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Reproductive strategies and life history traits of the Adder, *Vipera berus* (Serpentes: Viperidae), in southern England and central Wales

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THIS study of the Adder, *Vipera berus*, was unusual in that it spanned a very long period of time, from 1971 until 2003. The life histories of a significant number of snakes, particularly breeding cycles of females, were made known. This sample included a large number of Adders recorded from birth to old age or death. A total of 2200 males and 1934 females were identified throughout the period of research. Results confirm the findings of other researchers with regard to large male advantage, and furthermore define a clear hierarchic structure within the male population. The length of the study period revealed that a biennial female breeding cycle was the exception, and that a more irregular cycle was the norm with positive benefits relating to survival and longevity.

The life history traits of the Adder, *Vipera berus*, are now well known, and it is arguably the most intensively studied snake in the world (Shine & Madsen, 1994; Phelps, 2004a). During the last three decades or so much has been revealed with regard to reproductive behaviour and seasonal movement, including pioneering work in England and Scandinavia (Viitanen, 1967; Prestt, 1971; Phelps, 1978; Nilson, 1980; Andren, 1981; Madsen, 1988; Andren *et al.*, 1997).

A fundamental feature of Adder ecology is fidelity to the hibernation site and associated mating areas. There has been some consensus with regard to site fidelity in the short term (Prestt, 1971; Phelps, 1978; Madsen & Shine, 1993; Luiselli, 1994). Volkl & Biella (1988) conducted a long term study of the Adder in the German highlands and found that the various mating areas were occupied by the same subpopulations each year, and this was confirmed for the duration of the study. More recently, subpopulations in southern Dorset have been defined as stable

autonomous mating and breeding units for a period of more than three decades (Phelps, 2004b).

Although this pattern of distribution could be described as the 'norm' where optimum conditions exist, it is equally likely that more dynamic habitats would exhibit fluctuations with regard to population numbers and site fidelity. Prey resources have a direct impact on population stability. Extreme examples of this have been found in insular populations off the coast of Sweden where numbers can range from ten to two hundred individuals, which can be directly attributed to a narrow adult prey spectrum, namely one species of vole, *Microtus agrestis*, which varies temporally in numbers (Andren, 1982; Andren & Nilson, 1983). Adder populations can also be dramatically affected by excessive predation. Again in the German highlands, Volkl & Thiesmeier (2002) found that a former stable population suffered a decline because of habitat loss and predation by Wild boar, *Sus scrofa*. Wild boars are also known to have a negative effect on snake populations in other areas (Filippi & Luiselli, 2002, 2003).

Climate and topography are also major influences. Kasewitter *et al.* (2004), in a study of a population in the Lech Valley in southern Bavaria, found no site fidelity and explains that this is caused by the dynamic habitat which changes after each spring flood. Human influences on Adder populations are exemplified by the fragments of heathland within urban areas of southern Dorset where there are high levels of disturbance most often in the form of regular fires, but also from other factors such as motorcycle erosion, persecution, and predation by domestic cats, *Felis catus*.

Recently, high levels of heathland management have introduced a new dynamic which has had a

significant impact on former stable populations with regard to disturbance and mortality (in prep.). Habitat dynamics have a direct influence on reproductive output and frequency (Capula *et al.*, 1992). Phelps (2004b) found that in a stable environment, population numbers hardly varied over a thirty year period and adult sex ratios were maintained. The main effect in more disturbed areas is an imbalance of the adult sex ratio, which disrupts the breeding cycle. Heath fires in the early spring can cause high mortality of adult males, which are the first to emerge from hibernation and therefore the most exposed. Such events are often quick surface fires, and females, which emerge later, appear to survive to a higher degree, although much depends on the availability and proximity of adequate cover (in prep.). This study embraces a range of habitats and conditions representative of a variable lifestyle for the Adder in southern England and central Wales

A number of viperids from temperate regions exhibit communal behaviour in that they form aggregations at winter dens, and are most obvious during emergence in the spring and again at ingress in the autumn. Spring aggregations are not necessarily associated with a spring breeding cycle. The North American rattlesnakes *Crotalus horridus* and *Crotalus viridis*, for example mate during summer when dispersed from the winter dens. This mating system is typical for a number of North American pitvipers (Duvall *et al.*, 1992). It has been hypothesized that communal hibernation may be a comparatively recent event and a summer mating system is a relict component that has survived to the present day. Duvall (1992) has suggested that summer mating in North America pitvipers evolved in response to (i) the pattern of the adult shed cycle (King & Duvall, 1990) and (ii) the Type IIFY female reproductive cycle (Rahn, 1942; Klauber, 1972; Aldridge, 1979). Another explanation is that females are not sexually receptive during the spring period (King & Duvall, 1990).

The Adder adheres to a spring breeding cycle, although within the Arctic Circle the mating period begins in June (Anderson, 2004). The mating period is triggered by the spring moult of the adult males which is more or less synchronised within a population. Agonistic behaviour of males following the spring moult is well known (Prest,

1971; Andren, *et al.*, 1997; Luiselli, 1995; Hoggren & Tegelstrom, 2002). My study has shown, however, that adult males within a subpopulation form a hierarchic group and competitive interaction exists at various levels in accordance with size and also age. This hierarchic structure is founded on first (large) male advantage with the result that as few as 30% of males actually mate successfully (Phelps, 2004a). Hoggren & Tegelstrom (2002) have also provided genetic evidence for first male advantage in the Adder.

Phelps (2004b) has shown that although birth litters consistently exhibit an even sex ratio the adult ratio is male biased. This is explained by the high mortality of young females that breed in the first year of maturity, and a corresponding lower cost of reproduction in males. A biennial breeding cycle has often been quoted to be the 'norm' for female Adders throughout much of its range (Smith, 1951; Saint Girons & Kramer, 1963; Prestt, 1971; Nilson, 1981) and this statistic is also quoted in more recent literature (Beebee & Griffiths, 2000; Arnold, 2002), although it is also noted by several of these authors that in Scandinavia females breed every third year. This study is perhaps unique in that the life histories of individual snakes for a period of over thirty years have been made known. An important consequence of this is the revelation that females do not maintain a biennial breeding cycle throughout life even in areas that contain a consistently high level and wide spectrum prey resource.

Information with regard to survival and longevity has been gathered mainly from Swedish studies where Adders existed as insular populations or occupied a variable environment (Andren, 1982; Madsen, 1988; Madsen & Shine, 1994; Forsman, 1995). These studies have suggested that Adders attain an age of around ten years and are sexually productive just two or three times during a lifetime. My study strongly indicates that Adders in a stable environment have the potential for a much longer lifespan and are not compromised by old age, and that a delayed and irregular female breeding cycle together with a hierarchic male structure suggests a successful strategy for survival and longevity.

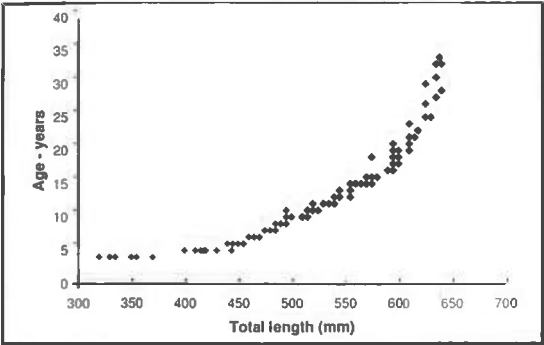


Figure 1. Size and age structure of adult males across six subpopulations at Studland, Dorset.

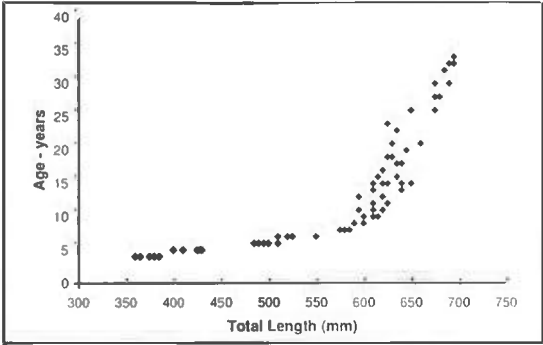


Figure 2. Size and age structure of adult females across six subpopulations at Studland, Dorset.

METHODS

Duration and study areas

The study was first initiated in 1971 and continued through until 1980, and then resumed again in 1986 until 2003. Six key sites in south east Dorset were established during 1971 and 1972, and all but one (Norden), are large areas of protected heathland with two (Furzebrook and Wareham Forest) being part of the original study areas of Prestt’s (1971) pioneering work. These areas have been shown to contain the most stable Adder populations, although in recent years there has been a negative impact because of to inappropriate habitat management (in prep.).

Three other sites represent more dynamic habitats subject to disturbance or other negative influences. One area situated in the Mendip Hills, Somerset, consists of a number of clearings with variable heather cover within a pine forest.

Table 1. General population numbers and stability of adult *Vipera berus* throughout the six key study areas in south east Dorset. Also showing a consistently male biased sex ratio.

Site Name	2004		1974 -		2003		No. of subpopulations
	males	females	males	females	males	females	
Furzebrook	48	35	52	41	42	30	6
East Creech	85	58	91	71	81	52	10
Norden	36	26	41	34	32	24	2
Studland	77	62	81	71	72	54	11
Wareham	59	44	64	52	50	38	8
Hartland	85	62	93	74	85	62	9

Another embraces Cors Caron, National Nature Reserve, a raised bog in Ceridigion, central Wales. The third site is a 45 ha fragment of urban heath near Bournemouth, southern Dorset. Although vulnerable, for various reasons these three sites all contain, or have contained, high density Adder populations. Study on these more dynamic sites began in 1989.

Identifying individual Adders

On first capture, individual immature and adult Adders were permanently and uniquely marked by clipping a series of four ventral scales (see Prestt, 1971 for details). Each Adder was also examined for unusual scalation, markings and scarring. Since 1989 each Adder has been photographed for identification of head and dorsal markings (see Sheldon & Bradley, 1989; Benson, 1999). Adders were measured in plastic tubes of appropriate size to an accuracy of ± 5 mm and weighed with a fine spring balance. From early on in the study non-invasive techniques were employed as far as possible. When it became possible to identify

individual Adders by sight alone much was achieved by passive observation. Most sampling, weighing, measuring, and identification photography took

place shortly after emergence with further recording in the summer grounds and again at ingress in the autumn. It was policy not to disturb any Adders engaged in mating activity, and sampling for this period involved only juveniles, immature and non-breeding females. During the latter part of gestation a number of females, average four to six each season, were held to record brood sizes, identification of neonates and physiological factors pertaining to the female. Most females were held for no more than six days. Females and their broods were returned to their place of origin shortly after parturition.

RESULTS

Population structure and site fidelity

A four year period of intensive mark and recapture at the six key study areas was sufficient to assess accurately adult population numbers. (Phelps, 2004b) gives details for two of these (Furzebrook and Norden). It also became clear that in a general area Adders are split into a variable number of distinctive groups, described here as subpopulations. These subpopulations may be separated by as little as 300 metres but adults have consistently exhibited a 100% fidelity and mating autonomy. In the key study areas the general population numbers have been remarkably stable (Table 1). Immature Adders, both males and females in their second season and older, never constituted more than 15% of the total population and at Furzebrook and Norden this was as low as 10% (Phelps, 2004b). This contrasts markedly with the Smooth snake, *Coronella austriaca*, and Grass snake, *Natrix natrix*, which occurred in the same areas in which immature snakes constituted 30% and 40% respectively of the general population (Phelps, 2004a). Phelps (2004b) also explains how, for a confined autonomous mating group, genetic integrity is maintained by the random dispersal of immature Adders and their final placement as young adults in subpopulations other than their birthplace. In other words, once an Adder, male or female, has been absorbed into a subpopulation then site fidelity is maintained through life.

males	females	breeding females
8	6	2 = 33.33%
9	7	4 = 57.14%
11	8	3 = 37.51%
8	5	1 = 20.00%
10	7	3 = 42.85%
12	9	5 = 55.50%
10	8	4 = 50.00%
8	6	2 = 33.33%

Table 2. Details of adult numbers within subpopulations at Hartland Dorset and breeding status of females at 2002 showing that 38.70% of the total adult female population were breeding ($n = 24$). This figure was fairly constant for this and the other key study areas in Dorset (range 32–42% $n = 287$ range 260 - 343).

Reproductive sex ratios

The total number of adults active during the mating period is described as the Operational Sex Ratio (OSR). This usually involved 100% of the adult males, regardless of size, and 32–42% of adult females (Table 2). At subpopulation level Table 2 shows that at Hartland in 2002 throughout the metapopulation, breeding females represented between 20% and 57.14%, which was found to be fairly constant for subpopulations in this and the other key study areas and reflects the irregular breeding pattern of adult females.

Negative influences impacted on the more dynamic areas in a number of ways. In the Mendip Hills, a metapopulation of 72 adults (40 males, 32 females) were divided into four subpopulations, two of which were close to a popular walking and picnic area. The main consequence was habitat degeneration through trampling, but also a fairly high level of persecution, particularly of exposed breeding females during the summer. One subpopulation lost eight females over a two year period (1998 and 1999), which represented 80% of the adult females, and has since shown little sign of recovery, and further degeneration of habitat has probably negated any recruitment from nearby subpopulations.

The Adder metapopulation at Cors Caron was spread over sphagnum bog and along the route of a disused railway and represented a total of 88 adults (52 males, 36 females), divided into five subpopulations. Three of the subpopulations hibernated just a few centimetres above the water

Date	Males	Females	Source	Distance (m)
2000	2	9	-	-
2001	3	9	subpopulation 3	400
2002	4	8	subpopulation 2	550
2003	4	8	-	-
2004	6	8	subpopulation 3 & 6	400 & 300

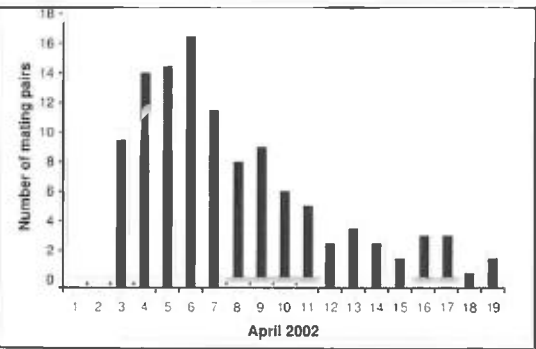
Table 3. The more dynamic habitats of *Vipera berus* often exhibited an extremely skewed adult sex ratio. Turbary Common, an isolated area of urban heathland, shows an example where for one subpopulation the ratio was as low as 2:9 and furthermore how this is being addressed via the recruitment of young males from other subpopulations.

table at the base of heather roots. Erratic seasonal flooding caused some mortality in winter, but also notable population shifts during active months. However, recent management (bunding) has alleviated much of this problem and future work will examine the full effect of this habitat enhancement.

At Turbary Common, spring fires (arson) caused high mortalities and local population shifts, and had a profound effect on the OSR for a number of subpopulations. An extreme case occurred during 1999 when a fire almost annihilated the adult male population. This subpopulation has been closely monitored since that time and Table 3. shows how the adult sex ratio is slowly returning to the former level as a result of ingress by young males from other subpopulations.

Despite the variety of negative influences, Adders in these more vulnerable areas still maintained a population structure virtually identical to that of the key study sites.

Figure 3. Dates and numbers of mating pairs at Hartland in 2002.



Age and size structure within a metapopulation is shown in Figs.1 and 2 for Studland in 2003, which was fairly typical of all the key areas throughout the study period. This structure was maintained at subpopulation level, although numbers of young adults were more variable because of erratic recruitment. Results have shown that age and size could be correlated with mating success in males and mortality and fecundity in females.

The mating period

During the last decade the timing of the male moult and dates of first mating in Dorset were significantly earlier than in previous years In the 1970s the first mating pairs were consistently observed during the third week of April with a peak around early May and then tailing off toward the end of that month. Since 1989 there has been a definite trend for earlier mating activity and Fig 3. shows Hartland as a typical example in 2002 when the highest numbers of mating pairs were observed during the first week of April. The Mendips, which are at a higher altitude, show a similar pattern to that of Dorset in the 1970s with a peak of mating pairs during the first week of May (Fig. 4). The mating period can extend to just over thirty days, however, mating activity for the majority of breeding adults occurred during the first seven to ten days.

Male reproductive behaviour

Close observation during the mating period showed that males formed a definitive hierarchic structure, with behaviour and mating success varying with size and age. All males with a total body size of 350 mm and above were assumed to be sexually mature (see Prestt, 1971), although a small number of males with a body size of around 320 mm were also seen to be active during the mating period. A first male advantage was achieved by larger males finding females very quickly and exhibiting mate-searching behaviour very different from smaller males.

Shortly before the start of the mating period breeding females undertook a local dispersal of distances varying between five and one hundred metres from the hibernation den. The same

locations were used each year by a variable number of females and the furthest positions dictated the outer limits of the mating area within a subpopulation. The fidelity of females to specific mating areas was a constant feature and provided a predictable pattern for searching males.

Mate-searching: Immediately following the spring moult males became alert and excitable and after a short session of basking around mid-morning moved around in earnest. Close observation at this time has revealed that males of various size and age groups exhibited different behaviour patterns. When expressed in terms of reproductive behaviour males could be divided into three distinct groups. This division calculated for all 46 subpopulations across the six key study areas over a ten year period showed small males in the 320 mm to 400 mm range with a mean of 2.65 per subpopulation (range 1–7, $n=122$). Large males in excess of 550 mm showed a mean of 2.26 per subpopulation (range 0–4, $n=104$). The majority of males were in the 420 mm to 540 mm size range with a mean of 8.23 per subpopulation (range 6–10, $n=379$). Male Adders are guided by pheromone trails exuded by the female which are both ground-based and airborne. Typical male searching behaviour was to move slowly over the ground, with much tongue flicking, and occasionally pausing raising the head and foreparts for visual cues. This visual awareness also served to confirm the presence, or otherwise, of other males. Although alert at this time male Adders were seen to be apparently oblivious of danger, often crossing and re-crossing open ground, and even roads. This behaviour was typical for all but the small number of older large males. Mate searching behaviour for large males was quite different and much more direct. Knowing the location of breeding females made it possible to assess the success rate of these large males. During the early part of the mating period males still mainly occupied the same surface dens as in previous weeks, and it was possible to follow the movements of individuals. Large males, after a short period of basking would leave the den and start to move purposefully at a moderate speed. It was relatively easy to track these males and it was noted that there was no pausing or tongue flicking and long distances were covered in a short amount

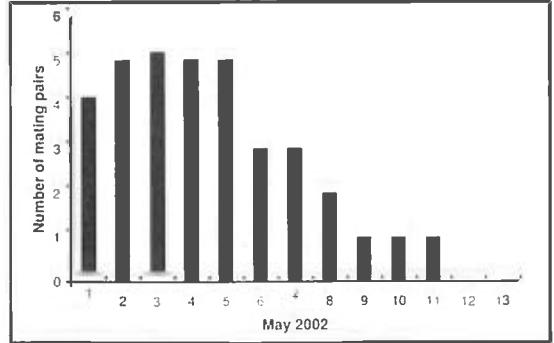


Figure 4. Dates and numbers of mating pairs in the Mendips in 2002.

of time. One male at Hartland in 2002 covered 80 metres finding a female in just fifteen minutes. This was typical for the small number of large old males and showed that this behaviour did not rely on chemical cues and although controversial, suggested imprinting or some kind of learning process. This strategy resulted in a high success rate with regard to first male advantage and for most years was seen to be virtually 100%. Although the remaining two groups each showed similar behaviour when searching, small males travelled longer distances per day and almost always with a negative outcome, and the group containing the majority of males travelled less and were more successful at finding females. Search patterns for the last two groups were partly linear, but became circular on entering a receptive female location. This involved much retracing of movement, and for small males the longest daily distance travelled was 600 metres, but all within a 120 square metre area. The maximum daily distance travelled by the majority of males was around 200 metres. The males at this time were closely observed, often by more than one person, and were seen never to venture outside their respective groups. This was unexpected as it had been predicted that males would disperse more widely in search of females. Andren *et al.* (1997) states that males are attracted by female pheromones at a distance of at least 500 metres. Most subpopulations throughout the study areas are separated by distances within this limit and in theory would have detected chemical cues from females situated outside the subpopulation. Although by no means conclusive, one

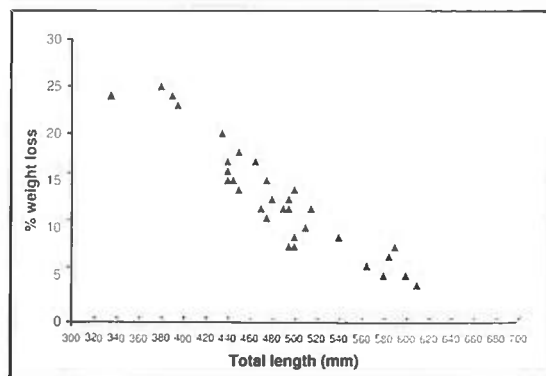


Figure 5. Percentage weight loss of adult males during the mating period, recorded at Norden in 1999, representing energy expenditure for the various size groups.

explanation is that perhaps ground-based pheromones are stronger and therefore over ride airborne chemical cues which may be at the limits of effectiveness. Even at this stage of the study, it would perhaps be not too unexpected if, in the future males were seen to interact with other nearby subpopulations, particularly during a year that exhibited a low number of breeding females within a particular subpopulation. However, the tenacity and familiarity of larger males to their respective subpopulation suggests that this would just involve the smaller males.

Combat and mate-guarding: Agonistic behaviour between rival males was a component part of Adder mating behaviour and this became manifest in spectacular bouts of combat. However, interaction between males was observed to exist at various levels which could be defined as size related. When small males encountered larger males this usually involved brief skirmishes lasting just a few seconds, often followed by a quick short chase by the larger male. Short bouts of combat were common during mate-searching by the majority of males, but increased in duration when in close proximity to a female. The most serious and prolonged bouts occurred when a male in possession of a female was approached by another male. At such times a male in company with a female would become highly agitated and would rush to meet the encroaching male and a long bout of combat would ensue. This often had a

negative outcome, for although the defending male almost always won such bouts, the female would move away and another period of mate-searching would be undertaken. In most cases the defending male was successful in finding the female again before another male could intrude. The minority group of large males most often employed a different tactic, and when approached by another male instead of leaving the female would go directly into combat mode, often raising the body to a height of 30 cm, which in most cases was sufficient to ward off other males. Females remained passive during such encounters, and on many occasions such pairs were actually observed to be copulating. Although there were an equal number of males participating during the mating period annually, the levels of combat varied from year to year and was directly in accordance with the number of available females. Although combat defined male superiority, the most effective method of promoting first male advantage were long periods of mate-guarding ranging from one to eight days; the longest sessions being undertaken by the larger males. The exclusion of other males was enhanced when in almost all cases after first mating such pairs would undertake a local dispersal, becoming cryptic and hard to find visually. In addition, after a period of seven to ten days females became unreceptive and did not invite any response from other males. Although such a long attachment by these large males to a single female represented other lost mating opportunities, the efficiency of prolonged mate-guarding probably guaranteed single male paternity for that particular pair. The majority group of males was more erratic with regard to duration of mate-guarding but periods of up to five days were recorded. This resulted in some females mating with more than one male but some males, those that exhibited in excess of three days mate-guarding, successfully maintained a single mating pair showing behaviour comparable to that of the largest males. At Hartland during 2002 in one subpopulation 25% of males ($n=2$) mated successfully with two females. In another, also at Hartland, 33.33% of males ($n=4$) mated successfully with five females. First male advantage strongly indicated that the most likely outcome of mating resulted in single male paternity for the smaller subpopulations, but in

subpopulations with larger numbers there probably existed a mix of both single and multiple maternity.

Male reproduction costs: Over a period of twenty five years a total of 2200 males were sampled during the early spring phase when in the premoult condition. Each male was assessed visually for fitness and then weighed and measured. With such a large sample it was ultimately possible to correlate weight and body size against mating fitness potential. As expected, this represented a wide range of weight and body size, (28 g–110 g 318–650 mm [$n=2200$]). Only a small number failed to meet this criteria (4%, $n=88$) and these were males that expressed a body weight $\pm 10\%$ under the expected fitness weight. Males were again sampled at the end of the mating period, although this proved more difficult and over the twenty five year period a total of 1200 males were recaptured at this time. This usually represented a recapture rate of between 40–50% but at Norden in 1999 88.88% of males ($n=32$) were accounted for at the end of the mating period. The results were almost identical to other study areas and Fig. 5 shows weight loss across the whole male spectrum which reflects the levels of activity for the various size groups in terms of energy expenditure. Other samplings were undertaken in July and August when males were in the summer (feeding) grounds, and again on return to hibernation areas. A total of 1750 males were sampled and 92% ($n=1610$) were seen to have regained the spring weight with 75% ($n=1260$) having exceeded this with some showing a maximum of 15% above the spring weight ($n=440$). However, even for those males that failed to meet the fitness criteria many were seen to survive into the following season and beyond. Results show quite clearly that energy expenditure and mortality are unrelated in male Adders which is proven by the ability to forage successfully during the post-mating period and regain condition rapidly as a consequence. Adult males do not feed during the mating period and Madsen & Shine, (1993) have stated that there is an 'opportunity cost' in that reproductive activities reduce feeding rates. However, it is doubtful if this can be regarded as a cost of reproduction as the

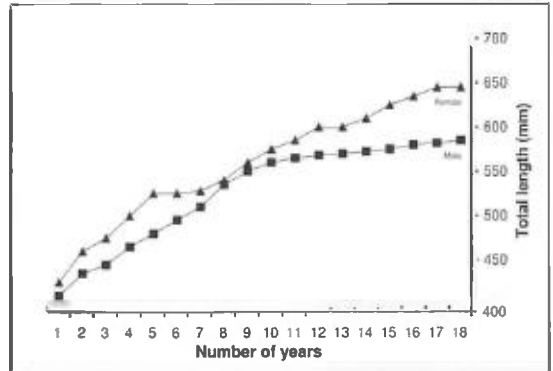


Figure 6. Growth of male and female Adder at Furzebrook from fourth season until 22 years of age. Shows female first breeding age of nine years, years of zero growth represent breeding years.

participation of 100% of adult males during the mating period in an inherent feature of all Adder populations. Mortality of male Adders expressed as a cost of reproduction was difficult to assess as many were found dead both within and outside the mating period. Immediately following the spring moult Adders were uncryptic and vagile and vulnerable to predation, and at both Hartland and Studland road kill was a significant cause of death. Mate-searching and combat had the potential to attract predators and throughout the study period male Adders were seen to be taken by Crows, *Corvus corone*, Magpies, *Pica pica*, and Buzzard, *Buteo buteo*. At Cors Caron the Polecat, *Mustela putorius*, was a significant predator of Adders typically leaving the head and skin. The domestic cat, was also known to take Adders at Turbary. Although a number of corpses were recovered each year, the only way mortality could be determined with any accuracy was to identify the surviving males on emergence the following spring. Although the time and cause of death could not be established in the majority of cases mortality measured across the active season was comparatively low. The situation at Hartland over a ten year period showed an annual mean of 12.94% across the general population ($n=11$). Studland showed an annual mean of 15.78% ($n=12$) and Furzebrook an annual mean of 9.72% ($n=7$). The significantly lower figure for Furzebrook can be explained by the consistent number of male road kills for the other two areas.

Location	TL (mm)	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	TL (mm)
Furzebrook	520		x			x		x		x		x			620
Furzebrook	550			x				x			x			x	680
Furzebrook	410						x		- presumed dead -						
East Creech	595				x			x				x			695
East Creech	490						x			x			x		610
East Creech	500	x		x			x		x				x		620
Norden	520	x			x		x			x			x		685
Norden	600		x		x			x		x			x		710
Norden	390					x			- presumed dead -						
Studland	650		x			x				x					720
Studland	500		x			x		x			x			x	620
Studland	400							x	- presumed dead -						
Wareham	520		x		x				x		x			x	630
Wareham	500	x		x			x				x			x	650
Wareham	390						x		- presumed dead -						
Hartland	600			x			x				x			x	680
Hartland	510				x			x			x			x	610
Hartland	490					x		x		x				x	600

Table 4. Breeding history of individual *Vipera berus* females in south east Dorset also showing increase in body length since first recorded. x = breeding years.

Female reproductive behaviour

In contrast to males, breeding females were passive and sedentary and once located in the respective mating areas daily movements were minimal. The daily movements for a number of breeding females were measured over a ten year period at Hartland, Studland and Furzebrook, irrespective of male influence, and showed a mean daily movement of >7.08 metres (range 1–15.5, $n=44$). Intense behaviour exemplified by mate-searching, combat and mate-guarding indicated that mate selection was purely male orientated. Close observation however, has shown that females responded to males of various sizes in different ways, which although controversial (see Duvall *et al.*, 1992; Andren *et al.*, 1997) suggests some form of mate choice. This was particularly noticeable with regard to the larger and older females. When a male with a total length of around 450 mm and above initiated courtship the female remained passive and positively responsive. Smaller males invited a very different reaction in that the female would move off, and even repeated attempts by such males resulted in the same outcome. This was a constant feature throughout

the study period, and it was concluded that this was mate choice by rejection, and in combination with combat success reinforced the concept of large male advantage. Smaller males often mated with young females, some of which were in their first year of maturity and more responsive and not usually the target for the larger males. These young females usually mated later than older females with a consequence of late parturition.

Female breeding cycle: The breeding history for eighteen females across the six Dorset study areas for a thirteen year period is shown in Table 4. and for thirteen females in the Mendips and Cors Caron for a ten year period in Table 5. The breeding histories of a further 68 females were recorded throughout the entire study period and results clearly show that only a small number of females maintained a biennial reproductive cycle for up to seven consecutive years of life ($n=4$) which represented 12.90% of those sampled in Tables 4 and 5. and 15.15% of the total recorded during the study ($n=15$). The total number of females sampled with regard to life histories were those that were recorded from birth ($n=28$) or as immatures and sub-adults ($n=71$). The majority of females were first recorded as mature adults ($n=1835$) and although some were in the 480–500 mm size range ($n=485$) it was not possible to state

age with a great degree of accuracy, although results have consequently indicated that many must have been virgin females. Of the 99 recorded life histories of females 18.18% ($n=18$) bred during the first year of maturity exhibiting a size range of between 390 mm and 420 mm. A further 235 females with a similar size range were recorded as first time breeders across the Dorset study areas. None of these females were recorded again after parturition and it was concluded that females that bred in the first year of maturity did not survive and represented 100% mortality. Although a high number of females with a size range of around 500mm strongly indicated that first time breeding occurred in later years following maturity, only the females with a complete known life history were included in the results. This showed a mean age of first time breeding of 8.25 years (range 6–11, $n=71$). Figure 6 shows growth of male and female from fourth season and indicates that the female bred for the first time in the ninth season and a further two times in a period of eighteen years. Result clearly show that a biennial cycle represents the absolute maximum periodic reproductive output for females and that two, three or even longer periods of non-reproductive years conclusively reveals a more typical breeding cycle, and this was at least consistent across all nine study areas. A similar breeding cycle for female Adders has been recorded in other parts of Britain (S. Sheldon, pers. comm.).

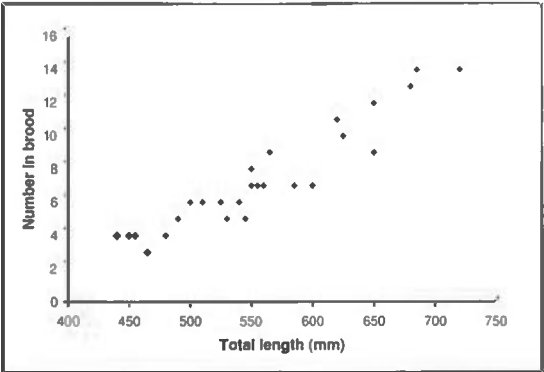


Figure 7. Litter sizes recorded across all age groups showing that this is correlated with body length.

Female reproduction costs: Energy expenditure and mortality was explicitly linked in females, and was manifest in the total non-survival of first time breeders in the early years of maturity. Adult females could be defined as three groups. Those that were of fitness weight and condition, and would breed that year, those that were of fitness weight and condition, and would not breed that year, and those that had bred the previous year. Females were examined on each spring emergence, and as with males the large sample

Table 5. Breeding history of individual *Vipera berus* females in the Mendips, Somerset, and Cors Caron, Ceredigion, also showing increase in body length since first recorded. x = breeding years.

Location	TL (mm)	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	TL (mm)
Mendips	480		x			-presumed dead-						
Mendips	550	x			x		x			x		590
Mendips	610		x				x				x	625
Mendips	520	x			x			x				580
Mendips	575		x		x					x		630
Mendips	650	x			x					x		685
Mendips	670		x				x				x	690
Mendips	420				x	-presumed dead-						
Cors Caron	450		x			-presumed dead-						
Cors Caron	550	x			x			x			x	610
Cors Caron	490		x		x	-presumed dead-						
Cors Caron	620		x		x			x			x	690
Cors Caron	600		x			x				x		650



Figure 8. Reproductive output, less two live young, of 430 mm female from Furzebrook.

made it possible to assess for fitness as expressed by body weight mass to body length. Excluding females that had bred the previous season, this represented optimum bodily condition for females and it was ultimately possible to predict body weight against length with only a small margin of error when assessing fitness. For example, a female with a total length (TL) of 550 mm would have a body mass of around 120 g, and it was this fitness weight minus the immediate post-parturition weight that was used to calculate reproduction costs expressed against body condition. Just prior to giving birth females were emaciated, and the general outward appearance of good condition was entirely due to the litter mass. This became apparent immediately at post-birth when the reduction in fat body was obvious. Reproduction costs were independent of litter mass, and litter sizes were in accordance with the TL of females (Fig. 7). Females between the 550–600 range with an average litter size of seven showed the same percentage weight loss as a 650mm female with a litter size of twelve. Over the study period females were sampled from spring emergence until post-birth. Just prior to birth litter mass represented between 42–52% of the spring fitness weight, (mean = 46.48%, $n = 120$). However, reproduction cost was calculated as a reduction in body condition (fat reserve), as illustrated in the example below, a breeding female from Hartland in 2002.

TL 550mm – Spring weight 120g – Pre-parturition weight 172g – Post-birth weight – 82g
Litter mass wet weight – 52g Actual fitness mass loss (weight = 38g) = 31.66%

This figure was fairly constant across the whole sample with a mean of 34.88% (range 29.56%–39.44%, $n=120$).

Because of the similar outward appearance of many females on emergence it was impossible to predict which would breed that particular year. However, during late March or early April close observation showed those females that would breed moved to the traditional mating areas, while non-breeding females left the hibernation areas, and many were seen foraging from early April onwards some significant distance away.

Although all first-time breeding females died as a result of breeding effort and consequent trauma, it was more difficult to attribute this cause when related to older females. Shortly after giving birth females began an intensive feeding regime which involved movement, often travelling distances of several hundred metres, and consequent exposure to predators. It was impossible to evaluate mortality as a cause of predation, but over the entire study period only fifteen females were known to have been killed by predators. During the gestation period females were sedentary, and as such did not attract natural predators. However, a number of mortalities were a direct cause of human persecution and predation by domestic cats. As with males, the number of survivors was established when recorded on emergence the following spring, or in some cases, later that same season.

Fecundity: The recording of birth litters over a long period of time showed quite clearly that the number of young per litter can be correlated with female body size and length. Figure 7 shows a sample of litter sizes for females from Hartland and Studland across the entire size spectrum, (440–730 mm), revealing a mean litter size of 7.42 (range 3–14, $n=26$). These results do not include stillborn or infertile eggs, however, the largest females produced just 4% of all stillborn recorded. Small litters and a large proportion of stillborn was consistent for females breeding in early years of maturity, Fig.8 shows a part litter, less two small live young, for a 430 mm female from Furzebrook. Litters from these young females accounted for 86.04% of all stillborn recorded during the study period ($n=148$). The significant number of non-reproductive years for a large number of females

may have suggested a low fecundity across the population as a whole. In fact this was not the case, firstly it was obvious that population numbers were maintained and remained stable for a long period of time. The duration of the study allowed life histories for a significant number of females to be examined. Four females at Norden, and five from Furzebrook, bred for the first time when between 520–555 mm and bred a further four times over a 15 year period producing a total of 485 young. This expressed as an annual fecundity rate produced a mean of 3.60 young, expressed as a biennial rate, a mean of 7.19, which is reasonably close to the mean litter size (7.42), as the sample shown in Fig. 7.

DISCUSSION

The study clearly shows that Adders exist as autonomous mating units at subpopulation level within a wider metapopulation. This was unexpected as other studies have shown that Adders, both males and females, can move long distances to mating areas (Forsman, 1997; Volkl & Thiesmeier, 2002). Although it is possible to overlook a wider dispersal of searching males, it seems fairly conclusive that over a thirty year period this has not thus far been recorded. The only long linear distances recorded was dispersal to summer grounds which involved all but the breeding females.

The hierarchic structure of adult males was a consistent feature at all sites and could be defined by size and age. Small males, many in the first year of maturity, engaged in long periods of negative mate-searching and were excluded from most females by the larger males. Some did mate late with small females and this may account for low fecundity and mortality of these females. The majority group, males those with a size range of 500–600 mm were successful at finding mates but exhibited high levels of combat. The minority of superior males in excess of 600 mm were 100% successful in finding mates because mate-searching techniques transcended conspecific trailing and strongly suggested a learning process which gave quick access to female breeding areas. This success was further enhanced by extended periods of mate-guarding. Females consistently rejected the advances of small males and it raises

the question how do they recognize 'inferior' males? Although not conclusive, it may be the weight difference between a 340 mm male at 30 g and a 550 mm male at 70 g. Once a small male mounted a female in preliminary courtship the female may just simply detect the substantial difference in weight. However, it also raises the question, is this really mate selection or choice by females?

Reproductive costs were significantly higher for females than in males, although the majority of mortalities largely affected young females, and explains the male bias with regard sex ratio throughout all areas. During the early years of the study it was expected that most females would show a biennial breeding cycle. The long duration of the study has revealed a very different pattern with most females breeding for the first time well beyond the year of maturity. This was unexpected, but not unique in temperate viperids, Martin (2002) in a study of timber rattlesnakes, *Crotalus horridus*, in West Virginia, states that females, breed for the first time between the ages of 9–14 years, although it is also stated that these females do not mature until eight years of age. This shows that although in good bodily condition, females are not obliged to breed during any one season and a choice is made with regard to energy expenditure. A biennial breeding cycle demands a high feeding regime during the following season, whereas long gap years provide flexibility with regard to negative influences, such as bad weather or fluctuation in prey resources. It is not known what triggers a female's choice to breed, but it is known that the ovarian cycle begins in the season prior to breeding (Nilson, 1981).

This study has shown clearly that female Adders have a reproductive strategy that is explicitly linked to survival and longevity. Males with lower reproduction costs have shown an equal degree of survival and longevity and there is no bias between the achievement of an upper age limit between males and females. In the spring of 2004, across all six study sites 34 males and 37 females were known to be in excess of 25 years of age with twelve now beyond the thirtieth season. This has dictated a low level of recruitment which is reflected in the low number of immature and subadults, the result of a high mortality, (92%),

during the first three years of life (Phelps, 2004b). In the absence of any other known literature this study may represent records for the oldest known wild snakes to date.

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