Intermittent breeding and the dynamics of resource allocation to reproduction, growth and survival

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Summary

1. In iteroparous organisms, the timing of reproduction varies greatly and reproduction may be intermittent. Here, we investigate the proximate determinants of intermittent breeding and their evolutionary significance in a viviparous snake, the meadow viper *Vipera ursinii ursinii*. We used individual life-history data collected over a 28-year capture–mark–recapture field study.

2. Among viviparous snakes, the meadow viper's almost exclusively insectivorous diet is remarkable. Breeding females maintain substantial foraging activity during gestation.

3. The life cycle is iteroparous, and female breeding frequency is essentially biennial. Breeding status is strongly associated with a threshold on female body condition prior to vitellogenesis.

4. Non-breeding females grow and store fat reserves needed for future reproduction. Breeding females convert reserves into eggs, the number of which is determined by maternal size and body condition prior to vitellogenesis. During pregnancy, females stop growing.

5. Females survive breeding and non-breeding years with equal probabilities. Our results suggest that income resources during pregnancy are used to fully cover the costs of gestation.

6. Integration of our data into a matrix population model allowed us to relate breeding pattern to fitness. According to the model, biennial breeding is strongly favoured by natural selection if consecutive breeding decreases maternal survival and/or fecundity. Growth cessation during breeding years generates weak selection pressures for intermittent breeding.

Key-words: growth, life-history trade-offs, reproductive investment, snakes, survival, temporal variation

Introduction

Patterns of resource allocation to maintenance, growth and reproduction are key attributes differentiating life histories and underlying variation in the timing of life-history events (Zera & Harshman 2001; Ricklefs & Wikelski 2002). Life-history theory for constant environments predicts an optimal switch point in individual's lifetime prior to which all energy is allocated to somatic growth and after which all energy is allocated to reproduction (e.g. Perrin & Sibly 1993). In reality, iteroparous species, in which adults reproduce repeatedly during life, show great variation in their breeding schedule. For many organisms living in seasonal environments, reproduction is intermittent, meaning that reproductively mature individuals do not use all breeding opportunities (Jouventin & Dobson 2002; Rivalan *et al.* 2005; Church *et al.* 2007; Skjaeraasen *et al.* 2012). Intermittent reproduction is intriguing from an evolutionary perspective because it combines the loss of current reproduction with the risk of not surviving until the next breeding opportunity.

Apart from intermittency due to occasional failures, life-history studies have produced two scenarios to explain intermittent reproduction (Bull & Shine 1979; McNamara & Houston 2008). First, organisms may have the physiological flexibility of skipping reproduction based on environmental cues: consecutive reproduction is physiologically possible, but skipping reproductive events reduces or eliminates the cost of reproduction (defined as a reduction in survival or future reproduction as a result of resource allocation to current reproduction, Williams 1966), which may be higher during unfavourable seasons (Erikstad *et al.*

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1998). The ability to skip reproduction may thus evolve as a life-history adaptation to temporal environmental variability. Alternatively, capital breeders, such as many reptiles, primarily allocate stored energy and material rather than income resources to reproduction, and it may take them one non-breeding season or more to store the capital needed for future reproduction (Bull & Shine 1979; Drent & Daan 1980; McNamara & Houston 2008; Stephens *et al.* 2009). This is particularly likely when reproduction is strongly constrained by resource availability and when the cost of breeding includes a large fixed component independent of reproductive output. Such a 'fecundity-independent cost of reproduction' (sensu Bull & Shine 1979) can be due to brooding, live bearing or migration associated with reproduction, whereby income energy is diverted from storage or reproductive individuals are exposed to extra-predation. We then expect breeding to take place when individuals can invest more capital than the amount needed to cover the high fecundity-independent cost of reproduction (Bull & Shine 1979). For example, the long and energetically costly migration associated with spawning in some pelagic fish species does not depend on fecundity and may select for intermittent spawning (Jørgensen *et al.* 2006).

Investigating the adaptive value of either mechanism requires, however, that the fitness costs and benefits of intermittent breeding be evaluated in the framework of a dynamic resource budget. In this framework, income resources can be used or stored, and income and stored resources are partitioned between maintenance, growth and reproduction throughout the individual's reproductive life (Perrin & Sibly 1993; Casas *et al.* 2005). Few empirical studies have examined the proximate determinants of breeding and their adaptive significance in such a framework because there are few species for which patterns of breeding in the field are documented along with variation in resource acquisition and variation in resource allocation to maintenance, growth and reproduction, over their lifespan. Viviparous snakes are ideal study systems to take steps forward in that direction. These species are often considered as typical capital breeders characterized by strong costs of reproduction and irregular breeding (Bonnet, Bradshaw & Shine 1998; Shine 2003). Viviparous snakes are primarily lecithotrophic (yolk only provisioning, Blackburn & Stewart 2011), but some degree of reliance on income energy during both vitellogenesis and gestation has been uncovered in various species (Lourdais *et al.* 2003; Van Dyke, Beaupre & Kreider 2012). Physiological costs of reproduction include the costs of acquiring and storing resources in the form of various nutrients, the costs of vitellogenesis, the maternal cost of pregnancy and the foetal cost of embryogenesis (e.g. Van Dyke & Beaupre 2011). Live-bearing reproduction is associated with substantial energetic expenditure during gestation (Ladyman *et al.* 2003; Schultz, Webb & Christian 2008), and several potential fecundity-independent costs of reproduction have been uncovered in cold-temperate vipers, including a

reduction in survival, a reduction in body growth and a depletion of fat reserves (Madsen & Shine 1993; Bonnet *et al.* 2002).

Here, we report the analysis of individual patterns of breeding in relation to lifetime variation in body condition, reproductive output, growth and survival in a viviparous snake, the meadow viper *Vipera ursinii ursinii* (Bonaparte, 1835), from a 28-year mark–recapture study in the field and 19-year study in the laboratory. Among viperids, the meadow viper is remarkable for its small size and almost exclusively insectivorous diet (Baron 1992; Baron *et al.* 1996). Specialization on insects implies that the snakes have no prey available until about a month after the time of vitellogenesis, because insects emerge late in the short active season (Baron 1992). This makes this species an obligate capital breeder early in vitellogenesis. Once available, insects form a predictable and abundant source of food that both non-reproductive and pregnant females can use. We show that reproduction generally conforms to a regular biennial cycle. Combining capture–recapture and laboratory data on reproduction, we analyse patterns of body condition, growth, survival, current reproduction of breeders and future reproduction of non-breeders to address three main questions: (i) what are the proximate determinants of the transition from non-breeding to breeding and from breeding to non-breeding states? (ii) is there evidence that environmental variation in resource availability influences the transitions between non-breeding and breeding states? (iii) what are the fitness costs and benefits associated with these transitions and what is the adaptive significance of *V. u. ursinii*'s predominantly biennial pattern of breeding?

Study species and methods

STUDY SPECIES AND SITE

The meadow viper *V. u. ursinii* inhabits open and dry calcareous grasslands between 900 and 2200 m elevation in the northern Mediterranean basin. This study was conducted in one population located in Mont Serein, France (1430 m a.s.l., 44°18′N, 5°26′E). The population occupies a 100 ha area and is isolated from the nearest populations 45 km away by inhospitable habitat. A study area of four hectares has been monitored continuously since 1979. The area is divided into two contiguous study sites of about 2 ha each: a north facing and mesophilic hillside (habitat A), and a south facing and xerophilic hillside (habitat B). Small home ranges averaging 0·09 ha (Baron *et al.* 1996), together with the presence of a 10 m-wide asphalt road separating the two sites, make snakes' movements between sites extremely rare (only two such movements reported during this study). In this population, females become sexually mature when 4–6 years old. Adult males and adult females emerge around mid-April and early May, respectively. Vitellogenesis starts after hibernation and lasts 4–8 weeks (Saint Girons 1992). Mating occurs during

the last two weeks of May soon followed by ovulation and fertilization. Parturition takes place between mid-August and mid-September depending on weather conditions. Hibernation begins during October.

DATA COLLECTION: LIFE HISTORY

Snakes were individually marked by scale clipping upon their first capture during 56 primary capture sessions between 1979 and 2007 ($n = 1081$ captures, mean duration per session = 10 days). Even though scale clipping is extremely reliable and leaves permanent black marks allowing unambiguous individual identification throughout life, we always recorded ventral and head scales to confirm the ventral scale clipping pattern. Primary capture sessions were conducted by 1–3 persons during 1–2 weeks twice a year including one session during the mating season and before ovulation and one session before the end of gestation. All spotted animals were captured, identified and measured (snout-vent length, SVL to the nearest mm and body mass to the nearest dg). Sexual maturity and reproductive status (non-reproductive, reproductive: post-ovulation, gravid or post-partum) of each female were assessed. During the second capture session, we counted ova by palpation of the abdominal cavity to obtain accurate estimates of litter size (Pearson's sample correlation coefficient with litter size in the laboratory, $r = 0.997$, $n = 116$; only one mismatch). Snakes were released at their capture location in the evening of the capture day or after parturition for gravid females (see below).

In 1983–1988 and from 1994 onwards, we obtained data on reproductive outputs by keeping gravid females in the laboratory until they gave birth ($n = 396$ offspring, $n = 109$ litters, 19 years). Gravid females were maintained in individual rearing boxes ($350 \times 180 \times 210$ mm) with a shelter, damp soil, free access to water and a heat source, allowing snakes to thermoregulate. Body mass was measured daily. Just after parturition, we counted the number of undeveloped ova, dead embryo, stillborn and healthy offspring to calculate litter size and litter success (all variables are precisely defined in Table S1, Supporting information). On average, females were kept 13 days (± 9 SD) in the laboratory prior to giving birth, which is a short captivity period that should not influence reproductive parameters. Newborns were measured (SVL), weighed and sexed by counting sub-caudal scales. On average 11 days (± 7 SD) after parturition, mothers were released with their offspring at the maternal capture location. Data on survival and growth during the juvenile stage have been reported elsewhere (Baron *et al.* 2010a; Baron, Tully & Le Galliard 2010b).

DATA COLLECTION: BEHAVIOUR

Vipera u. ursinii's specialized feeding strategy is unique in the genus. Diet composition, venom characteristics and foraging behaviour are highly distinctive (Saint Girons & Naulleau 1981; Baron *et al.* 1996). In this population, more than 99% of prey items in the snakes' diet are orthopteran (Baron 1992). Foraging activity begins mid-June and stops in late September, irrespective of age or sex (Baron 1992). Snakes do not feed during the mating season, making reproductive investment during early vitellogenesis entirely dependent on reserves accumulated during the previous summer. Energetic costs of reproduction could result from lower energy intake and higher energy expenditures if gravid females feed less and bask at a higher body temperature than non-gravid females (Ladyman *et al.* 2003). We measured feeding frequencies (proportion of females whose stomach contains some prey), the wet mass of stomach content during the end of gestation (log-transformed to achieve normality) and field body temperatures. Body temperatures were measured by forcing a type K thermocouple through the mouth and throat to the stomach. We used one-tailed tests of the hypothesis that gravid females would feed less and bask at higher temperatures than non-gravid ones.

DATA ANALYSIS: MATURATION, BREEDING PATTERN AND SURVIVAL

We modelled the transition to reproductive maturity based on longitudinal data where females of known age are classified as immature or adult. The Arnason–Schwarz parameterization was used to fit a multistate mark–recapture model (software MARK 4.3) including age-specific transition probabilities from immature to adult state, that is, first-breeding probabilities conditional on survival (Brownie *et al.* 1993; Nichols *et al.* 1994; White & Burnham 1999). Detailed mark–recapture histories of sexual maturation were available for 87 females of known age recaptured until the age of 7 years. Parameters were estimated with a maximum likelihood approach. We included age-dependent first-breeding probabilities for age 4, 5 and 6 years with different intercepts between sites A and B. Based on previous findings (Baron *et al.* 1996, 2010a), we started the analysis with the Arnason–Schwarz model that included a linear effect of age on capture and survival probabilities, irrespective of breeding state. We identified the best model for capture and survival probabilities and used it to test whether first-breeding probabilities differ between sites A and B.

We also used mark–recapture data for adult females captured in August–September ($n = 161$, 302 observations, 1979–2007) to analyse breeding frequency and survival (see Fig. 1 for raw data). We used a multistate Arnason–Schwarz parameterization to estimate capture and annual survival probabilities conditional on current breeding state and transition probabilities between breeding and non-breeding states conditional on survival. The initial model included spatial and state-dependent variation but no temporal variation in capture, survival and transition probabilities. Goodness-of-fit (GOF) tests of this initial model performed with U-CARE 2.2 (Choquet
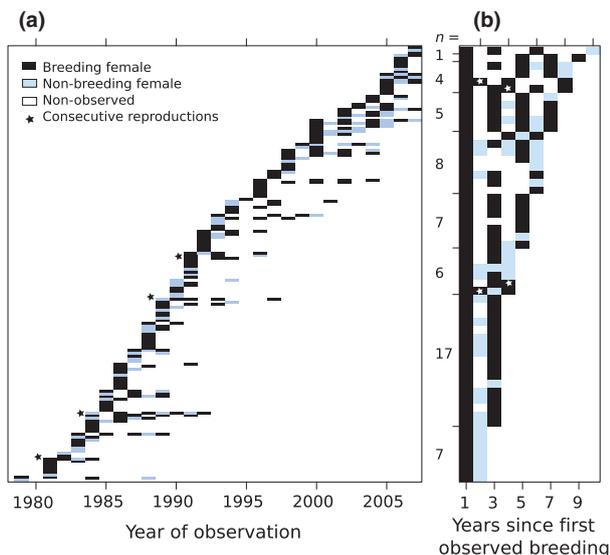
Fig. 1. Individual capture histories and breeding state. Each line represents an individual. Black rectangles represent years during which a female is breeding, while grey rectangles represent a reported non-breeding year. Year during which the female is not observed is in white. On the left (a), all capture histories are plotted ($n = 161$) organized by first year of observation and by increasing duration of observation. On the right (b), capture histories of females that have bred twice are plotted ($n = 56$). These histories are lined-up with their first-observed reproduction and are arranged in order of increasing observed maximum age after first-observed reproduction. Of the 138 reproductive events observed, only four females bred during two successive years (emphasized with a star symbol).

et al. 2005) were satisfactory (summed test, $\chi^2_{96} = 47.7$, $P > 0.99$). A bootstrap GOF test also supported the initial model (1000 simulations, $P = 0.33$), and the median c-hat test found no evidence for overdispersion. Model selection and hypotheses testing were conducted with the Akaike Information Criterion corrected for small sample size (AICc, Lebreton *et al.* 1992; Anderson & Burnham 1994). We first selected the models with the lowest AICc describing variation in capture probability and next selected the best models describing variation in survival and/or transition probabilities. We tested all additive models between the initial model and the constant model (Burnham & Anderson 1998).

DATA ANALYSIS: BREEDING STATUS AND REPRODUCTIVE OUTPUTS

We estimated stored reserves potentially available for breeding by body condition at the onset of vitellogenesis (BCV, Naulleau & Bonnet 1996; Aubret *et al.* 2002). We tested for the effects of BCV on breeding probabilities and reproductive traits (litter mass, mass loss at parturition, post-partum body condition). Body condition of adult females measured shortly after winter emergence but prior to ovulation (May) is similar to condition measured in September of the previous year, in accordance with the facts that females do not feed substantially in September

–October and do not lose much body mass in the winter period (Baron *et al.* 1996). Thus, we obtained estimates of BCV for 80 females for which either pre-wintering or post-wintering body condition data were available. We also compared annual change in body mass and body size between breeding and non-breeding years.

We further used mixed-effects models to investigate between years, spatial (between sites A and B) and inter-individual variation in clutch size, litter success, clutch mass (including water and residual tissues from amnion and allantois) and post-partum body condition (Table S1, Supporting information). We analysed residual clutch mass from a covariance analysis including body mass after parturition instead of ratios to correctly standardize for body mass (Van Dyke & Beaupre 2011). We followed the methodology of Pinheiro & Bates (2000) for general linear models (normally distributed data) and of Bolker *et al.* (2009) for generalized linear models (binomially distributed data). Site (A vs. B) was included as a fixed effect, and year was included as a random effect. Variance component was used to calculate the ratio of yearly variation on the sum of yearly and residual variation, or relative temporal variation (RTV). To address potential spatial differences in inter-individual variation, we included heterogeneous residual variances between sites (see chapter 5 in Pinheiro & Bates 2000). Female snout-vent length (SVL) was included as fixed covariate. Initial models contained all factors, and model selection was performed backward by removing non-significant terms ($P > 0.05$). Fixed effects were tested with conditional *F*-tests based on REML, and random effects were tested with asymptotic likelihood ratio tests.

Results

MATURATION AND BREEDING PATTERN

Our observations indicate that females reproduce for the first time between 4 and 6 years when their SVL reaches about 300 mm. The best multistate model of first breeding (Table S2, Supporting information) has constant annual survival probability of 0.69 (0.63, 0.74) (95% confidence limits) and capture probabilities that increase linearly with age from 0.15 (0.08, 0.24) at age 1 to 0.80 (0.62, 0.92) at age 7. Conditional on survival, the first-breeding probability is roughly constant from 4 to 6 years and averages 0.80 (0.59, 0.92). Thus, most females start reproducing when 4 years old.

Patterns of subsequent breeding were examined for adult females (Fig. 1). According to the best model for capture probabilities (Table S3a, Supporting information and Fig. 2a), adult females are more likely to be captured during their breeding years [odds ratio = 8.0 (3.7, 17.2), $\chi^2_1 = 32.5$, $P < 0.0001$] and slightly more likely to be captured in habitat B [odds ratio = 1.7 (0.8, 3.3), $\chi^2_1 = 2.39$, $P = 0.12$]. The analysis further shows that females alternate between breeding and non-breeding states (Table S3b,
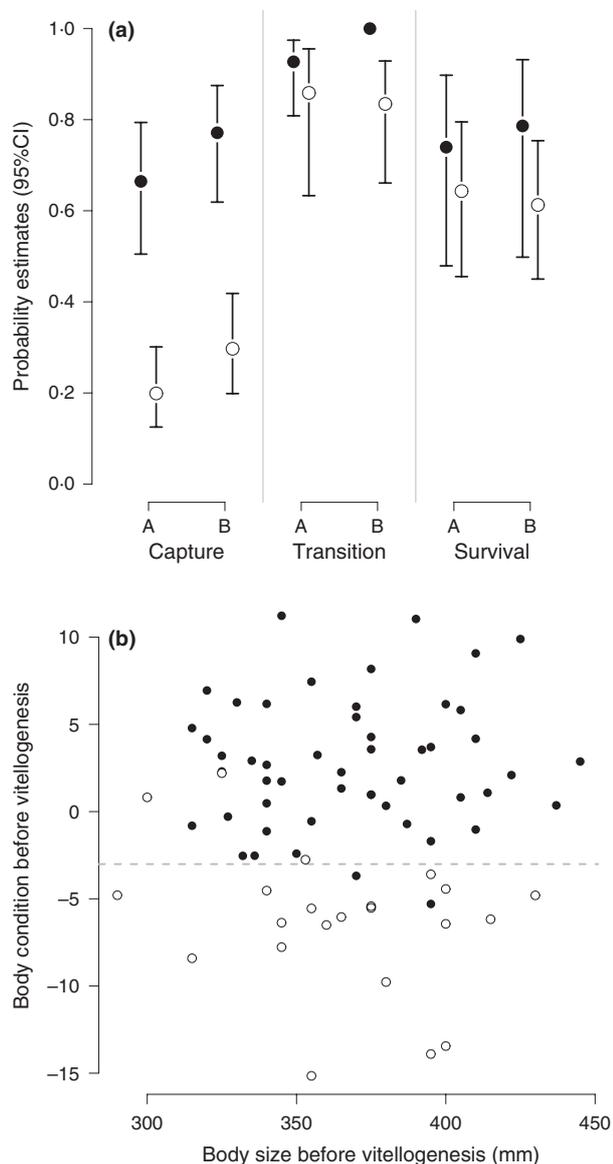
Fig. 2. (a) Survival and reproduction frequencies in female meadow vipers (breeding years: filled circles, non-breeding years: open circles). Estimates (±95% CI) of capture, transition and survival probabilities in habitat A and B were obtained from model 15 in Table S3c (Supporting information) and were grouped by breeding states and habitats. Capture estimates measure the probability to capture a female, survival estimates measure proportion of females surviving from one year to the next, and transition estimates measure the probabilities to change breeding state conditional on survival to the next year. (b) Body condition threshold for breeding (breeding females: filled circles, non-breeding females: open circles). Body condition (residual of body mass against body size) and body size (snout-vent length) were measured prior to vitellogenesis (*n* = 72). The dashed line corresponds to the body condition where the predicted breeding probability from a logistic regression is 50%.

Supporting information and Fig. 1). In habitat A, the probability of changing state is the same for either current state and averages 0·90 [from breeding to non-breeding: 0·93 (0·81, 0·97), from non-breeding to breeding: 0·86 (0·63, 0·96)]. In habitat B, all breeding females change

state conditional on survival (consecutive reproduction never occurs), while transition probability from non-breeding to breeding averages 0·83 (0·66, 0·93) (habitat × breeding status: $\chi_1^2 = 4{\cdot}47$, $P = 0{\cdot}03$, Fig. 2a). We could not test for inter-annual variation in transition rates because we had too few observations per year, but inter-annual fluctuations in the observed fraction of breeders are narrow and have no obvious structure (pers. obs.).

BODY CONDITION AND BREEDING STATUS

Among mature females, the breeding probability increases with body condition prior to vitellogenesis, or BCV (logistic regression, $\chi_1^2 = 57{\cdot}78$, $P < 0{\cdot}0001$, $n = 72$), while body size has no effect ($\chi_1^2 = 0{\cdot}26$, $P = 0{\cdot}55$; Fig. 2b). The relationship between breeding probability and BCV is similar between habitats (BCV × habitat: $\chi_1^2 = 1{\cdot}72$, $P = 0{\cdot}10$). In addition, adult females with a larger BCV produce heavier litters ($F_{1,34} = 6{\cdot}11$, $P = 0{\cdot}02$) and have a larger mass loss during parturition ($F_{1,36} = 13{\cdot}10$, $P = 0{\cdot}0009$) while retaining a greater post-partum body condition (BCV: $F_{1,36} = 12{\cdot}65$, $P = 0{\cdot}001$; habitat: $F_{1,36} = 20{\cdot}31$, $P = 0{\cdot}0001$).

FORAGING AND THERMAL ACTIVITY OF BREEDERS VERSUS NON-BREEDERS

Breeding and non-breeding females forage at the same frequency (Fisher's exact test, $P = 0{\cdot}40$; 31% in breeding females and 34% in non-breeding females). Non-breeders had on average a slightly heavier stomach content wet mass than breeders ($n = 30$, $t_{28} = 1{\cdot}778$, $P = 0{\cdot}04$; breeders: 1·12 g ± 0·06 SE, $n = 13$; non-breeders: 1·53 g ± 0·06 SE, $n = 17$). Despite wide variation in body temperatures across observations (median=29 °C, range=16–36 °C), a small but significant difference in basking temperature between breeding and non-breeding females was detected: breeding females bask at slightly higher temperatures during late gestation ($n = 194$, Wilcoxon rank sum test, $P = 0{\cdot}03$; breeders: 28·4 °C ± 0·1 SE, non-breeders: 27·4 °C ± 0·3 SE).

SURVIVAL, GROWTH AND RESERVE STORAGE OF BREEDERS VERSUS NON-BREEDERS

In adults, the annual probability of survival is on average 0·69 (0·64, 0·73). Annual survival is affected neither by breeding state ($\chi_1^2 = 1{\cdot}12$, $P = 0{\cdot}29$, Fig. 2a) nor by habitat ($\chi_1^2 < 0{\cdot}001$, $P > 0{\cdot}98$, Table S3c, Supporting information). Yet, a higher investment in reproduction causes a lower body condition (effect of litter mass on post-partum body condition: $F_{1,94} = 5{\cdot}65$, $P = 0{\cdot}02$) and thus may compromise future survival. This putative delayed survival cost of reproduction was assessed by studying the relationship between post-partum body condition and future survival. Post-partum body condition (measured for the first parturition of 72 snakes) has no detectable effect on

the mean probability of future annual survival (Table S4, Supporting information, model 6 vs. model 8, $\chi_1^2 = 0.23$, $P = 0.63$) nor on the annual survival probability during the year following reproduction (model 5 vs. model 7, $\chi_1^2 = 0.87$, $P = 0.35$).

We compared annual change in body size (SVL) between breeding and non-breeding years. Annual change in SVL is affected by initial SVL, breeding status and their interaction (initial SVL: $F_{1,73} = 3.54$, $P = 0.06$, breeding status: $F_{1,73} = 61.56$, $P < 0.0001$; initial SVL × breeding status: $F_{1,73} = 4.33$, $P = 0.04$, $n = 77$; see Fig. 3a). Females do not grow during breeding years (-0.58 mm ± 1.17 SE), whereas females gain on average 15.76 mm (± 1.79 SE) during a non-breeding year. Body size change during a breeding year did not correlate with relative clutch mass ($F_{1,35} = 1.68$, $P = 0.20$, $n = 37$). The annual gain in body length during non-breeding years is larger in smaller females (slope $= -0.13 \pm 0.06$ SE, $t = -2.41$, $P = 0.02$). Females also lose and gain mass during breeding and non-breeding years, respectively ($F_{1,58} = 224.9$, $P < 0.0001$, $n = 62$, Fig. 3b). The annual change in body mass is consistently smaller in habitat B than in habitat A (-6.1 g ± 1.32 SE, $F_{1,58} = 21.6$, $P < 0.0001$), irrespective of breeding status (habitat × breeding status: $F_{1,57} = 0.47$, $P = 0.49$). On average, annual body mass gain is smaller in initially heavier females ($F_{1,58} = 24.8$, $P < 0.0001$, Fig. 3b).

REPRODUCTIVE TRAITS AND INVESTMENT

Clutch size (mean $= 3.8 \pm 1.23$ SD, range $= 1-8$) is relatively invariant across years ($\chi_1^2 = 2.26$, $P = 0.13$, relative temporal variation RTV $= 17\%$, $n = 181$) but is larger (contrast $= 0.56 \pm 0.17$ SE; $F_{1,179} = 10.51$, $P = 0.001$) and more variable ($\chi_1^2 = 11.87$, $P = 0.0006$) in habitat A than B. However, spatial variation in clutch size is fully explained by a positive correlation between clutch size and maternal body size (body size: $F_{1,179} = 69.3$, $P < 0.0001$; habitat: $F_{1,178} = 0.35$, $P = 0.55$). On average, clutches are made up of 81% healthy offspring, 7.4% fully developed but stillborn embryo, 10% aborted eggs and 1.6% undeveloped ova. This high litter success [mean $= 81\%$, inter-annual range $= (0.4, 1)$] varies significantly between years ($\chi_1^2 = 82.4$, $P = 0.001$), irrespective of habitat ($\chi_1^2 = 0.09$, $P = 0.82$), maternal body size ($\chi_1^2 = 1.94$, $P = 0.29$) or clutch size ($\chi_1^2 = 2.29$, $P = 0.25$).

The average relative clutch mass (ratio of mass loss to post-partum body mass) is 0.55 ± 0.19 SD, and the residual clutch mass does not vary among years ($\chi_1^2 = 1.3$, $P = 0.25$, RTV $= 7\%$, $n = 116$) or between habitats ($F_{1,86} = 0.001$, $P = 0.97$), although there is more inter-individual variation within habitat A ($\chi_1^2 = 5.76$, $P = 0.02$). In contrast, post-partum body condition varies strongly among years ($\chi_1^2 = 11.6$, $P = 0.0007$, RTV $= 34\%$, $n = 116$). Post-partum females are in better condition in habitat A ($F_{1,94} = 9.99$, $P = 0.002$) and when females give birth earlier in the season ($F_{1,94} = 9.27$, $P = 0.003$).

We examined the annual body mass loss and the mass loss at parturition scale with reproductive investment in viable offspring, measured by litter mass (Madsen & Shine 1993). Mass loss at parturition increases linearly with litter mass (Fig. 3c) with a slope larger than one [standardized major axis regression, slope $= 1.48$ (1.39, 1.57)] and an intercept not significantly different from zero [intercept $= 0.03$ (-1.05, 1.10)]. Thus, energetic investment in the clutch increases solely with energetic investment in offspring. Testing for a difference in slopes between habitats A and B further indicates that the regression slope was slightly higher in habitat A [slope A $= 1.52$ (1.39, 1.67); B $= 1.34$ (1.23, 1.47), $P = 0.05$; Fig. 3c]. Similarly, annual mass loss during breeding years increases linearly with litter mass [Fig. 3d; standardized major axis regression, slope $= 1.36$ (1.02, 1.83)]; again, the intercept is not significantly different from zero [-3.26 (-7.89, 1.36), $P = 0.14$]. Thus, reproductive investment is proportional to reproductive output (litter mass) and shows no sign of a 'fecundity-independent cost' that would be independent of reproductive output.

Discussion

We have shown that our study population of the meadow viper exhibits a predominantly biennial pattern of breeding (Fig. 1). The meadow viper is a true iteroparous species: the adult life expectancy is three years, and adult females breed on average two times. Among females that survive more than three adult years, most individual histories alternate breeding and non-breeding years. For a few individuals, breeding in consecutive years has been recorded. The absence of year or habitat effects on reproductive investment and the regularity of biennial breeding over the 28 years of study indicate that breeding frequency was not confounded by consistent individual or spatial differences or by some inter-annual variability in environmental conditions. In addition, breeding status is strongly predicted by a threshold on body condition. During their non-breeding years, adult females, especially small ones, accumulate reserves and grow significantly in length. During their breeding years, females stop growing in structural size but their survival probability is as high as in non-breeding years. In stark contrast with sister species *Vipera aspis* and *Vipera berus* that forage on much larger prey and completely cease feeding during pregnancy (Shine 2003), *V. u. ursinii* does not feed during vitellogenesis but forage substantially throughout gestation. Food intake during gestation is only reduced by 25% compared with non-breeding years. Future survival of breeders is not affected by their current reproductive investment.
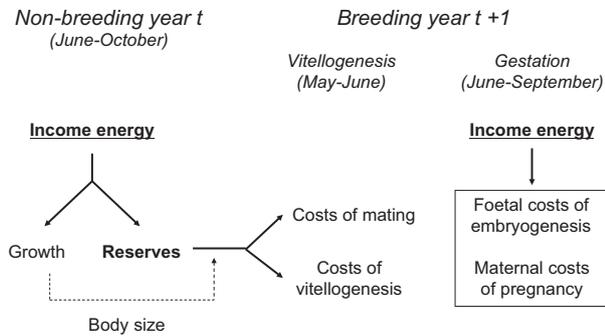
PROXIMATE DETERMINANTS OF BREEDING

Breeding is associated with a loss of body mass that parallels the body mass gain during non-breeding years. The energy acquired by a non-breeding female is invested in
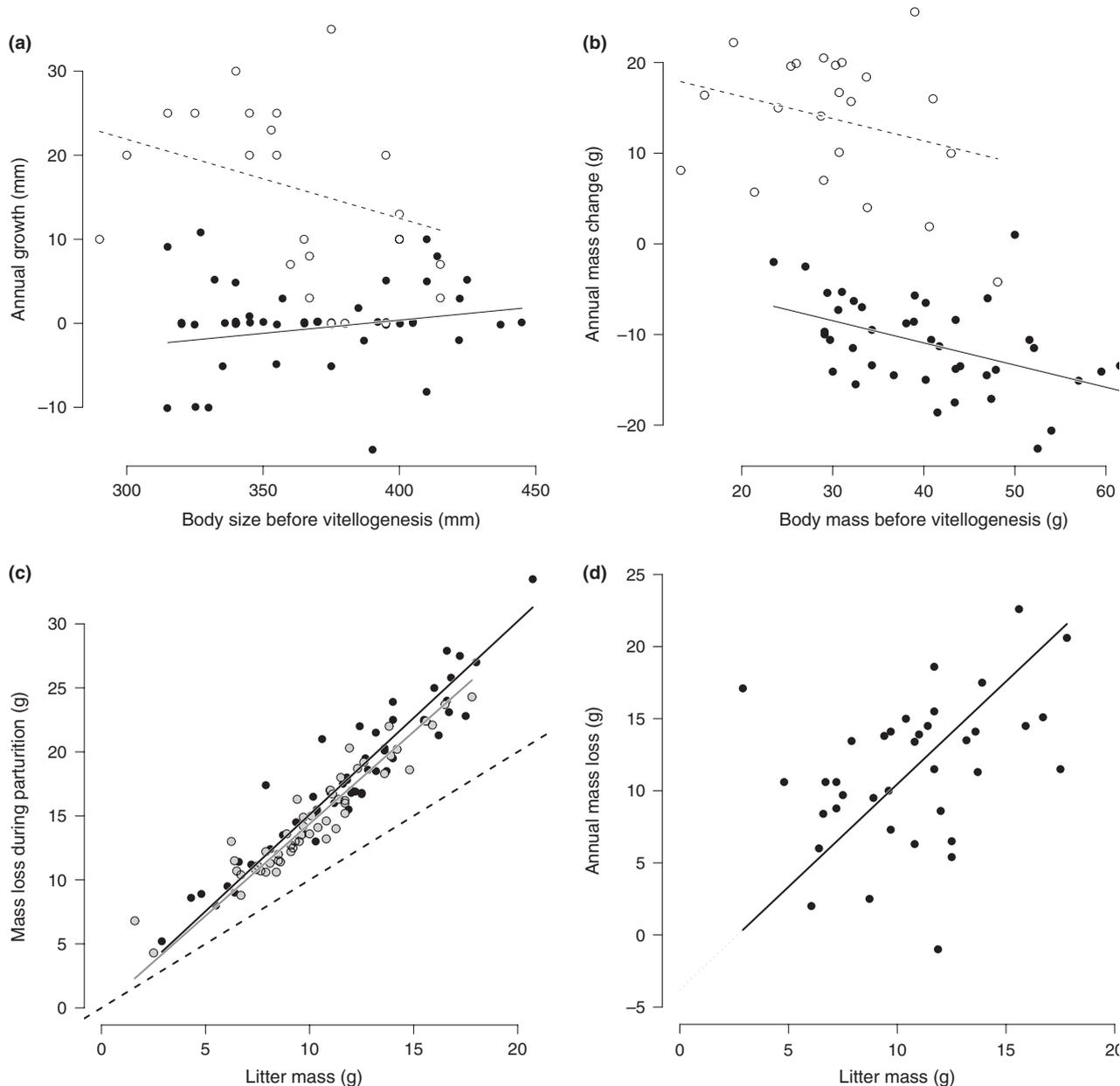
Fig. 3. Body growth (mm per year, a) and body mass change (b) during breeding and non-breeding years as a function of size and mass prior to vitellogenesis, respectively. Negative values of body growth were caused by measurement errors associated with pregnancy or by body shrinkage (see main text). Change in body mass was calculated from early spring to post-parturition for breeding females (filled circles) and from early spring to late summer for non-breeding females (open circles). (c, d). Analyses of energetic investment of reproduction show a linear scaling with mass investment in the litter (total litter mass) and provide no evidence of fecundity-independent energetic costs. Energetic costs of reproduction were measured either as total mass loss during parturition (c) or total mass loss during the breeding year (d, from early spring to post-parturition). Lines represented standard major axis regressions. In the case of mass loss during parturition, the regression lines differed slightly significantly between habitat A (black circles) and habitat B (grey circles) and the line $y = x$ was drawn for the sake of interpretation.

basal maintenance, body growth and reserves for future reproduction (Fig. 4). Because foraging activity does not start until after vitellogenesis, females require body reserves for maturing follicles and for mating (Baron 1992). Breeding depends more on body condition than on body size, and we uncovered a critical condition threshold above which most mature females reproduce. Breeding thresholds were also found in *V. aspis* (Naulleau & Bonnet

1996) and in a rattlesnake (Diller & Wallace 2002). However, unlike other viviparous snakes, the net mass changes at parturition and during gestation are almost perfectly proportional to litter mass, which indicates that there is no fecundity-independent component to the expenditure of reserves or the consumption of income energy. In the sister species *V. berus*, there is a minimum body mass loss of 25 g during gestation (Madsen & Shine 1993).

Non-breeding year t
(June-October)

Breeding year t +1

Vitellogenesis
(May-June)

Gestation
(June-September)

Fig. 4. Hypothetical dynamics of resource allocation to reserves, reproduction, growth and survival. A non-breeding female at the beginning of the active season averages 30 g in mass and 350 mm in length. During the feeding season, the average non-breeding female mass will increase by 13·7 g, which includes an expected growth in size of 15·8 mm equivalent to a structural mass increase of about 2–3 g (based on structural mass–length relationship, unpublished data); thus, the annual mass increase amounts to 2–3 g structural growth and 11–12 g of reversible mass increase (e.g. reserves). In the following year, the average 11–12 g of reversible mass available prior to vitellogenesis is used by the breeding female to produce an average 11 g of litter mass. Reserves are thus invested in vitellogenesis and survival. Maternal costs of pregnancy and foetal costs of embryogenesis are covered by resource income during pregnancy.

Does resource availability influence the breeding threshold on body condition? Madsen & Shine (1999) predicted that capital breeders should decrease their threshold in response to lower resource levels. This prediction can be examined in the light of the consistent differences found here between sites A and B that form two adjacent but essentially disconnected patches of habitat. In habitat B, females gain less body mass during non-breeding years, lose more body mass during breeding years, are smaller on average, and produce clutches with a smaller slope of the major axis regression of clutch mass to litter mass. As off-spring mass at birth does not differ between habitats (Baron, Tully & Le Galliard 2010b), the lower slope in habitat B either means a lower relative egg hydration, or a lower investment in egg membranes and uterine fluids. Thus, the xeric habitat B is less productive than the meso-philic habitat A, and we would predict that females from habitat B should decrease their threshold for breeding (Madsen & Shine 1999). Yet, the breeding threshold on body condition and size-independent reproductive invest-ment is similar between habitats. Rather, females are less successful at passing the breeding threshold and have lower post-partum body condition in habitat B. This suggests that the breeding threshold on condition is set basically by the amount of energy needed to mature the number of eggs.

RESOURCE ALLOCATION PATTERN IN BREEDING STATE

Like other cold-temperate vipers (Naulleau & Bonnet 1996; Aubret *et al.* 2002; Bonnet *et al.* 2002), the meadow viper shows elements of capital breeding early in vitello-genesis, where capital breeding is defined as reliance on stored resources to finance expenditure in reproduction during a given time period (Stephens *et al.* 2009). The sharp body condition threshold for breeding and the biennial dynamics of body reserves is typical of capital breeders (Drent & Daan 1980; Bonnet, Bradshaw & Shine 1998), but do not imply that income energy is unimpor-tant during breeding years (Stephens *et al.* 2009; Van Dyke, Beaupre & Kreider 2012). The contribution of resource income to cover high energetic costs of vitello-genesis has been shown in viviparous snakes (Van Dyke & Beaupre 2011; Van Dyke *et al.* 2012). This does not apply to the meadow viper, however, because vitellogene-sis takes place several weeks before the onset of foraging. All costs of vitellogenesis must therefore be supported from the capital.

During pregnancy, breeding females show no reduction in feeding frequency and only a relatively small reduction in stomach content, implying that pregnant females acquire resources at 75% of the foraging rate of non-breeders. In theory, the maintenance, metabolic costs of pregnancy, body growth and even reserve storage may be financed from food intake during gestation similarly to other mixed capital and income breeding vertebrates (Stephens *et al.* 2009). In fact, the annual growth rate varies among breeders from small positive to small negative with a mean close to zero without any correlation with reproductive investment. Thus, at most a small amount of resource income is invested in maternal growth. Whether the cessation of body growth during breeding is the expression of a resource allocation trade-off remains uncertain however. Alternatively, embryo development may directly signal to shut down growth metabolic pathways (Harshman & Zera 2007) because orthopteran may not provide the amount or quality of nutrients that gestation requires. Some of the nutrients needed during gestation might instead be catabolized from maternal structural capital including tissues such as muscles and bones. This would be consistent with the observation of negative growth observed in several breeding females (Fig. 3a).

We do not have direct measurements of whether and how much resources acquired during pregnancy can be stored as fat reserves, but our analysis of body mass dynamics during a breeding year (see Fig. S1, Supporting information) suggests some physiological ability to convert resource income during pregnancy into reserves. All these results indicate that the basal cost of maintenance and the metabolic and behavioural costs of pregnancy are covered by income resources during gestation. It remains to be investigated whether food intake during gestation might contribute to the offspring mass and energy balance (Van Dyke & Beaupre 2012). This is untested in most snakes, even though mother-to-embryo nutrient transfer has been found in viviparous snake species long thought to be lecithotrophic (Blackburn & Stewart 2011).

INTER-ANNUAL VARIATION IN REPRODUCTION STRATEGY

The meadow viper in this population is exposed to environmental conditions that vary across years. For example, monthly averages of daily maximum temperatures over the summer vary between 15 °C to 25 °C across years (unpublished data), which is likely to impact the snakes' physiology and behaviour and their insect prey as well (Le Galliard *et al.* 2012). However, the biennial cycle of individual breeding is regular (see Fig. 1) and inter-annual fluctuations in the proportion of breeders are narrow, which shows no tendency for breeding synchrony across years. This suggests that breeding threshold and transition rates vary little between years. Clutch size and residual mass loss at parturition also show little variation among years compared with variation among females. Clutch size correlates primarily with body size and body condition prior to vitellogenesis. Reproductive investment remains constant even though body condition varies across years because females with larger body condition lose more mass at parturition but also score higher post-partum mass for their length.

The invariance of clutch size and reproductive investment contrasts with inter-annual variation in post-partum body condition and litter success. These traits are expected to co-vary with weather and food availability, which may influence both energy income and the speed and cost of embryo development (Le Galliard *et al.* 2012). Inter-annual variation in post-partum body reserves without significant variation in breeding probability suggests that the corresponding range of variation remains for the most part below the breeding threshold. The meadow viper thus expresses a life-history strategy in which key reproductive components (clutch size, reproductive investment, breeding threshold) are buffered against environmental variation, whereas other reproductive traits appear to be less 'environmentally canalised' (Gaillard & Yoccoz 2003; Baron *et al.* 2010a).

COSTS OF REPRODUCTION AND THE EVOLUTION OF INTERMITTENT BREEDING

Costs of reproduction are defined as a reduction in survival or future reproduction as a result of resource allocation to current reproduction (Williams 1966). We found neither immediate nor delayed reduction in survival associated with reproduction. In other snakes, high mortality during gestation and after parturition is documented and attributed to increased predation and increased energy expenditure during vitellogenesis and gestation (Madsen & Shine 1993; Bonnet *et al.* 2002; Shine 2003). In *V. u. ursinii*, females bask at slightly higher body temperatures (this study), are more exposed and visible than non-breeding females, and their vitellogenesis and pregnancy must also be associated with increased metabolic expenditure (Schultz, Webb & Christian 2008; Van Dyke & Beaupre

2011), which should result in higher energetic costs and predation risks. This trade-off between breeding and survival, mediated by the energetic costs of gestation, has been demonstrated in other viviparous snakes (Ladyman *et al.* 2003; Van Dyke & Beaupre 2011). Our data suggest that breeding females are able to finance expenses of gestation from resource income. As a consequence, the trade-off is cryptic (i.e. no apparent reduction in current or future survival of breeders) under normal field conditions.

Existing theory (Bull & Shine 1979; McNamara & Houston 2008) predicts the evolution of reproductive frequency towards annual breeding when (i) there is no fecundity-independent energetic costs of reproduction, (ii) resources are acquired in breeding years and, as a consequence, (iii) the metabolic and behavioural costs of pregnancy can be covered by income energy. Annual breeding may also yield fitness benefits by means of bet-hedging (e.g. Church *et al.* 2007) against stochastic fluctuations in juvenile life-history traits (Baron *et al.* 2010a). Meadow vipers seem to fit these conditions because they have the physiological capacity to breed in consecutive years, yet they follow a regular biennal breeding cycle. The pause in body growth during breeding years may represent a significant cost of breeding that could select against annual reproduction (e.g. in other viviparous snakes, Bonnet *et al.* 2002; Shine 2003). In the meadow viper, larger females produce larger clutches (this study), as well as larger and fattier offspring that subsequently survive and grow better (Baron *et al.* 2010a). A non-breeding year implies an average growth increment of about 16 mm, which translates into an increase in future reproduction of ca. 0·4 eggs conditional on annual survival ($n = 48$). However, the actual fitness cost caused by growth loss during breeding years must be evaluated over the individual's life span (see below).

We also found a positive correlation between body condition prior to vitellogenesis and reproductive output (litter mass and mass loss during parturition), which implies lower reproductive output if consecutive breeding depletes stored resources. The second clutch in the few observed breeding–breeding sequences is indeed smaller than the first by an average 1·75 eggs ($n = 4$). This may hint at a cost of consecutive breeding mediated by reduced fecundity. To evaluate the impact on lifetime fitness of a growth cessation during breeding and of a reduction in fecundity and/or maternal survival potentially associated with consecutive breeding, we integrated our data into a matrix population model (Appendix S1, Supporting information). Numerical analysis of the model led to the following conclusions: (i) a non-zero non-breeding to breeding state transition rate is always selected for; (ii) the growth cessation during breeding cannot by itself select for a non-zero breeding to non-breeding transition rate; and (iii) a cost of consecutive breeding on fecundity or maternal survival favours a non-zero breeding to non-breeding state transition rate (see Fig. S2, Supporting information). The breeding to breeding state transition rate is close to

zero if consecutive breeding reduces both fecundity and maternal survival by ca. 40%. In this case, the growth cessation during breeding selects for an even lower breeding to breeding state transition rate, but the effect is relatively small (Fig. S2, Supporting information). We thus conclude that even though non-breeding is associated with significant growth, the fitness cost of breeding mediated by growth loss is minor. In contrast, reductions in fecundity or maternal survival associated with consecutive breeding are major factors of lifetime fitness.

Conclusion

The reproductive strategy of the meadow viper contrasts markedly with other seasonal viviparous snakes, in which (i) feeding ceases completely during gestation; (ii) there are large fecundity-independent costs of reproduction, some of which are financed by investing fat reserves, while others cause high mortality during gestation; (iii) inter-breeding intervals are frequently longer than one season; and (iv) direct and future mortality caused by reproduction is so high that most females are functionally semelparous. In these species, breeding is thus strongly constrained by resource availability. In the meadow viper, a diet of small and abundant prey makes higher breeding frequency physiologically possible. Our data suggest that substantial resource income during pregnancy can fully cover the metabolic and behavioural costs of pregnancy. This intriguing pattern and the underlying mechanisms warrant detailed physiological studies. Body growth accrued in non-breeding years selects only weakly for intermittent reproduction, while strong selection pressures arise from the reduction in fecundity and/or maternal survival that may be associated with consecutive breeding. Even in organisms in which breeding is not strongly constrained by resource availability, intermittent breeding can therefore evolve adaptively in the form of a regular alternation of breeding and non-breeding states. This may provide a general evolutionary explanation for the evolution of regular patterns of biennial reproduction known in many vertebrates (Bull & Shine 1979; Jouventin & Dobson 2002; McNamara & Houston 2008).

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Variables and parameters: names, definitions, dimension
Table S2–S4. Mark–recapture models for age at first breeding (S2), breeding probabilities and survival costs of reproduction (S3), and survival effects of post-parturition body condition (S4).
Fig. S1. Body mass dynamics during a breeding year.
Fig. S2. Optimization of breeding frequencies.
Appendix S1. Life-history model.