

Do female northern vipers (*Vipera berus*) really stop feeding during pregnancy?

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ABSTRACT – A temporary reduction or even cessation of feeding has been documented in a wide range of vertebrate species and is usually attributed to conflicts between foraging and other activities. It is generally recognised that females of Old World vipers (*Vipera* spp.) reduce or even stop feeding during pregnancy, even though detailed quantitative information for most species is limited. We conducted a long-term (2000 – 2017) and intensive mark–recapture study in a large population of northern vipers (*Vipera berus*) and employed two indices of feeding frequency in adult females during their breeding years. The first index uses cross-sectional data and estimated that a strict minority (7 %) of captures of females in breeding years revealed detectable signs of recent food intake (swelling of the mid-body, voiding of solid faeces). A second index is based on the magnitude of increases in body mass over recapture intervals of individual females, which can be attributed to the intake of food. Depending on the criteria used to consider an increase in body mass as a consequence of prey consumption, about 12 % (range: 2 – 29 %) of recaptures revealed indications of prey consumption. Overall, we estimated that ca. 20 % of the reproductive females fed at least once before parturition. We thus confirm that most pregnant female *V. berus* fail to feed, but also point out that the number of females that feed occasionally during pregnancy is higher than has often been assumed. We suggest that reduced foraging by pregnant northern vipers is, presumably in part, a consequence of their behaviour of residing in habitats where feeding opportunities are rare because prey encounter rates are low.

INTRODUCTION

Organisms feed to secure the resources needed for fuelling the metabolic demands of maintenance, growth and reproduction. Hence, organisms dedicate considerable amounts of time and effort to foraging activities. However, conflicts between foraging and other activities can result in the temporary interruption of feeding. For instance, reduction of food intake during the reproductive season has been observed in a wide range of vertebrates (Mrosovsky & Sherry, 1980; Sherry et al., 1980; Shine, 1980; Brivio et al., 2010), including males and females of both oviparous and viviparous species of snakes (Shine, 1980; Gregory et al., 1999; Lourdais et al., 2002a; O'Donnell et al., 2004; Brischox et al., 2011; Webber et al., 2012). Two broad categories of proximate mechanism may reduce feeding in reproductive animals: intrinsic factors that trigger anorexia (i.e., a loss of appetite; Mrosovsky & Sherry, 1980), or extrinsic conditions that reduce feeding occasions (i.e., spatial or temporal fluctuations in food availability; Shine et al., 2003; O'Donnell et al., 2004).

Reduced feeding by reproductive female snakes seems to be a general condition in Old World vipers (*Vipera* spp., Bea et al., 1992). These are typical live-bearing 'capital' breeders (Drent & Daan, 1980) that alternate breeding with non-breeding years. During reproductive years, females initially invest their energy reserves in vitellogenesis and subsequently use any remaining lipids to cope with metabolic costs as they diminish, or even cease feeding during pregnancy. After

giving birth females are emaciated, must restore their fat reserves before they can reproduce again, and therefore produce litters only biennially or even less frequently (Bea et al., 1992; Madsen & Shine, 1993; Bonnet et al., 2001; Lourdais et al., 2002a; 2002b; Pleguezuelos et al., 2007).

Reproductive investments and costs, and prey consumption by reproductive females have been particularly well studied in the aspic viper (*Vipera aspis*). Field data indicate that, depending on prey availability, females may feed during the egg production phase in spring, but they tend to cease feeding during the two months of pregnancy (Bonnet et al., 2001; Lourdais et al., 2002a). However, pregnant females readily accept prey in captivity, indicating that their appetite was not completely lost, so that there are other reasons for their failure to feed in the wild (Lourdais et al., 2002a).

Reduced feeding rates in gravid females have also been reported for the northern viper (*Vipera berus*). Examination of specimens in collections indicate that reproductive females feed occasionally during the period of vitellogenesis, but do not eat during pregnancy (Prestit, 1971; Nilson, 1981; Bea et al., 1992). However, published data from field studies are fragmentary, such that quantitative information on the extent of food intake by pregnant females is largely lacking. Moreover, pregnant females readily take food in captivity (Madsen & Shine, 1992; Völkl & Thiesmeier, 2002) and during our own field study we have sometimes noted that pregnant females exhibited considerable increases in body mass, which we tentatively attributed to food intake.

These considerations warrant a detailed and comprehensive examination of information gathered during our intensive field campaigns.

We present here data on the frequency of feeding by reproductive female *V. berus*, collected during a long-term (2000 – 2017) field study in a large population in northern Belgium. We used cross-sectional and longitudinal data to estimate the frequency of food intake during different phases of the reproductive cycle. Firstly, we recorded instances of food intake on the basis of visible signs (e.g., distension of the mid-body, voiding of solid faeces). However, the detection of prey remnants in living snakes is restricted in time, depending on the digestion rate, which would tend to underestimate the frequency of feeding occasions. We therefore also examined changes in body mass during recapture intervals of individual females. Increases in body mass during pregnancy have been shown to be the result of prey consumption and can thus be used as an index of food intake (Bonnet et al., 2001; Lourdais et al., 2002a).

MATERIAL AND METHODS

Study species and phenology

Vipera berus is a small, stout-bodied venomous snake that has a huge distribution area covering large parts of Europe and Asia. At our study site males and females reach maximal sizes of 55 cm and 60 cm respectively. Females are live-bearing; litter size varies between 4 and 12 and increases with female size and newborn snakes measure 13 – 16 cm SVL (Prestit, 1971; Madsen & Shine, 1992; own observations).

The annual cycle of the vipers in our study area coincides generally with that observed in other regions (Prestit, 1971; Nilson, 1980; Andr n, 1985; Madsen & Shine, 1993; Madsen et al., 1993; V lkl & Thiesmeier, 2002; Phelps, 2004). Adult females emerge from hibernation around mid-March, and those that have accumulated enough reserves initiate vitellogenesis during April. Follicular growth involves an intensive mobilisation of maternal reserves and is finalized upon ovulation around mid-May. The reproductive females stay near the overwintering areas, where they spend the summer carefully thermoregulating to enhance development of the embryos. The fully developed young are born during the second half of August or the beginning of September. Hibernation starts during October.

Study area and data collection

Data were collected during a long-term citizen science population study (2000 – 2017) of northern vipers in the "Groot Schietveld" (ca. 1570 ha; N 51° 20'22" – E 4° 32'37", province of Antwerp, Belgium; detailed description in Bauwens & Claus, 2018).

Snakes were located by sight while walking slowly and erratically through the terrain, captured by hand and released immediately after handling. A digital photograph of the upper side of the head allows individual identification of vipers, on the basis of the number, shape and arrangement of the head scales (Bauwens et al., 2018). At every encounter we recorded date, time, exact location (GPS coordinates), sex, snout-vent length (SVL) (to the nearest 5 mm), and body

mass (to nearest 1 g). To obtain an index of body condition (BCI) for females, we first calculated the baseline relation between logMass and logSVL for female vipers, excluding measurements taken after recent food intake or recent parturition ($\log\text{Mass} = -2.678 + 2.732 \log\text{SVL}$, $r^2 = 0.968$). Next we estimated body condition as the difference between the observed mass and the mass predicted by the baseline relation, a procedure that is analogous to the calculation of regression residuals (Schulte-Hostedde et al., 2005).

Reproductive status (reproductive/breeding versus non-reproductive/non-breeding) of potentially mature adult females (in at least their fourth activity season, $\text{SVL} \geq 38$ cm; D. Bauwens & K. Claus, unpublished data) in a given year was determined by palpation of the abdomen to detect oviductal eggs or developing embryos during May – August and/or by signs of postparturient body condition (i.e., presence of flaccid abdomen and extensive skin folds) in August – October. To avoid false judgements of non-breeding in a given year, this status was assigned only to females that did not show signs of pregnancy during June – August or indications of recent parturition in September – October.

Evaluating feeding status

We addressed the incidence of food consumption by reproductive females in two complementary ways: 1) by direct indications of food intake, and 2) by examining changes of the body condition index (BCI) at successive measurements of individual females.

Adult vipers feed primarily on prey (mice, voles, frogs) that are large relative to their body width (Prestit, 1971; Bea et al., 1992; V lkl & Thiesmeier, 2002) such that the recent swallowing of prey can be detected by a conspicuous swelling of the mid-body, by the presence of touchable prey remnants (bones) in the digestive tract and/or by voiding solid faeces. However, the oviductal eggs and developing embryos result in swelling of the abdomen in breeding females, and may hamper detection of prey remnants, especially of small prey, in the gastric tract. This may lead to an underestimation of feeding intake by reproductive females. We therefore also used the difference in BCI between successive recaptures within the same year of individual reproductive females as an indication of food intake (Bonnet et al., 2001; Lourdais et al., 2002a). In a first step, we examined the distribution of changes in BCI in females with clear indications of recent prey consumption and identified the 50 %, 66 % and 75 % percentiles of this distribution. These P50, P66 and P75 values were considered as thresholds to judge on the likelihood that changes in BCI resulted from a recent feeding event. Next, the changes in BCI of reproductive females that were recaptured before giving birth and that did not show marked signs of prey ingestion, were compared to these threshold values to detect presumed unnoticed feeding events. Increases in BCI that surpassed the above defined P50, P66 and P75 values were categorized as "possibly", "likely" and "very likely" to result from an otherwise unnoticed feeding event.

To estimate the timing of the presumed feeding events, we assumed that they occurred during the half-month corresponding to the central date within the interval between two successive captures.

A considerable proportion (28 % of $n = 263$) of the recaptured reproductive females were caught more than twice in a given year and thus yielded 2 - 4 observed changes in BCI in that year. To avoid pseudoreplication, we randomly excluded duplicate records from these animals to retain only a single change in BCI per combination of female and year. This procedure was repeated 50 times. Comparison of the full with these reduced datasets revealed no noticeable differences (Chi²-tests, all $P > 0.20$), so that we report results from the complete dataset only.

RESULTS

During the period March – August only a minority (7 % of $n = 1377$) of captures of females in breeding years revealed detectable signs of recent food intake. This number increased abruptly to 57 % (of $n = 90$) in the short period after parturition (September – October; Fig. 1). By contrast, captures of adult females that were in their non-reproductive years showed high and equal rates of food intake during March – August (45 % of $n = 325$) and September – October (50 % of $n = 94$).

Changes of BCI at successive captures of females with obvious indications of recent prey consumption did not differ between females in reproductive and non-reproductive years (ANOVA: $F = 1.07$, $df = 1$ and 39 , $P > 0.30$). We therefore combined the data of both groups. Although most of these females showed an increase in BCI, important differences were observed among individual females (range = $-20.3 - 56.8$ g; $n = 41$; percentiles: $P50 = 6.0$ g, $P66 = 10.0$ g, $P75 = 16.0$ g).

In a vast majority (72 % of $n = 353$) of the recapture events of reproductive females without marked signs of prey consumption, the change in BCI did not exceed the $P50$ value and, according to our criteria, provided no indication of unnoticed feeding. Increases of BCI that surpassed the $P50$, $P66$ and $P75$ thresholds were detected in respectively 16 %, 10 % and 2 % of the recapture events. These were considered respectively as “possibly”, “likely” and “very likely” to result from a putatively unnoticed feeding event. Among these recapture events, the increase in BCI was positively correlated with female SVL ($r = 0.434$, $df = 95$, $P < 0.001$).

These presumed prey intake events were observed throughout the period May – August and thus included the main periods of ovulation (May) and gestation (June – August) (Fig. 2). There was no correlation between the increase in BCI and the central date within the recapture interval ($r = -0.011$, $df = 95$, $P > 0.90$). We note that due to low recapture probabilities of reproductive females at the onset of the activity period (April) and end of gestation (August), data availability is truncated and the frequency of presumed feeding events possibly underestimated.

DISCUSSION

Only a small proportion (7 %) of captures of reproductive female northern vipers revealed direct indications of recent food intake. Thus apparently confirming the widely accepted view that most female northern vipers do not feed during the years that they reproduce (Prestiti, 1971; Nilsson, 1981; Bea et al., 1992; Madsen & Shine, 1992; Völkl & Thiesmeier,

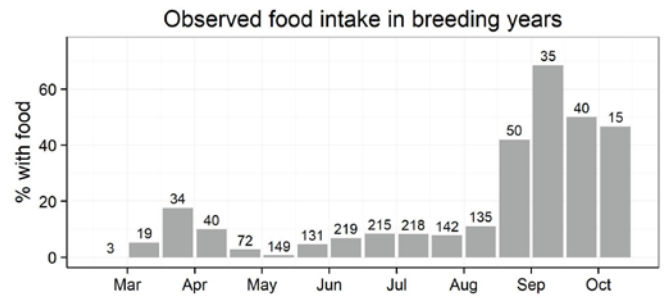


Figure 1. Relative frequency of reproductive females with visible signs of recent feeding in distinct half months throughout the annual activity period. Numbers indicate the number of captures per half month. Labels on the x-axis denote the midpoint of each month.

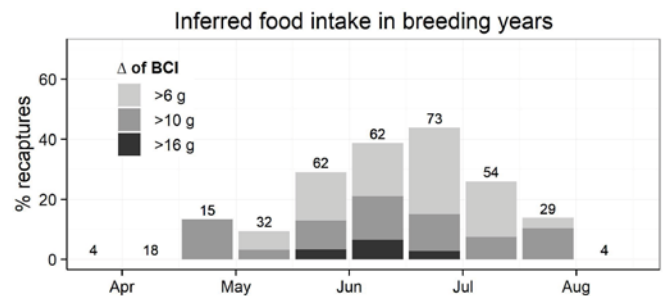


Figure 2. Relative frequency of recaptures of reproductive females that exhibited increases of the body condition index (Δ of BCI) above three threshold values. These thresholds indicate the likelihood of a recent food intake (see text for explanation). Numbers indicate the number of recapture events assigned to each half month. Labels on the x-axis denote the midpoint of each month.

2002). However, examination of changes in BCI suggests that a number of food intake events may have gone unnoticed by the commonly used indications. The frequency of these ‘concealed’ feeding occasions ranges between 2 – 29 % of recapture events, depending on the criteria used to consider an increase in BCI as a result of prey consumption. Thus, conclusions about the extent to which reproductive females are feeding require consideration of the factors that influence changes of body mass.

Changes in BCI of reproductive females should be interpreted cautiously as they may occur due to at least three major processes with opposing effects, namely metabolism-induced mass losses, food intake, and water uptake. These have been studied in detail in the closely related aspic viper (*V. aspis*). First, female aspic vipers experience a decrease in BCI during pregnancy (Lourdais et al., 2002a), due to an increase in metabolic rate and the mobilisation of remaining fat stores and structural proteins (Bonnet et al., 2001; Dupoué & Lourdais, 2014). Hence, decreases in BCI should be ubiquitous in reproductive females while increases in BCI should be attributed to intake of food and/or water.

Prey consumption appears to be the main factor causing increases in body mass of reproductive female aspic vipers both before (Bonnet et al., 2001; Lourdais et al., 2002a) and after ovulation (Lourdais et al., 2002a). Particularly relevant are the results of the experiment by Lourdais et al. (2002a)

who offered pregnant aspic vipers none, one or two mice and recorded the vipers' body mass at the onset and end of gestation. The feeding regime clearly influenced the change in body mass: it equalled -13.0 g for snakes fasting during pregnancy, -1.9 g for snakes that consumed one prey, and +5.6 g for snakes that consumed two prey items. These results are consistent with the hypothesis that mass changes reflect feeding rate. We note that the increase in body mass in aspic vipers that ate two prey items (i.e., 5.6 g) is very similar to the median value (i.e., $P50 = 6.0$ g) for the increase in BCI in our field-sampled females with indication of food intake. This coincidence would justify using the latter value as a threshold for 'concealed' prey consumption in our northern viper population.

Pregnant snakes may increase their body mass due to water uptake which is allocated to the developing embryos as embryonic sac fluids (Bonnet et al., 2017). In food-restricted aspic vipers, Lourdais et al. (2015) found an average increase in body mass of 4.4 g during pregnancy, but important differences were observed among individual females (range = -11.2 g – 30.2 g). Most embryonic water uptake takes place during the second half of pregnancy and increases with the number of developing embryos (Lourdais et al., 2015; Bonnet et al., 2017). In our study, the largest increases in BCI were found in the biggest females, which generally produce the largest litters (Prestit, 1971; Nilson, 1981; Madsen & Shine, 1992), but did not occur near the end of pregnancy. Assuming that the findings for aspic vipers apply to our northern viper population, then we cannot rule out that increases of BCI in some of our breeding females resulted from embryonic water uptake.

Considering the possible effects of both food consumption and water uptake, we take a conservative view and consider a relatively high value (i.e., $P66 = 10.0$ g) as the set-point for 'concealed' food intake in our viper population. Accordingly, we estimate that some 12 % of recapture events of breeding and apparently unfed females revealed an increase in BCI that was indicative of prey consumption. Including the females with obvious signs of food intake, we estimate that ca. 20 % of the reproductive females fed at least once before parturition. Our data thus confirm that most pregnant northern vipers fail to feed, but also indicate that the number of females that feed occasionally during pregnancy is higher than has often been assumed (Prestit, 1971; Nilson, 1981; Bea et al., 1992; Völkl & Thiesmeier, 2002). Moreover, the ingestion of small prey such as the common lizard (*Zootoca vivipara*; adult body mass = 3 – 5 g), will go unnoticed by the methods used here and may result in further underestimation of feeding frequency.

Reduction of feeding in gravid snakes has been interpreted as being proximally caused by a loss of appetite that is intrinsically associated with gestation (Gregory et al., 1999). This may ultimately be a consequence of morphological constraints (i.e., abdominal space limitation to accommodate both embryos and prey items (Bea et al., 1992) or as an adaptation to reduce susceptibility to predation (Seigel et al., 1987; Brischoux, Bonnet & Shine, 2011). However, a reduced food intake may simply be a consequence of low prey encounter rates during specific periods or in particular habitats. Male red-sided garter snakes (*Thamnophis sirtalis*

parietalis) provide a well-documented instance. They do not feed while at their courting habitats, where food is scarce, but readily accept experimentally offered prey items, indicating that the cessation of feeding in the reproductive habitats is a facultative response (Shine et al., 2003). In addition, the males initiate foraging as soon as they disperse to their food-rich feeding grounds, after crossing distances as short as 250 meters. Hence, the lack of feeding by reproductive males is due to a scarcity of prey items and/or a cessation of foraging behaviour, rather than by some intrinsic anorexia (Shine et al., 2003; O'Donnell et al., 2004).

Old World vipers typically catch prey that are large relative to their own size and consequently feed at low frequency (Bea et al., 1992). An exception is the meadow viper (*Vipera ursinii*) that forages almost exclusively on grasshoppers, a highly abundant food resource during the summer months. Gravid females of the latter species exploit this unique condition by feeding frequently throughout the gestation period (Baron et al., 2013). By contrast, northern vipers are ambush (i.e., sit-and-wait) predators that feed on large prey, a strategy that precludes a high feeding rate (Greene, 1983). They will take prey that moves within striking range, such that the rate of food ingestion is highly dependent on prey availability (Andrén, 1982; Andrén & Nilson, 1983; Forsman & Lindell, 1997). Of particular relevance in this respect is the spatial separation between breeding and foraging habitats. Northern vipers of all age and sex-classes forage predominantly or even exclusively in the 'summer' or foraging grounds (Prestit, 1971; Völkl & Thiesmeier, 2002). For instance, adult males do not feed during the period March – half May when they stay in the winter habitats; they only start feeding upon arriving in the summer habitats. These are spread out over a large area, include diverse habitat types, and provide more abundant food to the vipers (Viitanen, 1967; Prestt, 1971; Luiselli et al., 1994; Völkl & Thiesmeier, 2002; Phelps, 2004). Pregnant females typically reside in the winter habitats that are favourable for thermoregulation, but have low primary productivity and hence low food availability. Thus, we suggest that the reduced and opportunistic foraging by pregnant vipers is, presumably in part, a consequence of their behaviour of residing in habitats where prey encounter rates are low so that feeding opportunities are rare.

ACKNOWLEDGMENTS

DB and KC are voluntary researchers at the Functional Morphology research group, University of Antwerp. We thank Tina De Swert, Bart Hoeymans, Wim Mathijssen and Jurgen Melis for their company and skilled help in the field. Roger Avery, Xavier Bonnet and Rick Hodges gave constructive and encouraging comments on a previous version of the manuscript. All aspects of this citizen science project were carried out on a voluntary basis without funding or any other form of financial support. The military commander of the Groot Schietveld and the Agentschap voor Natuur en Bos (ANB) (ANB/BL-FF/16-00002) gave permits to access the area and to study northern vipers. All applicable institutional and national guidelines for the care and use of animals were followed.

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Accepted: 24 February 2019