Population dynamics and spatial distribution of the adder *Vipera berus* in southern Dorset, England

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Zusammenfasssung

Populationsdynamik und Verbreitung der Kreuzotter Vipera berus *im südlichen Dorset, England.*

Die Kreuzotter, *Vipera berus*, hat die weiteste Verbreitung aller Landschlangen und wurde als gewöhnlichste Schlange Großbritanniens angesehen (SMITH 1973), obwohl ihre Verbreitung in England, Schottland und Wales in neuerer Zeit als lückenhaft bezeichnet wurde. In Südengland ist sie am häufigsten (BEEBEE & GRIFFITHS 2000).

Eine Langfriststudie wurde über einen Zeitraum von 30 Jahren an mehreren Populationen von *V. berus* in Südost-Dorset, England, unternommen. Die Ergebnisse zweier dieser Populationen werden hier vorgestellt. Aufgrund der Dauer der Untersuchung war eine detaillierte Erfassung der Populationen und Subpopulationen möglich, was wiederum die Lebensgeschichte einer Reihe von Individuen aufdeckte. Ein Schwerpunkt lag auf der Struktur und den Lebenszyklen von Subpopulationen im Vergleich zu der Gesamtpopulation, wobei Aspekte der Fortpflanzung, der Hierarchie, der Lebenserwartung, der saisonalen Wanderungen, der Ortstreue und der Stabilität der Population berücksichtigt wurden. Obwohl bedeutende Daten zur Fortpflanzung gewonnen wurden (PHELPS, in Vorbereitung), werden hier nur Beobachtungen zum Sozialverhalten wiedergegeben.

Die Ergebnisse werden mit solchen aus anderen Teilen des Verbreitungsgebiets der Kreuzotter verglichen, und Schlussfolgerungen für adäquate Schutzmaßnahmen werden diskutiert.

Schlagwörter: Kreuzotter; *Vipera berus*; Ortstreue; Hierarchie; Wanderungen; Lebenserwartung.

Abstract

The adder, *Vipera berus*, has the widest distribution of any terrestrial snake and has been stated as being the commonest snake in Britain (SMITH 1973) although it is more recently described as having a patchy distribution in England, Scotland, and Wales, and is most abundant in southern England (BEEBEE & GRIFFITHS 2000).

A long term study of *V. berus*, spanning thirty years, was undertaken in south east Dorset, England, of a number of populations for which the results of two are presented here. The duration of the study has allowed detailed recording of the general population and subpopulations, resulting in the known life histories for a number of individual snakes. The wider emphasis has been on the structure and life cycles of subpopulations in relation to the general population embracing the aspects of reproduction, hierarchy, longevity, seasonal movement, site fidelity, and population stability. Although important data with regard to reproduction was obtained (PHELPS, in prep) only that which was pertinent to social behaviour is included here.

Results are compared with those from other parts of the adder's range and the implications for appropriate conservation measures are discussed.

Key Words: adder; *Vipera berus*; site fidelity; hierarchy; movement; longevity.

1 Introduction

It is only in recent years that snakes have become popular for field research and this is borne out by the fact that our current knowledge regarding behaviour still only extends to a handful of species. It has now however been well demonstrated that snakes are good subjects for studies of social structure as reflected in mating systems (DUVALL et al. 1992).

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The adder has a wide distribution in Europe (ARNOLD & BURTON 1978) and was an obvious candidate for pioneering field studies for a number of workers through various parts of it's range (SAINT GIRON 1952, VIITANEN 1967, PRESTT 1971, NILSON 1980, ANDREN 1981).

Having a predictable spring breeding cycle, and also exhibiting pronounced site fidelity, has made the adder a highly suitable subject for long term field study.

CORBETT (1989) stated the need for field investigation into the status of *V.berus* in Britain in order to identify its conservation requirements. To allow appropriate conservation measures to be implemented such an investigation needs to go beyond just surveying and establishing presence, and would essentially identify hibernal and vernal assemblages, probably the very heart of all adder populations. Furthermore, it is now well known that *V. berus* can occupy different habitat types during its annual cycle (VIITANEN 1967, PRESTT 1971, PHELPS 1978, LUISELLI 1994) which can involve both local and long distance dispersal to and from each respective focal area.

The annual cycle for *V. berus* is now well known and typically the mating period usually lasts about three weeks and takes place within a relatively confined area at, or close to the hibernations site, although some workers have stated that males move long distances when searching for females (ANDREN 1986, MADSEN 1988, FORSMAN 1997, VÖLKL & THIESMEIER 2002).

The few short weeks of the mating period is the only phase of the annual cycle when most aspects of social structure and behaviour are apparent; for example, there is no way of assessing male hierarchy outside the breeding season. From May through to September adders are well dispersed and can be considered as solitary, although the exception are breeding females which remain in the breeding area and can exhibit gregarious behaviour.

Although *V. berus* has been well studied it is still not clear how groups distributed throughout an extended area of suitable habitat relate to each other. There has been some consensus regarding site fidelity in the short term (PRESTT 1971, PHELPS 1978, MADSEN & SHINE 1993, LUISELLI 1994) but only very little has been recorded where known populations persist at a site for more than one or more seasons (VÖLKL & BIELLA 1988, VÖLKL & KORNACKER 2004).

MADSEN (1988) and CAPULA & LUISELLI (1994) hypothesised that the vast majority of adders do not live longer than eight to nine years. There has been an almost complete lack of data with regard to the longevity of individual adders and until now much has been left to speculation. This study attempts to further promote this aspect and that of site fidelity and shows firstly, that adders have the potential for a long life, certainly spanning two or more decades, and also that individual snakes exhibit a pronounced attachment to their respective focal area. The study also points out that much depends on the nature and long term security of individual habitats with regard to the survival and stability of adder populations.

2 Materials and Methods

Study areas

The two study areas are situated in the district of Purbeck which lies in the southern part of the county of Dorset near the south coast of England (Figures 1 & 2). One area, Furzebrook, is typical lowland heath which has been sympathetically managed over the last thirty years and covers approximately 50 hectares. Wet heath and mire are a

feature adjacent to much of the dry heath and represent summer ground for *V. berus*. All six species of British reptiles are present in good numbers including a high density population of *Coronella austriaca*.

The second area, Norden, is situated just three kilometres south of Furzebrook on the site of old clay workings and covers approximately 35 hectares. The area has a history of heathland in the pre 1960s but since that time has been transformed by bracken and birch encroachment. However, the tree invasion has not been total and sufficient open area has persisted allowing the adder population to flourish.

Although the most intensive study has taken place over the last sixteen years fieldwork was first initiated in 1971 and continued through to 1980 and resumed again in 1986.

Identifying individual adders

Individual adult adders were permanently and uniquely marked by clipping a series of four ventral scales and each given a hypothetical field number (see PRESTT 1971 for details).

Additionally, individual distinguishing features, such as scarring, (e. g. from predator attacks), were noted. No neonate or juvenile of less than 25 centimetres in length were marked so as to prevent injury or infection. Since 1989, each adder captured was photographed for an identification by individual head and dorsal markings (SHELDON & BRADLEY 1989, BENSON 1999). This reliable method also allowed for the identification of neonate and juvenile adders.

3 Results

Population numbers

An initial intensive capture and marking effort during the early spring and late summer periods over four years, 1971 to 1975, resulted in the identification of 78 individual adult adders at Furzebrook, (46 males, 32 females), and 62 at Norden, (36 males, 26 females). From 1975 it was thought that much of the adult population for both areas had been accounted for and new snakes recorded at that time were mainly young adults in their first potential breeding season. This has since been confirmed in that the current situation (2002) is: Furzebrook 43 males, 30 females; and Norden 32 males, 27 females. Both populations have been seen to be remarkably stable throughout the study period, (Figures 3 & 4).

The overall sex ratio for both areas was consistently male biased although the actual breeding sex ratio within individual groups was closer to 1:1.

The proportion of immature adders, (second and third season with a length between 25 and 30 centimetres), never exceeded 15 % at Furzebrook and 20 % at Norden of the total population and showed no bias between male and female.

During 2001 at Furzebrook the number of new records for young adult males in their first potential breeding season represented just under ten percent of the total male population (n=4). Young adult females were also around ten percent (n=3). For the same period at Norden young adult males represented just under twenty percent (n=6) and the number of young adult females was almost identical (n=5).

The numbers of both adult and immature *V. berus* were consistent throughout the study period, and given the duration of the study is deemed to be an accurate assessment of the general population for both study areas.

Fig. 1. Adder habitat at Furzebrook. Photo T. Phelps.
Untersuchungsgebiet Furzebrook.

Fig. 2. Adder habitat at Norden. Photo T. Phelps.
Untersuchungsgebiet Norden.

Annual life cycle

The annual cycle of the adder in the study areas does not differ significantly from results obtained in other regions of the snake's range, although this study has revealed the behaviour and life histories for individual snakes over an extended period of time.

Males leave their hibernation sites usually during early March but remain close to the winter dens. There, they usually form basking aggregations and establish surface

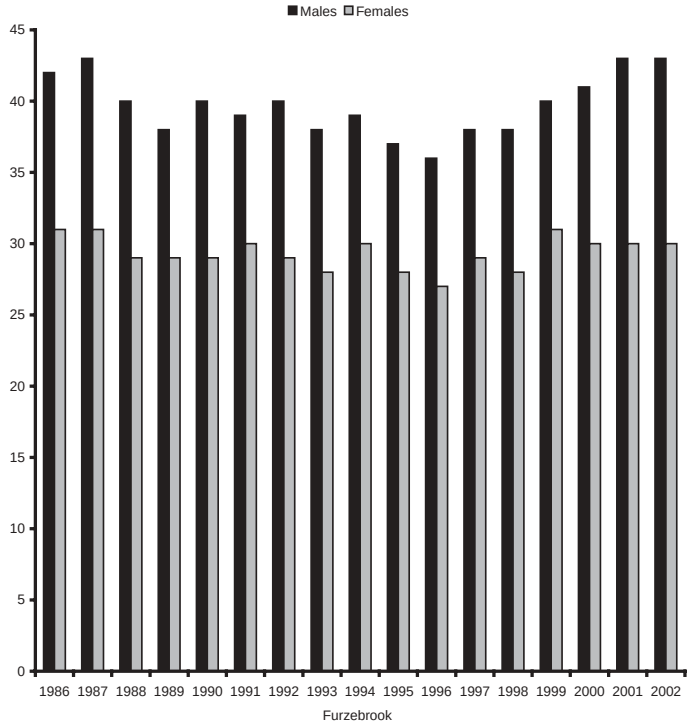

Fig. 3. Overall population numbers of adult *Vipera berus* at Furzebrook, for the period 1986-2002.

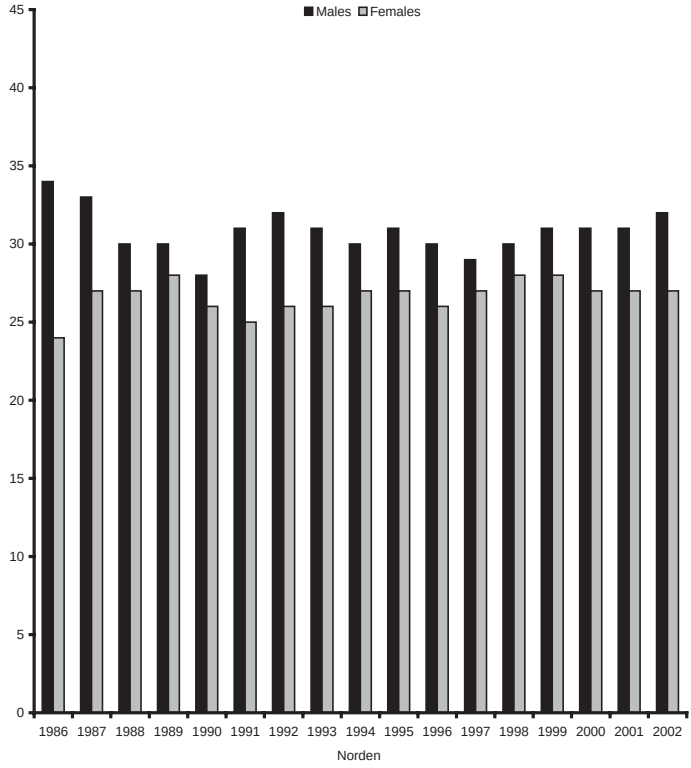

Fig. 4. Overall population numbers of adult *Vipera berus* at Norden, for the period 1986-2002.

dens which provide good cover and security. Females leave the hibernation sites around the end of March and may bask both singly and communally. The adult male spring moult, the trigger for the mating period, takes place during the first weeks of April and is more or less synchronised throughout the population. The mating period lasts for about three weeks and males exhibit the well documented behaviour of combat and mate-guarding. The mating areas are situated at, or close, to the hibernation site. At the end of the mating period males disperse to the summer grounds and most breeding females remain in the vicinity of the hibernation area where they give birth during late summer or early autumn.

Site fidelity

During the initial four years of the study it was revealed that the general population at both areas was divided into a number of individual adult groupings, six at Furzebrook and two at Norden. These individual groups were situated in dry areas with good cover and a southerly aspect, and being occupied for around seven months of the year represented the hibernal and breeding area for that particular group. The locations, numbers of adults, and sex ratios, are shown in Figures 5 and 6.

It also became apparent quite early on in the study that individual adult adders showed a pronounced tenacity to their respective group. Even though, at Furzebrook, some groups were separated by as little as two hundred metres no interaction between adults from the six groupings has ever been recorded and adult fidelity is thus thought to be one hundred percent. Adult fidelity was also one hundred percent at Norden, even though the population was divided into just two groups.

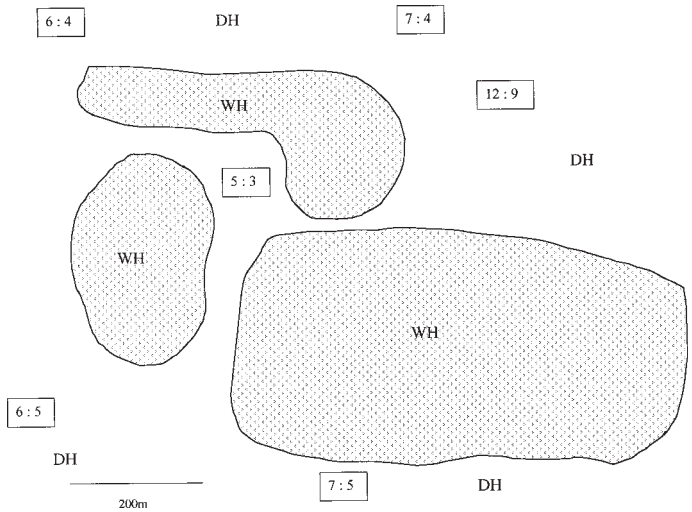

Fig. 5. Distribution of *Vipera berus* at Furzebrook Heath, Dorset. The boxes represent the six reproductive autonomous groups and the number of adult males and females. The wet heath (WH) areas represent communal summer grounds for all six groups.

Verteilung der Kreuzottern im Untersuchungsgebiet Furzebrook Heath. Die Kästen stehen für die sechs autonomen Fortpflanzungsgruppen und die jeweilige Anzahl von Männchen und Weibchen. WH sind Feuchtgebiete, die allen sechs Gruppen als gemeinsame Sommerquartiere dienen.

Individual identification of neonate adders did not take place until 1989 and it was hypothesised that young adults presented as first records were probably those returning to their place of birth. This has since been seen to be the case in other parts of the adder's range (see VÖLKL & KORNACKER 2004).

During the early spring of 1995 at Furzebrook two young male adders, identified as neonates in 1991, were found in groups at other than their place of birth. That same year a young male recorded in group one was known to have been born in group two. Careful examination of adults since that time has revealed an irregular pattern whereby just one or two at both sites represent known neonates born to other groups. These records, although still few in number, have been consistent and it is thought to have provided an insight as to how immature adders can move at random throughout a population.

Although young adders moved at random throughout the population their activities could not be considered as entirely independent from the adults. Research on timber rattlesnakes, *Crotalus horridus*, has shown that there is a strong association between neonates and chemical cues given off by conspecific adults (BROWN & MACLEAN 1983, REINERT & ZAPPALORTI 1988). It is likely then that adder neonates followed scent trails to the summer grounds and again on return to hibernation, and as results have shown hibernation areas are selected at random during the first three years of life. Two records have identified young adders in outlying areas between two and three kilometres away from their place of birth. This was unexpected and even this low number indicates that some adders have a potential for a wider dispersal.

During the mating period males were seen to maintain fidelity. This was unexpected and it was predicted during the early part of the study that males would be likely

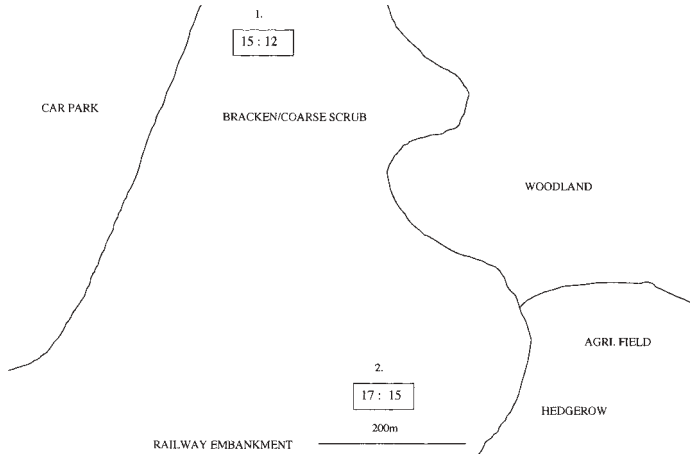

Fig. 6. Distribution of *Vipera berus* at Norden, Dorset. The boxes represent the two reproductive autonomous groups and the number of adult males and females. The woodland edge, hedgerow and railway embankment represent communal summer ground for the two groups.

Verteilung der Kreuzottern im Untersuchungsgebiet Norden. Die Kästen stehen für die zwei autonomen Fortpflanzungsgruppen und die jeweilige Anzahl von Männchen und Weibchen. Woodland edge (Waldrand), hedgerow (Hecke) and railway embankment (Bahntrasse) dienen beiden Gruppen als gemeinsame Sommerquartiere.

to disperse more widely in search of a mate. But over the years, and working with several people observing individual groups, the adults, both males and females, were seen to exhibit total fidelity.

A pronounced tenacity to respective groups is further surprising when ANDREN et al (1997) have stated that males are attracted by female pheromones at a distance of at least five hundred metres. All groups throughout both areas are separated by distances within this limit and in theory would have detected chemical cues from females outside their group. Although by no means conclusive one explanation is that perhaps ground-based pheromones are stronger and therefore override airborne cues which may be at the limits of effectiveness.

Social behaviour and hierarchy

The most obvious communal behaviour was during the early spring when adult males could be seen in the immediate area of the hibernation den in aggregations of up to ten individuals at Norden, although it was more usually two or three at Furzebrook.

This was a passive time for males, although some individuals showed some agitation when apparently competing for basking position. Around mid March males established surface dens between two and twenty metres distant from the hibernation dens proper. These second dens had both good cover and basking facilities, and although involving fewer males, were still mostly communal. Large males used the same surface dens each year but young males, particularly those under 45 centimetres, were seen to select dens at random. These smaller males nearly always chose a den occupied by a larger male and although not yet proven, it may be possible that they are guided by both visual and chemical cues from the older males.

During the last week of March, or very early April, breeding females were seen to move through the ground occupied by the males and become locally dispersed throughout the area. The distance moved from the hibernation site for these females ranged from zero to 50 metres at Furzebrook, and zero to 100 metres at Norden. This philopatric behaviour was consistent throughout the study and defined the limits of the mating area through all groups at both study areas.

Immediately after the spring moult adult males exhibited a dramatic change in behaviour and became alert and aggressive and highly vagile in the search for females. It was during this time that hierarchy within the adult male population became apparent. Although male combat was a feature at both study areas it was more pronounced at Norden, and could be explained by the two more densely populated groups. The intensity of male combat was seen to exist at varying levels. If a large male encountered a small male then this involved a brief skirmish followed by a short chase lasting just a few seconds. More prolonged combat occurred when two large males met, resulting in bouts lasting up to twenty minutes. This includes the most serious combat when one male would already be in company with a female. Throughout the study, particularly in later years, it has been possible to determine which individual males were most successful during the mating period. Careful observation has shown that the larger males, (in excess of 55 centimetres), were those that exhibited first mating, and in particular mated with the large females. It was also observed that although engaged in a number of combats very little time was spent in actual mate searching, and in fact, without exception the large males appeared to find females very quickly. Mate-guarding, for up to five days, was an aspect of consistent behaviour in the large males. Breeding females became secretive after the first mating and often undertook a local dispersal. This, combined with the behaviour of the males suggests that multiple

mating is unlikely in both populations. Mating success in relation to large size has also been demonstrated in Scandinavian and alpine adders (ANDREN 1986, MADSEN 1988, MADSEN & STILLE 1988, LUISELLI 1993, 1995).

Small males spent a great deal of time and energy in negative mate searching, but some often mated later with young females.

During the first weeks of May male adders were seen to have vacated the breeding areas. At Furzebrook distances travelled to the summer grounds were variable, but during the early part of May some males were seen to have traveled as far as 400 metres. It was routine to search the summer ground at this time (and through summer), and about half the adders recorded during any one year showed evidence of having recently fed. This number also included non-breeding females and the immature.

Male adders at Norden moved to surrounding hedgerows and woodland edges, and a number also moved along a railway embankment. Snakes from both groups shared the mutual summer ground as described above. Evidence of feeding was observed from early May onwards. Adders were seen to be mainly solitary when in the summer grounds but on occasions two or three of mixed age and sex could be seen basking together.

Breeding females remained secretive and hard to find at both Furzebrook and Norden until early June when they were made more obvious by prolonged periods of basking in prominent and open situations. At Furzebrook most females remained in the breeding area and some showed a degree of communal behaviour when observed basking in groups ranging from two to five snakes. This behaviour was even more pronounced at Norden and it was not unusual to see up to nine females basking together (This phenomenon has also been observed in other populations in southern England, and the highest number recorded was in the county of Surrey during the summer of 1975 when fifteen gravid females were found under a sheet of corrugated iron [pers. obs.]). This communal behaviour ceased around mid August when the females dispersed locally and gave birth.

Longevity and survival

This study has shown quite clearly that adders have the potential for a long life. Currently at Furzebrook, seventeen percent of adult males and twenty six percent of adult females are over twenty five years of age. Similarly, at Norden, sixteen percent of males and twenty nine percent of females are in this age group. There are also exceptional cases where individuals recorded as adults during the mid 1970s are still alive today. The oldest female, recorded in 1974 at Norden, and measuring 58 centimetres, gave birth to fourteen young in 2001 and exhibited a length of 68 centimetres. Also in 1974, a male from Furzebrook measured 48 centimetres and was still alive in 2001 showing a length of 61 centimetres. Tables 1-4 show the current situation with regard to size and age of adults at both Furzebrook and Norden.

The study has shown that male hierarchy and female fecundity does not diminish with age, but the lack of adders in excess of thirty years of age strongly suggests that this is the upper age limit. What remains unknown is why old adders that were seen to be active and prominent during a season just disappeared. In fact, these adders were so prominent and predictable if they were not seen during a season they were deemed to be dead.

The longevity of adders as shown for both areas, plus the recorded stability of individual groups, suggests that recruitment of young adults would be accordingly low. Tables 1-4 show that adults of 50 centimetres and below are indeed in the

Group No.	Field No.	Size mm	Age group (years) 4-6	6-10	10-20	20-30
One	009	610				x
One	023	590			x	
One	040	590			x	
One	067	510		x		
One	073	500		x		
One	102	480	x			
Two	005	620				x
Two	017	610				x
Two	054	520			x	
Two	068	520			x	
Two	084	490		x		
Two	114	475	x			
Two	189	400	x			
Three	012	630				x
Three	025	580			x	
Three	033	580			x	
Three	046	580			x	
Three	052	570			x	
Three	057	520		x		
Three	094	490		x		
Three	115	490		x		
Three	173	450	x			
Three	182	410	x			
Three	185	390	x			
Three	186	375	x			
Four	014	650				x
Four	037	520		x		
Four	044	520		x		
Four	062	510		x		
Four	155	400	x			
Five	004	610				x
Five	010	550			x	
Five	018	545			x	
Five	036	510		x		
Five	045	510		x		
Five	183	390	x			
Six	003	600				x
Six	017	560			x	
Six	028	560				x
Six	029	555				x
Six	077	510			x	
Six	179	450	x			
Six	191	360	x			

Tab. 1. Ages and size of male *Vipera berus* at Furzebrook within individual reproductive autonomous groupings (as at summer 2001).

Altersgruppen und Gesamtlänge männlicher *Vipera berus* aus sechs autonomen Fortpflanzungsgemeinschaften im Gebiet „Furzebrook“.

Group No.	Field No.	Size mm	Age group (years) 4-6	6-10	10-20	20-30
One	010	660				x
One	011	620				x
One	043	500		x		
One	111	480	x			
Two	006	620				x
Two	012	610				x
Two	029	610				x
Two	086	480	x			
Three	005	680				x
Three	017	620				x
Three	027	610				x
Three	039	610			x	
Three	044	610			x	
Three	062	540		x		
Three	066	535		x		
Three	068	540		x		
Three	102	440	x			
Four	024	610			x	
Four	038	620			x	
Four	094	490	x			
Five	007	690				x
Five	016	620				x
Five	037	590			x	
Five	047	600			x	
Five	101	450	x			
Six	022	620				x
Six	035	600			x	
Six	042	620			x	
Six	104	490	x			
Six	105	480	x			

Tab. 2. Age and size of female *Vipera berus* at Furzebrook within individual reproductive autonomous groupings (as at summer 2001).

Altersgruppen und Gesamtlänge weiblicher *Vipera berus* aus sechs autonomen Fortpflanzungsgemeinschaften im Gebiet „Furzebrook“.

minority. This has meant that during any one season one or two young adults of either sex would be recorded for each group. Sometimes no young adults were recorded in a group and the long term nature of the study has concluded that recruitment is erratic. For example, in group two at Norden, no young adult males were observed between 1998 and 2000, and then two were recorded in the spring of 2001. Similarly in groups three and five at Furzebrook, no young adult females were observed between 1997 and 2000, and then one in each group was recorded in the spring of 2001.

PRESTT (1971) stated a mortality rate of 88 % during the first three years of life for adders which if translated to this study would suggest a recruitment of around thirty adults for each area. However, PRESTT's figure was calculated using a hypothetical

Group No.	Field No.	Size mm	Age group (years) 4-6	6-10	10-20	20-30
One	008	620				x
One	014	620				x
One	029	630				x
One	032	610				x
One	038	600				x
One	066	600			x	
One	068	580			x	
One	077	600			x	
One	082	575			x	
One	089	600			x	
One	104	540		x		
One	116	520		x		
One	155	480	x			
One	166	390	x			
One	172	390	x			
Two	005	640				x
Two	017	610				x
Two	022	610				x
Two	030	620				x
Two	072	600			x	
Two	081	610			x	
Two	084	590			x	
Two	088	600			x	
Two	091	590			x	
Two	094	580		x		
Two	102	590		x		
Two	114	540		x		
Two	125	500	x			
Two	133	510	x			
Two	152	490	x			
Two	177	370	x			
Two	179	360	x			

Tab. 3. Ages and size of male *Vipera berus* at Norden within individual reproductive autonomous groupings (as at summer 2001).

Altersgruppen und Gesamtlänge männlicher *Vipera berus* aus zwei autonomen Fortpflanzungsgemeinschaften im Gebiet „Norden“.

model and because actual results for this study have shown erratic and therefore low recruitment, it was thought that mortality during the first three years of life is probably significantly higher. This is also reflected in that immature adders have consistently formed the population minority.

Since 1990 six gravid females have been taken from each population shortly before parturition. This represented around 25 % of the breeding females each year at Furzebrook, and 20 % of those at Norden. Over an eleven year period 550 neonates from Furzebrook and 310 from Norden have been identified. Although a number of females have been recorded more than once selection was random and has resulted in reliable data with regard to fecundity and post-partum condition across a wide size and age range.

Group No.	Field No.	Size mm	Age group (years) 4-6	6-10	10-20	20-30
One	011	640				x
One	018	650				x
One	019	630				x
One	025	640				x
One	027	680				x
One	033	625				x
One	065	610			x	
One	070	620			x	
One	073	590			x	
One	076	600			x	
One	133	540		x		
One	156	510	x			
Two	004	635				x
Two	007	660				x
Two	013	680				x
Two	024	620				x
Two	026	610				x
Two	028	630				x
Two	029	620				x
Two	060	620			x	
Two	066	630			x	
Two	100	600		x		
Two	10	600		x		
Two	112	580		x		
Two	140	550	x			
Two	151	520	x			
Two	154	500	x			

Tab. 4. Showing ages and size of female *Vipera berus* at Norden within individual reproductive autonomous groupings. (as at summer 2001)

Altersgruppen und Gesamtlänge weiblicher *Vipera berus* aus zwei autonomen Fortpflanzungsgemeinschaften im Gebiet „Norden“.

Between 1994 and 1998 of the 550 neonates identified at Furzebrook nine have now been recorded as young adults, and for the same period of the 310 at Norden, six have been recorded. Allowing for neonates identified between 1998 to 2001, which have still to reach maturity, this represents a recapture rate of around 2 % for both areas. This figure represents 25 % of the total young surviving, the survival rate can be expressed simply thus 2 % × 4 = 8 % = mortality 92 %. Even though this was a crude calculation it does show how similar the two populations were even though they occurred in different habitats and densities. Although these figures appear close to PRESTT's hypothetical model the difference of around 4 % is thought to be significant when related to actual numbers of snakes. Once recorded as young adults, adders, both male and female, showed the pronounced tenacity to their respective group consistently throughout the study.

The male bias suggests a higher mortality in females, and this has much to do with reproduction costs (PHELPS in prep). A brief explanation is that the highest mortality occurs with those females that breed during the first years of maturity with a length

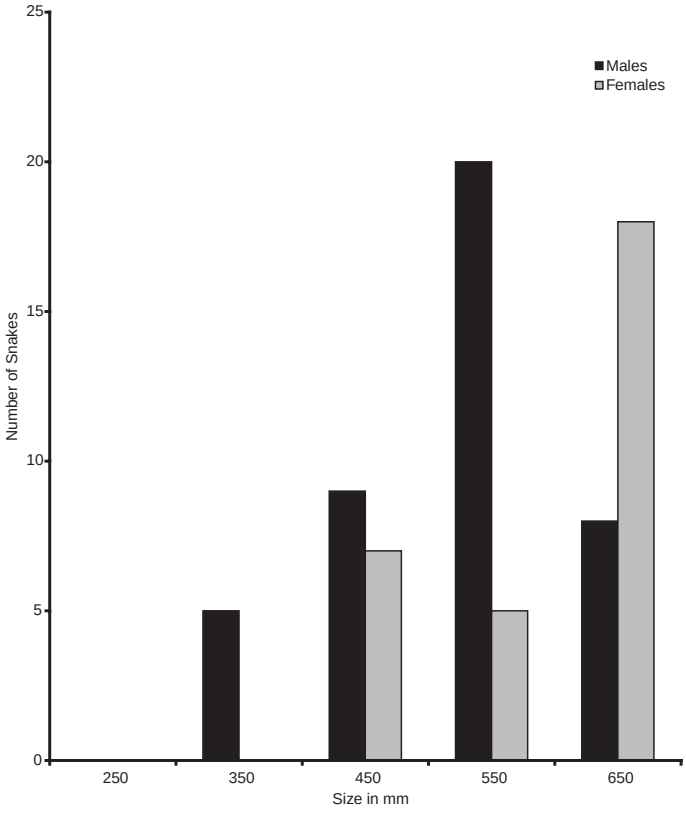

Fig. 7. Combined size structure of adult *Vipera berus* at Furzebrook across all six groupings.

Größenklassenverteilung der adulten Kreuzottern in Furzebrook (alle sechs Gruppen).

of around 41-45 centimetres. These females typically gave birth to small broods and a high proportion of stillborn and deformed young, and most often gave birth late and just could not gain condition. As a consequence most were never seen again, mortality obviously occurring before or during hibernation. A notable number of females at both Furzebrook and Norden were seen not to breed until their seventh or eighth year. These females showed a rapid increase in growth and most have since exhibited a high degree of survival.

During the study a number of predators were known to have preyed on adders. The buzzard, *Buteo buteo*, is said to be a major predator of adders in Britain (FRAZER 1983) and was seen to take both adults and smaller adders during the study period. The most consistent predators, particularly of smaller adders, were crow, *Corvus corone*, magpie, *Pica pica*, and pheasant, *Phasianus colchicus*. The smooth snake was a significant predator at Furzebrook and was seen to take adders of up to 30 centimetres. Predation of adders by smooth snakes has also been recorded in other areas of southern Dorset (SPELLERBERG & PHELPS 1977).

Human impact was minimal due to the secluded nature of both areas, but a number of females were killed in one day at Norden during 1996. Also at Norden part of the migration route for both groups involved crossing a busy road and a number of snakes, five adults and three immature were found dead over a four year period.

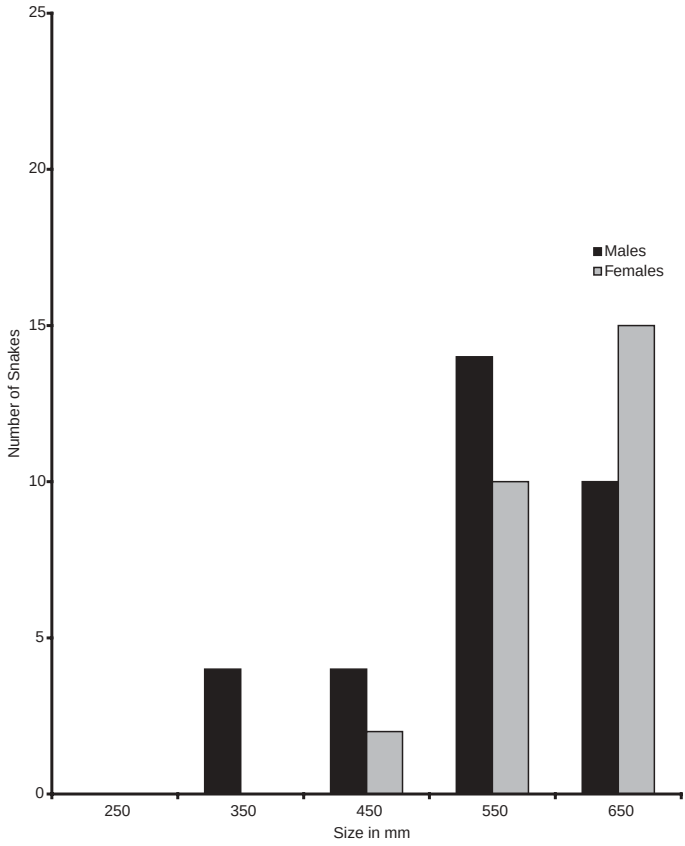

Fig. 8. Combined size structure of adult *Vipera berus* at Norden across both groupings.

Größenklassenverteilung der adulten Kreuzottern in Norden (beide Gruppen).

4 Discussion

Adders occur throughout a wide range of habitats and conditions and as such are subject to a variety of both positive and negative influences. Just how adder populations react to these various influences has been studied by a number of workers. Andren et al. (1997) in a study of adders on the island of Stora Hastholmen estimated that the population ranged from fewer than ten to about two hundred adults. This notable fluctuation was due to a narrow prey spectrum consisting of just the one species, the field vole *Microtus agrestis*, the numbers of which were seen to be highly variable. A study of adders in the German highlands (Völkl & Thiesmeier 2002) revealed a similar situation to this study in that numbers in the population were seen to be stable between 1982 and 1990. However, the population has since suffered a decline explained by habitat loss and predation by wild boar, *Sus scrofa*.

The two locations in this study represent a habitat that has remained stable and even enhanced by positive and selective management and this is reflected in the constant numbers of adders that have existed there for at least three decades. Such pristine habitat also presents a wide prey spectrum and adders are probably not adversely affected by possible fluctuations in numbers of any one prey species.

Although there are many areas within the general region of south Dorset which contain pristine habitat for the adder there are more than an equal number of habitats which can be described as more dynamic. These are typically fragmented areas of heath that have become isolated due to either urban development or forestry operations. There are a number of negative influences on urban heathland sites for example. Many such sites have become 'islands' amongst a conurbation of urban sprawl. Adder populations here often flourish if allowed to do so, but most suffer due to such events as regular fires, human disturbance, and even predation by domestic cats, *Felis catus*. Such populations often exhibit shifts in population, as a result of fire or disturbance, or else an imbalance in sex ratio which results in an erratic breeding cycle. One current study on a urban heathland site has shown that in one sub-population females outnumber the males by almost four to one. These females hardly ever breed and put their energies into feeding and some have been recorded as reaching more than average size, 84 centimetres being the largest so far recorded (PHELPS unpublished data).

The pronounced fidelity by adults to their respective groups was, and still is, a constant feature. This consistency gave the overall impression that these groups were reproductively autonomous and that the only interaction between groups was represented by mutual use of the summer grounds. The status of immature adders was not revealed until 1995 when a number of recaptures showed them to be erratic in their movement and that they select and integrate with groups at random. This contrasts with VÖLKL & BIELLA (1988) and VÖLKL & KORNACKER (2004) where although there is agreement regarding the fidelity of adults young adders were seen to return as adults to their place of birth.

KÄSEWIETER et al. (2004) found no site fidelity for a population in the Lech Valley in Southern Bavaria and explain this difference by the dynamic habitat which changes after each spring flood.

MADSEN (1988) and CAPULA & LUISELLI (1994) hypothesised that the vast majority of adders do not live beyond nine years of age and only reproduce once or twice during a lifetime. This study has shown quite clearly that adders have the potential for a long life which can reach an upper limit of around thirty years of age. Furthermore, careful observations have also revealed that adders are not compromised by old age, in fact the opposite appears to be the case. There is some consensus with regard to old adders and other viperids. A long term study of adders in Wyre Forest in the British West Midlands has shown that adders can attain an age in excess of twenty five years (SHELDON unpublished data). It has also been stated that timber rattlesnakes, *Crotalus horridus*, can reach ages in excess of twenty five years (BROWN 1993, MARTIN 2002).

Close observation of individual adders over a long period has shown that both males and females maintain good health in to old age and in addition retain prominence over younger (smaller) individuals. Visible signs of old age were typically of wear and tear, particularly torn ventral scales, and trauma scarring, including bits of tail missing.

Results regarding the annual cycle are largely in agreement with other studies, and also that of reproductive behaviour, in that the larger adders are the most successful with regard to hierarchic behaviour and fecundity. Figures 7 and 8 show current (2002) adult size structure for the general population for both areas, the study has also shown that there is a correlation between size and age for both male and female adders, although some females have exhibited a more rapid growth during their early years of maturity.

The long term aspects of fidelity and longevity highlight the importance of hibernation sites, and thus being occupied by specific groups of snakes for extended periods of time should be regarded as traditional, or even ancestral, and should be given the same consideration as badger setts or bat colonies. The problem is that adder hibernation sites are never obvious and many remain unrecognised, even in protected areas such as National Nature Reserves.

There is also evidence to suggest that inappropriate management has caused some populations to become extinct (WILD & ENTWISTLE 1997). Adders that occur on the heaths of south Dorset fare better as they exist alongside target conservation species such as the smooth snake and sand lizard, *Lacerta agilis*. But even here all reptiles can suffer due to excessive scrub clearance which leaves key sites exposed and vulnerable. Elsewhere in Britain the fate of adders is often left to chance and many populations now face local extinction.

To summarise, the stable number of adult adders throughout all groups over a long period of time for both study areas strongly suggests that an optimum limit has been reached and maintained. The longevity of adults has dictated low levels of recruitment which is erratic and subject to random movement and selection by immature (young adult) snakes.

The study also reveals that where suitable habitat exists young adders have the potential for dispersal to outlying areas. This has obvious conservation implications when for example considering the creation or enhancement of habitat close to existing populations.

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