are linked to the high thermal/metabolic requirements of vitellogenesis and gestation (Bonnet et al. 1994; Bonnet and Naulleau 1996). Each year, most of the adult males undertake reproductive activities whereas only a fraction of the females are reproductive. As a result, male captures outnumbered female captures in spring but not later in the year when males were no longer involved in reproduction, whereas female reproductive activities continued through the end of summer. Overall, when comparing males and females, both the difference in the absolute values and the temporal shift in catchability are explainable in the light of their respective system of alloca-

tion of energy to reproduction (gradual versus threshold dependent).

In the course of the study, total population size fluctuated widely, and year-to-year variations in rodent abundance (voles) appeared to be an important regulator. A sex-specific analysis revealed that interannual fluctuations in population size were mainly driven by the female population, notably reproductive females. These variations are linked to the annual recruitment rate of reproductive females among nonreproductive adults and subadults and to the annual survival cost of reproduction. As reproduction requires a female to have attained a high body condition threshold, and because food availability influences the accumulation of body stores, food availability thus influences the proportion of reproducing females in the following year (Bonnet et al. 2001). However, the proportion of reproducing females was also elevated the year of particularly high food availability (1996; see Fig. 4), and this absence of a temporal delay between food availability and reproduction suggests a more direct influence of prey availability on reproductive status. We hypothesized that some females (e.g., those close to the threshold) may respond positively to high food levels (1996) and reproduce under such favorable condition. This complex reproductive decision process that involves both long-term storage and facultative food intake is well illustrated in the multiple regression analysis (see Table 3).

In this population, survival costs of reproduction are high and most females die during or shortly after reproduction (Bonnet et al. 2000, 2002b). Part of this mortality is attributable to exposure to avian predation (Naulleau 1997) whereas part is the result of the extreme emaciation of postparturient females (Bonnet et al. 2000a). A similar effect of reproduction on survival through predation and body reserves depletion has been reported in a similar adder, *Vipera berus* (Madsen and Shine 1993). A direct consequence of this high mortality of reproducing females is that a fluctuation in the proportion of reproducing females will generate substantial variation in absolute annual mortality. This result was clearly confirmed in our data set as the proportion of reproducing females in a given year n negatively influenced the annual changes in total female population over this year n (see Table 4). However, current food levels also positively affected annual changes in female population size (Table 4).

Because most female vipers die after reproduction, positive changes in adult population size can be attributable to the recruitment of new adult females. Therefore, this positive relationship between food availability and adult population size suggests a strong linkage between food levels and maturation, as is largely confirmed by field data. Growth rate and reserve storage are directly dependent on fluctuation in food levels. In 1996, the best year in terms of food availability, we recorded the highest growth rates, up to 20 cm in juveniles (Bonnet et al. 1999a), and several females reached maturity in 2.5 years (instead of the typical 3.5) and reproduced in 1997 (Bonnet et al. 1999a). Hence, demographic patterns in female vipers were clearly understandable in the frame of their particular reproductive biology,

combining delayed reproduction (precise body condition) and a short reproductive life (tendency toward semelparity).

In strong contrast to females, annual changes in male population size were limited and apparently not affected by food levels. Although food levels influence growth in this sex as well (Bonnet et al. 1999a), they did not directly affect population dynamics. In males, the gradual system of energy allocation to reproduction does not impose extended phases of energy gathering; thus, most males can initiate reproductive activities even with limited body reserves. Furthermore, reproductive activities are concentrated in spring and do not entail prolonged exposure to predation as observed in reproductive females, as a result, most males reproduce repeatedly during their life span. This gradual system of energy allocation (no body condition threshold, iteroparity) offers a likely explanation for the stable male population size.

The differential effects of food abundance on each sex within a population led to marked fluctuations in both absolute and operational sex ratio (see Table 3). To our knowledge, such a strong effect has never been documented in snakes. Because the operational sex rate influences sexual selection gradients and the reproductive strategy of males (Duval et al. 1992; Madsen and Shine 1992), it deserves further study.

In conclusion, although differential catchability is classically viewed as a confounding factor complicating population size analysis, in ectotherms it rather offers opportunities to explore complex relationships between the energy budget of reproduction, seasonal catchability, and population dynamics. Our study of aspic vipers shows that within the array of capital breeders and within a given population, two subpopulations (males versus females) nonetheless exhibit marked differential sequences in the links between various life history traits. Sexual differences in ecology (i.e., diet, behavior, and habitat selection) or demography in relation to climatic or resource fluctuations have been reported in endotherm species, notably ungulates (Clutton-Brock et al. 1987; du Toit 1995; Myseterud 2000; Oakes et al. 1992; Owen-Smith 1993). The clear dichotomous system revealed in the present work, however, contrasts sharply with results gathered on endotherms. The temporal dissociation between the phases of energy acquisition and allocation to reproduction exhibited by ectotherms provides a unique opportunity to better unravel the complex effects of resource-fluctuating environments on reproductive strategies (Pough 1980; Shine and Bonnet 2000). Finally, the present study also emphasizes the complementary aspects of ecological and physiological approaches to interpret capture–recapture data (Bonnet et al. 2002a).

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