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Natural History of the Barred Grass Snake *Natrix helvetica*: Insights from a Study in Southern Britain 1958–1962

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Edited by Simon Townson

FRONT COVER: The barred grass snake *Natrix helvetica*. Photograph by Brett Lewis.

Contents

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Natural History of the Barred Grass Snake *Natrix helvetica*: Insights from a Study in Southern Britain 1958–1962

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[†]Deceased. Ian Prestt (26 June 1929 - 24 January 1995, Obituary 01/02/1995, Independent) was the originator of this project but it was carried out in absentia by RES. It followed the methods of Ian's ground-making research on the adder which he undertook from the former Nature Conservancy, Furzebrook Research Station on mostly farmland, south of the River Frome, Wareham, Dorset

ABSTRACT – This report presents, for the first time, the results of an intensive study of individual grass snakes carried out in Dorset, southern England, between 1958 and 1962. About 500 grass snakes were individually marked, and data were obtained on seasonal and daily activity, breeding behaviour, egg laying and hatching, feeding, and population characteristics. The population is likely to have comprised about 1,000 snakes that displayed wide-ranging movements over a large area. Indeed, three snakes were observed to move at least 4 km. Large numbers of eggs and hatchlings were collected from a longstanding sawdust heap that appeared to provide the main oviposition site. The data collected correspond with more recent studies, and there is no evidence that grass snakes have markedly shifted their seasonal patterns of behaviour in the 60 years since this research was carried out. A recent visit to the study area found that much of the original habitat remained intact. Although the primary sawdust heap oviposition site has disappeared, the water bodies that support the toads that provided the bulk of the diet of the grass snakes still exist and local fisherman continue to report sightings of grass snakes in the area. Although the study site is no longer regularly monitored, records of grass snakes have continued to be submitted from the area in recent years, confirming the persistence of the species after sixty years.

INTRODUCTION

On 21 October 1980 one of us (RES) presented a lecture at the British Herpetological Society meeting in London: 'The Natural History of the Grass Snake in Dorset'. This described a pioneering field study carried out two decades before the date of the meeting. Although the intention was to publish the research, other pressing commitments meant that RES was unable to do so. Nearly two decades later, RES provided some of his unpublished data from the study for inclusion in the grass snake section of the third New Naturalist volume on amphibians and reptiles (Beebee & Griffiths, 2000). Over twenty years after the publication of that book, RES – now retired – unearthed the original data, photographs and field notes presented at the 1980 BHS meeting and contacted the society to explore the possibility of publication. In this report we present, for the first time, the detailed findings of this intensive field study of grass snakes that was carried out over 60 years ago.

The research was conducted on the Isle of Purbeck, Dorset, from 1958 to 1962. The research continued some preliminary work by Ian Prestt who was working mostly on the ecology of the adder *Vipera berus* (Prestt, 1971). RES was able to take over in October 1960 using similar methods to discover aspects of the life history of barred grass snakes *Natrix natrix*, now *Natrix helvetica* (Kindler et al., 2017). The core study area was a mixture of heath and woodlands surrounding lakes, formed by a ball clay extractive industry and these had become breeding sites for the common toad *Bufo bufo*, the principal food of that snake population. In addition, an estate timber yard producing mostly fencing posts sawn from larger tree trunks yielded large quantities of sawdust which was deposited in a heap annually. In summer, this heap of decaying sawdust, being exposed to the sun, became hot with internal temperatures reaching 40 °C. The grass snakes burrowed into the sawdust and laid their eggs in the moist warm substrate. About 500 adult snakes were marked individually and the study also involved dissections of animals which had died through the active season of March to October.

For this report, we have not carried out an extensive reanalysis of these historical data as we believe that it is important to demonstrate the tools and methodologies that were used in herpetological field research at the time. In the interim, legal and ethical frameworks relating to fieldwork have changed, so we accept that some protocols described here may not be appropriate in the present day. Nevertheless, we relate the findings described here to later studies of grass snakes that have used methodologies which have been developed in recent years.

METHODS

Study sites

The field study was carried out at two contiguous areas known as Creech and Cotness about 4 km south of Wareham, Dorset. This area was termed the 'core' area. A larger area totalling about seven square kilometres stretching mostly to the north and east was surveyed at approximately ten-day intervals, following any features such as lines of scrub or wet areas and former clay industry railway lines. This was mostly featureless wet heathland. Additional observations were made on Furzebrook Heath, Redcliffe Farm (Wareham) and Ridge to the east, including the River Frome

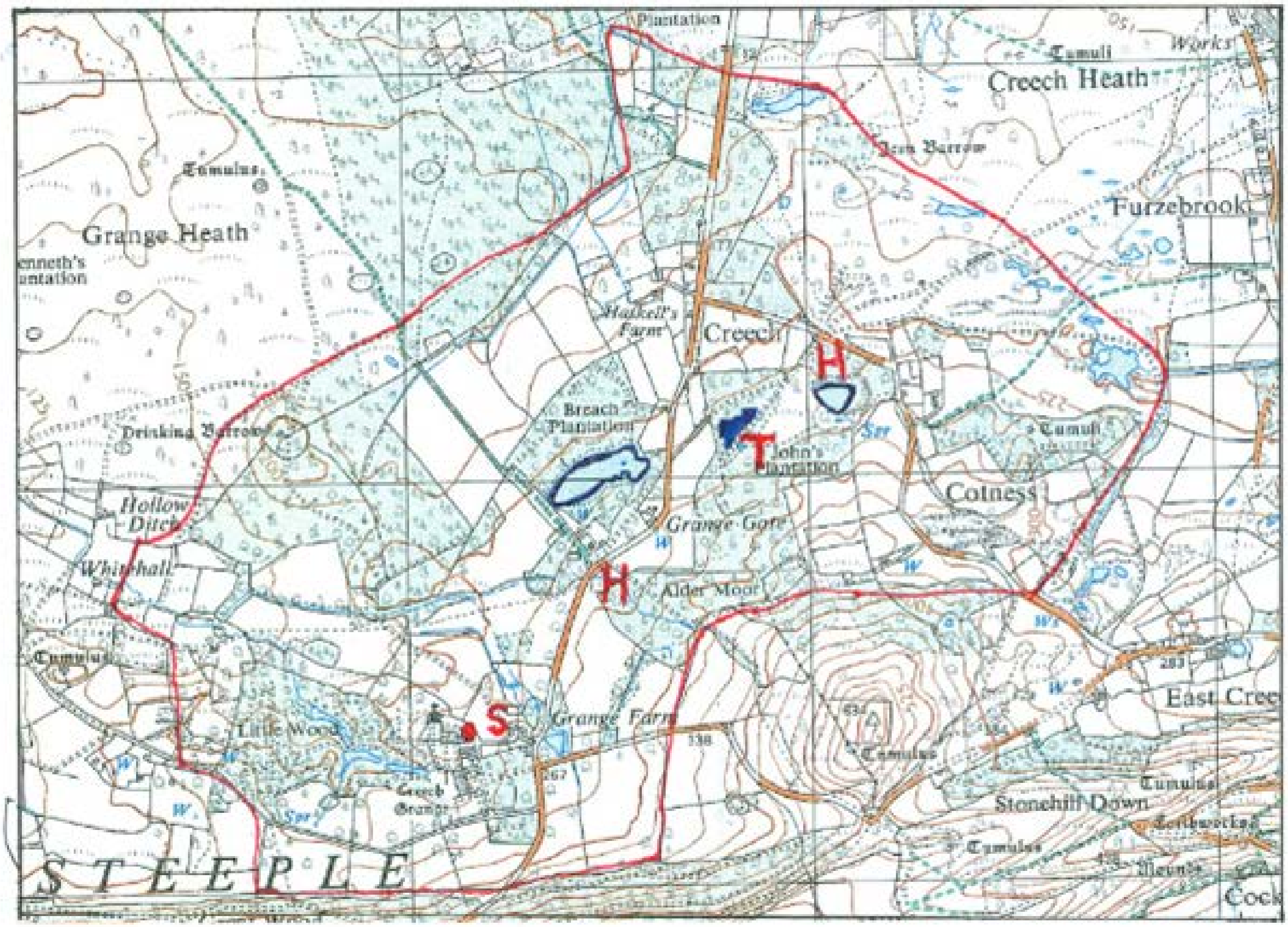

Figure 1. 1:25,000 OS Map of the core survey area outlined in red line. The OS map survey was conducted between 1952–1960 with this edition published in 1970 incorporating minor revisions. The National Grid lines are 1 km apart. The actual field boundaries for the grass snake surveys showed no variation from this OS edition. S - sawdust heap beside sawmill to its south. H - known hibernation areas with deep layers of dead bracken *Pteridium aquilinum* accumulations, typically 300 mm depth. T - The principal shallow toad breeding pond with other deeper ponds to east and west highlighted with blue outline.

Figure 2. View of principal survey site in 1961 at Grange with the sawdust heap approximately in the centre and surrounded by woodland.

flood plain, and at Hartland Moor and Morden Bog National Nature Reserves. These sites were about 3, 5 and 8 km away from the core study area. Experiments and observations of captive snakes were made in an enclosure at the former Furzebrook Research Station. The principal study area around Creech totalled about 235 ha and included 34 km of ditches, banks and hedgerows (Fig. 1). The area consisted mostly of pasture with occasional arable fields with heathland, scrub and woodland, the latter mostly being on former ball clay spoil heaps (Fig. 2).

The ball clay mines were often open cast pits which when abandoned became water filled with the adjacent large tips of poor-quality clay mixed with sand. Some of these tips were planted with oak, *Quercus robur*, and several conifer species and *Rhododendron* spp. Heathland vegetation developed on others including heathers and gorse, *Ulex* spp.

There were three large ponds in the centre of the area extending to 1.95, 0.34 and 0.49 ha.

Many of the ditches around the fields were water filled throughout the year. The fields were mostly used as pasture and grazed by cattle with occasional use being ploughed and planted with a cereal crop for a single year.

Snake capture and recording

Most snakes were found by stalking and then captured in a gloved hand. Some animals were caught by guide netting and traps in the method described by Prestt (1971). The traps were placed across hedgerows or edges of woodland with guide fences up to 6 m long. Traps were double-ended so the direction of travel could be indicated. Traps were inspected at least once a day. On first capture each snake was given a personal mark by ventral scale clipping in different combinations (Carlström & Edelstam, 1946; Prestt, 1971;

Luiselli et al., 1997). After this the animals were released immediately where caught. Some 112 grass snakes were dissected postmortem, mostly in 1962. Some of these had been killed by people and by other animals or run over on roads. Unfortunately, local people often killed any snake they found, with grass snakes being killed as well as adders.

Individual adult snakes were caught live on 718 occasions and of these 538 were caught only once. In all, there were 423 occasions when adult snakes were re-captured (Table 1).

Table 1. Number of occasions individual grass snakes were re-captured after initial marking.

No. of captures per snake	Males	Females	Total
2	22	36	58
3	16	19	35
4	8	13	21
5	2	7	9
6	1	0	1
7	1	2	3
8	0	0	0
9	0	0	0
10	2	1	3
16	1	0	1

Survey and marking protocol

Survey. Searches were made at all times of the day from shortly after sunrise to sunset, but most were between 08:00–18:30 hrs GMT. A visit was made almost daily from April to September through 1961 and 1962. There were some visits in March and October but not in an intensive way. There was no precise record of the amount of time spent or distance walked in the field survey but it is estimated that approximately 3,900 hours was spent in 1961 and 1962 with about 1,500–1,700 km walked. In addition, several visits were made at night on warm occasions because a few people, especially firemen, had remarked that they saw snakes in the open at night, perhaps escaping a heathland fire. The search consisted of walking quickly up to 30 km of hedges, ditches and woodland edges. The search effort over the entire area was kept as representative as possible, except the principal egg laying site was always visited daily in the season. It had been found that the stealthy slow approach which was most successful in catching adders (Prestt, 1971) was less effective for grass snakes. Because of their keen eyesight a slow approach invariably resulted in the snake moving away before being close enough for capture. In hot weather it was

Figure 3. The U-shaped grass snake enclosure in 1961 showing the observation hide.

found the snakes proved virtually impossible to catch safely by hand after about 08:00 hrs GMT. After dawn the snakes often climbed hedges and fences to get the first rays of sun and stayed on top of bushes to 'sun' themselves until their bodies were warm enough for activity.

Marking. Snakes were individually marked in the field by clipping differing combinations of ventral scales similarly to the method described by Prestt (1971) but using only single scales for each clip. It was found, when done carefully, each mark remained clear for at least four years. The cloaca was '0' and anterior to that the rows were numbered 1–30. To achieve sufficient number of combinations each scale was notionally divided into left and right sides and so the right side was the master number and left the running individual. In this way up to 900 individuals could be individually marked and identified. The snakes were held in bare hands which allowed them to wrap themselves around with least restraint pressure. (At the time of this study there were no legal restrictions on how these reptiles were caught and marked. The aim always was to minimise stress and to release the animal at the point of capture as quickly as possible).

Observations of grass snakes in captivity
A U-shaped enclosure with plain flat vertical walls 1.4 m tall and constructed of smooth asbestos cement was created in the grounds of the Furzebrook Research Station. The enclosed area totalled 18 m^2 and was equipped with vegetation and underground holes as hiding places. Because the snakes were easily disturbed by any movement of observers, a hide was constructed adjacent to the enclosure and observations made through small holes (Fig. 3).

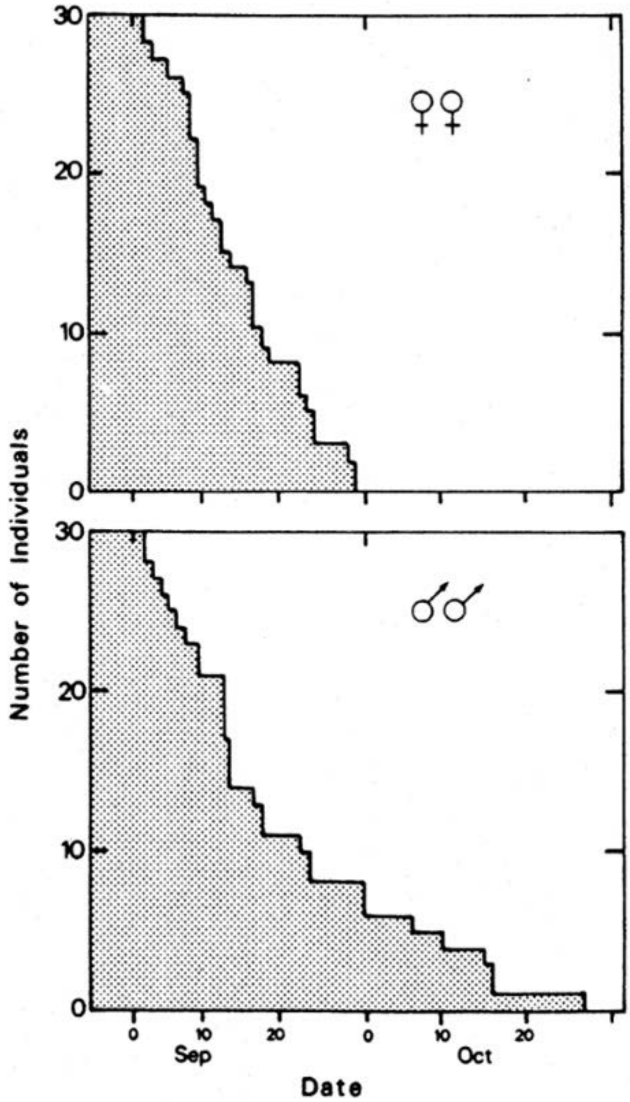

Figure 4. Entry into hibernation and termination of the active period. Figure shows the dates of the last 30 adult grass snakes to be recorded out of hibernation during 1961 and 1962.

RESULTS AND DISCUSSION

Seasonal activity
Annual behaviour cycle. Hibernation lasted about five months in this study area close to the south coast of England. The active period comprised three phases including laying out in spring and mating, the second period included feeding and egg laying and the third, return to hibernation and hatching of young.

Hibernation sites. These places were generally on ball clay spoil banks often with deep accumulations of bracken litter, *Pteridium aquilinum*. Many sites were banks topped by hedges with ditches filled with water, especially in winter. The tops of the banks were always above flood levels. Some banks were clearly occupied by many snakes but a few apparently had only one or two animals.

Throughout the autumns of 1959–1962 all study areas were visited almost daily to record the entry of snakes into hibernation. It was apparent that few animals remained active after the end of September (Table 2). The last 30 individuals seen are shown in Figure 4. The females were in hibernation by the end of September while some males continued to be found up to a month later. Twenty-eight days after seeing the last female the last male was seen.

Table 2. Numbers of captures of adult grass snakes per sex per month in 1962.

Month	Males	% males	Females	% females	Males + females
April	35	27	16	8	51
May	29	22	26	13	55
June	24	19	72	35	96
July	17	13	60	29	77
August	6	5	18	9	24
September	18	14	13	6	31
Total	129	100	205	100	334

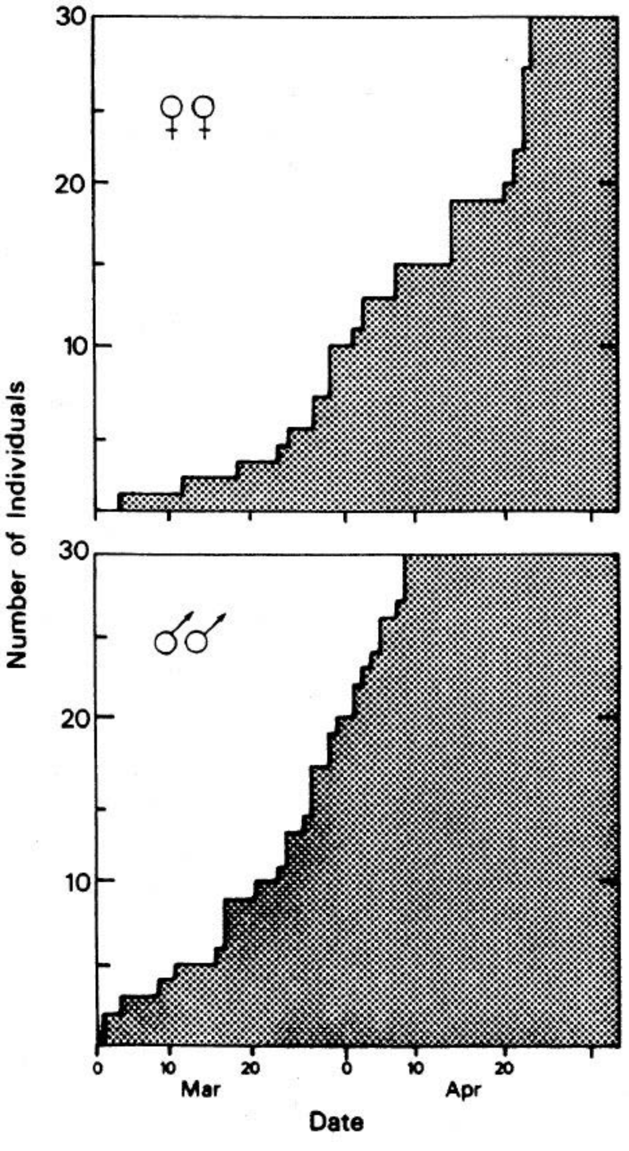

Figure 5. Start of the active period. Figure shows dates of the earliest 30 adult grass snakes found out of hibernation in 1961 and 1962.

Emergence. The pattern of emergence from hibernation was recorded. Figure 5 shows the earliest 30 dates when adult males and females were recorded 1959–1962. The earliest male was on 2 March and earliest female on 4 March. On average males emerged fifteen days earlier than females. Hibernation therefore extended from late September to end of March for adult males and from mid-September to the beginning of April for adult females, (188 and 207 days respectively) (Table 2).

These patterns of hibernation and emergence correspond with those observed in more recent studies. At other study sites in Dorset, Phelps (1978) also found grass snakes to start emerging in March with females later than males. Likewise, Brown (1991) observed grass snakes in Hampshire to emerge in mid-March, but in contrast to the present study and along with Phelps (1978), found no evidence of males emerging earlier than females.

Summer movements. The two major hibernation sites are shown in Figure 1. Most grass snakes did not move away from the hibernation area for a few weeks but a small number moved away and dispersed shortly after emergence. Although there was considerable variation, most animals had moved at least 100 m away from those sites by the end of May (Fig. 6).

After laying out and mating, the adult females began to move towards the egg laying sites. Distances between capture locations were

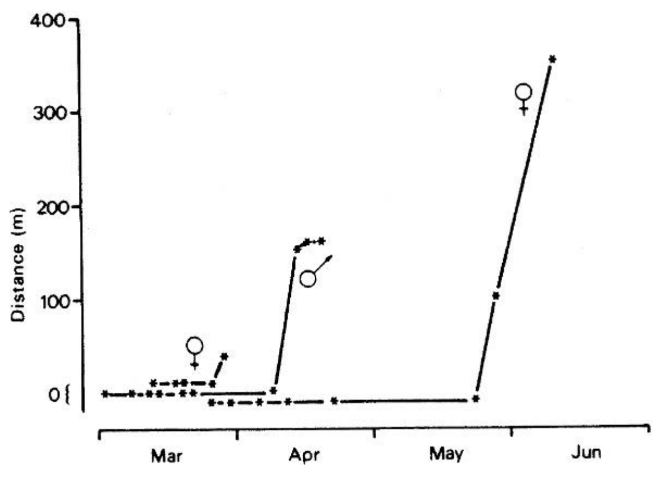

Figure 6. Laying out time for three marked individual grass snakes before dispersal. * = dates observed/ captured.

measured as straight lines but in reality it was thought movements would follow ditches and hedge lines rather than crossing open fields. Snakes disturbed near to field edges invariably turned towards tall vegetation even if this meant passing closer to the observer. Therefore, actual distances travelled were probably substantially longer than recorded here. Movements over 100 m are summarised in Table 3.

Table 3. Movements of over 100 m by individual grass snakes in all study areas.

	No. of movements	
Distance (m)	**Males**	**Females**
100–200	9	18
201–500	22	24
501–1000	12	17
1001–2000	3	8
2000+	1	2
Total	47	69

Of 292 recaptures, 116 were more than 100 m from the previous site and two females and one male had moved over 4 km straight line distances. There was no significant difference between the sexes in the distances between captures. However, grass snakes showed a distinct preference in orientation of long-distance movements with most moving in SS West or NN East direction (males: χ 2 22.1, df = 3, $P < 0.001$; females: χ 2 18.6, df = 3, $P < 0.001$; Fig. 7).

Males seem to wander haphazardly throughout the summer before finally returning to their traditional hibernacula. Breeding females moved to egg laying sites and returned to hibernation and those movements appeared to be consistent from year to year.

These observations correspond with later radiotelemetry studies that have shown considerable variation in movements and home range sizes. Working at the same site as the present study over three decades later, Reading & Jofré (2009) observed home ranges to vary between 0.18–9.41 ha over two years of radiotracking. In Hampshire, Brown (1991) found that although most daily distances moved were small, grass snakes could travel as much as 300 m per day. This is consistent with the maximum daily distances moved by grass snakes

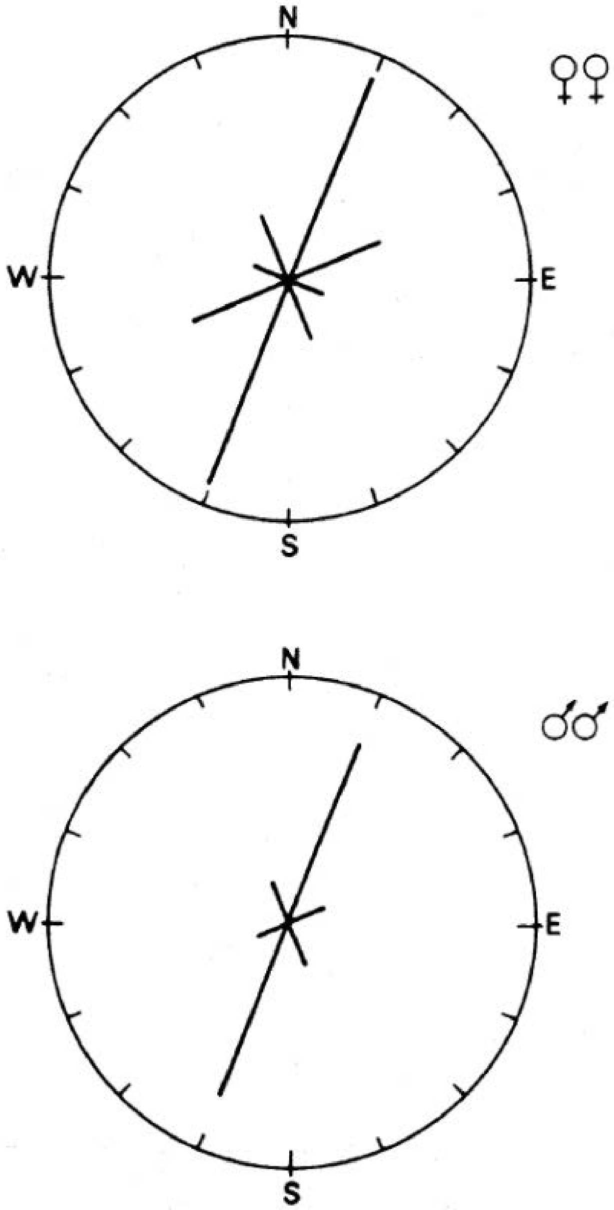

Figure 7. Orientation of long-distance movements between successive captures with length of line shown as a percentage of all movements per sex.

in Jersey (Ward et al. 2017). However, such estimates of movements and home range are heavily influenced by the duration of the tracking study and habitat structure (e.g. Madsen, 1984; Brown, 1991; Ward et al. 2017). Nevertheless, given the low detectability of grass snakes, the observation in the current study that three snakes moved over 4 km during the course of observations is noteworthy.

Daily cycle. Grass snakes emerged shortly after dawn to sun themselves before moving off. In cold weather they could be found at any time of day, usually coiled up in sheltered places facing south but snakes were not seen in wet weather. This contrasts with adders which were found in such conditions (Prestt, 1971). Searches for grass snakes were made on warm nights, typically over 18 °C, because we had reports of people seeing snakes at night. Despite searching for several hours of the night in areas where concentrations of snakes were known to be living, none were found. The comments had been made by people fighting heath fires, so perhaps these were animals escaping from disturbance. Beebee & Griffiths (2000) comment that grass snakes may actively hunt during the early hours of the night if the weather conditions are warm enough.

Sloughing. From field observations and postmortem evidence, it was possible to identify individuals which were preparing to slough or had recently done so, using the methods described by Prestt (1971).

The number of adult males found in pre- and post-slough conditions are shown in half monthly periods (Fig. 8). It shows the males shed twice each year (n = 90) with the peak times being assumed as the mid-point in the peaks. Therefore, sloughing occurred at the end of May and in mid-August with the interval being about 70 days. Records for a single adult male with a length of 840 mm shows this pattern of sloughing. On 27 June 1962 the ventral scales were blue and by 19 July it had sloughed. It was recaptured on 29 August with blue ventrals and by 4 September it had sloughed. This interval was around 50 days.

Similar observations for adult gravid females show a single slough occurring just before egg laying (Fig. 7, n = 104). Thus, peak sloughing is at the end of June (Fig. 9). However, there is another small peak in the second half of August, it seems this could be due to non-breeding animals but there were few records so this was inconclusive. Brown (1991) observed that movements of radio-tracked grass snakes were severely curtailed immediately before sloughing and increased significantly afterwards.

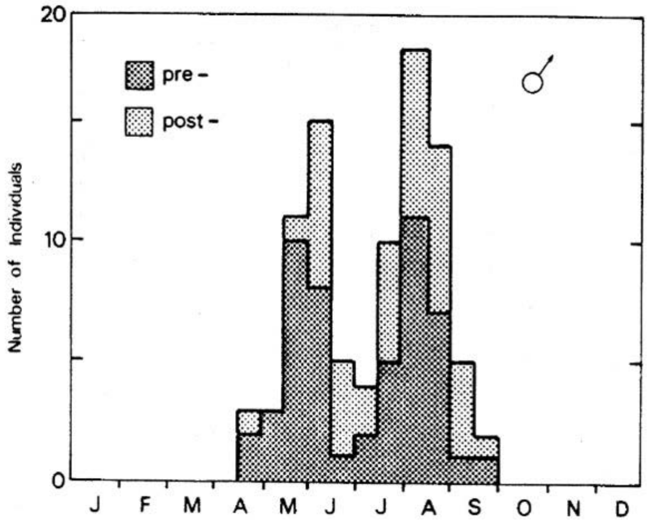

Figure 8. Periods of skin sloughing in adult male grass snakes. These results were obtained from field observations with pre-sloughing shown by dull colour and blue colour of eyes and post-sloughing by very bright clean scales.

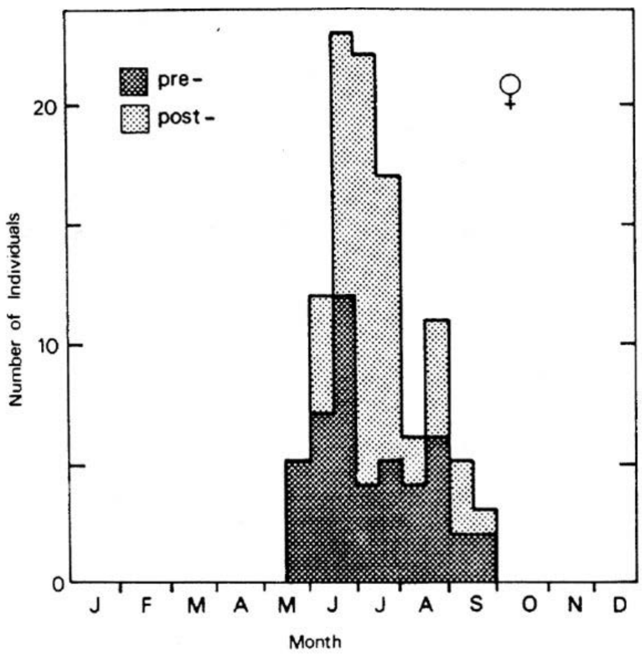

Figure 9. Periods of skin sloughing in adult female grass snakes. These results were obtained from field observations with pre-sloughing shown by dull colour and blue colour of eyes and post-sloughing by very bright clean scales.

Figure 10. Death feigning in a grass snake (photo: Brett Lewis).

Feigning death. It is well known some grass snakes feign death upon capture. Typically, the head is turned partly upside down with mouth open and tongue hanging out. Information on death feigning was assembled for 132 males and 163 females. There was no significant difference between the sexes with 36 (27.3%) feigning death for males and 56 (34.4%) for females. Gregory et al. (2007) observed a higher rate of death feigning in grass snakes in Kent (66%) although this may have been a result of a different handling regime.

Breeding

Mating and interactions between males. Field observation of mating was observed only three times, on 25 and 28 March 1962 and 11 April 1962. In addition, postmortem examinations were made to check for the presence of sperm or fertilised ova in females. Sperm were found in two females each on three dates, 23 April, 14 and 17 May 1961. Fertilised ova were found in females on 23 and 24 April as well as 14 and 17 May. The few observations suggest that mating can be in late March but probably most occur in April.

Although interactions between males is well known in adders *V. berus* and smooth snakes *Coronella austriaca* (e.g. Smith, 1951; Beebee & Griffiths, 2000), at the time of the study no similar behaviour was recorded for grass snakes. Keen eyesight in grass snakes meant that they were rarely found in the field while they remained unaware of the observer.

One large male (845 mm long and 138 g) was introduced into the enclosure with an adult female at the end of September 1961 and the two snakes hibernated together. In the following spring, another adult female was put in together with three males (655 mm and 60 g; 660 mm and 62 g; 680 mm and 74 g). The males were introduced and then removed in differing combinations to observe whether any interaction occurred.

A new male was introduced when the incumbent was patrolling the opposite side of the enclosure so that the two males did not have visual contact. The new male caused no disturbance to the patrolling male who was moving rapidly at approximately 0.5–0.7 m/second. When the new snake was encountered both males froze, then within 5–10 seconds both raised their heads 10–100 mm off the ground, keeping heads horizontal and directly facing each other. No tongue movement occurred. After periods of 10 to 50 seconds, one of the snakes, usually the 'new' male, slowly swayed sideways to and fro, and then putting his head down turned away and moved off, usually into dense vegetation. The remaining male then gradually dropped its head, first flicking the tongue and then purposely resuming patrolling, sometimes finding and staying with a female.

When this behaviour was witnessed on six occasions, it was the incumbent male who resumed patrolling. But twice, when a much larger male was introduced, the incumbent male backed away. No other interactions were observed and no mating was seen to occur in captivity. It was thought these encounters were a 'test' of dominance but more experiments were needed to test this hypothesis. Later observations of mating behaviour of grass snakes in outdoor enclosures in Italy by Luiselli (1996) found that larger males achieved more copulations than smaller males and that larger females are more attractive to males than smaller females. Indeed, mating balls of grass snakes were sometimes observed.

Spermatogenesis. Postmortem examinations searched for the presence or absence of mature sperm with results shown in Table 4. The first 5 mm of the vasa differentia, immediately posterior to the testis was removed, the contents examined microscopically (x600), and classified as abundant sperm, small amounts or none.

It appeared that abundant spermatozoa was found in a few animals in the autumn so it seemed that mating was possible after emergence in spring. Results showed it was apparent that mature sperm were present in at least some snakes each month.

The postmortem results of measuring testis lengths and their mass are shown in Figure 11. Most testicular growth occurred in July and August. Then snakes entered hibernation with testes at maximum mass and length and these regressed to a minimum by early April. There was no evidence of an additional increase in size immediately after emergence from hibernation as occurred in adders living in the similar area (Prestt, 1971). The results showed only a few male snakes contained mature sperm in late summer and because all male animals in spring had abundant sperm, it seemed probable that spermatogenesis occurred mostly while the animals were in hibernation. In spring these males

Table 4. Sexual maturity in male grass snakes. Figures show the minimum length of males producing mature spermatozoa and estimated age.

Date	Length (mm)	Presence of spermatozoa	Estimated age (yrs, months)
14 Sept 1961	210	Nil	0, 1
12 Sept 1959	200	Nil	0, 1
15 June 1962	230	Nil	0, 11
22 August 1962	250	Nil	1, 0
30 May 1962	320	Nil	2, 9
29 April 1962	290	Few in testes	1 or 2, 8
21 July 1962	330	Some	2, 11
24 April 1962	420	Abundant	3 or 4, 8
10 August 1962	440	Some	4,0
17 August 1962	450	Some	4, 0
20 April 1962	460	Abundant	4, 0
13 April 1962	490	Abundant	4 or 5, 8
20 July 1962	490	Abundant	4, 11
22 April 1962	510	Abundant	5, 8
22 April 1962	520	Abundant	5, 8
1 June 1962	510	Abundant	5, 9
24 August 1962	520	Abundant	6, 0

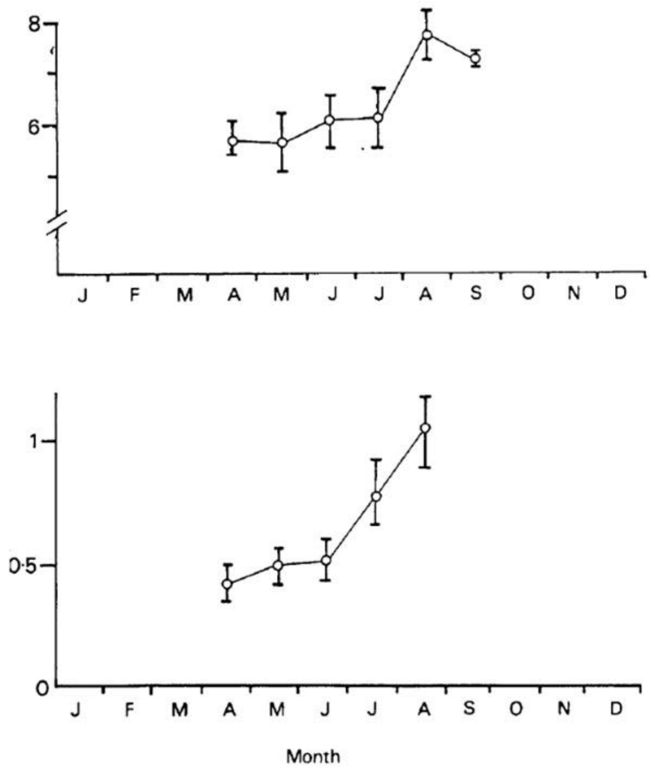

Figure 11. Changes in testis size and mass through the year, showing the variation in testis length expressed as mean percentage of the body length + SE (top) and similarly for testis mass and snake mass (bottom); n - values per month, 11 April, 6 May, 8 June, 8 July, 12 August and 2 September.

Figure 12. A pair of grass snakes (male: right; female: left) photographed soon after emergence from hibernation in Kent. Note the diminished yellow collar in the larger female (photo: Brett Lewis).

had regressed testes. According to Saint Girons (1982), spermatogenesis during the summer is the prevalent type of reproductive cycle in snakes occupying cool, temperate regions, with spermatozoa being stored in the vas deferens over the winter for use during the following spring. This was later confirmed in *Natrix natrix* from northern Iran (Faghiri et al., 2011).

Sexual maturity. With no known method of accurately ageing grass snakes in the field, the presence or absence of mature spermatozoa in the vasa differentia was compared with total body length. Postmortem examination of 17 males of different lengths showed mature sperm was present in some individuals of 290 mm length. Snakes over 420 mm all contained mature sperm. The onset of maturity usually occurs when a body length of 300 mm is reached. Nevertheless, it is unlikely such small snakes achieve successful mating (Table 4).

Confirmation of the body size at which females first breed was easier to determine than in males. Snakes that had previously bred could be separated from those about to first breed by examining reproductive tracts during postmortem. Those

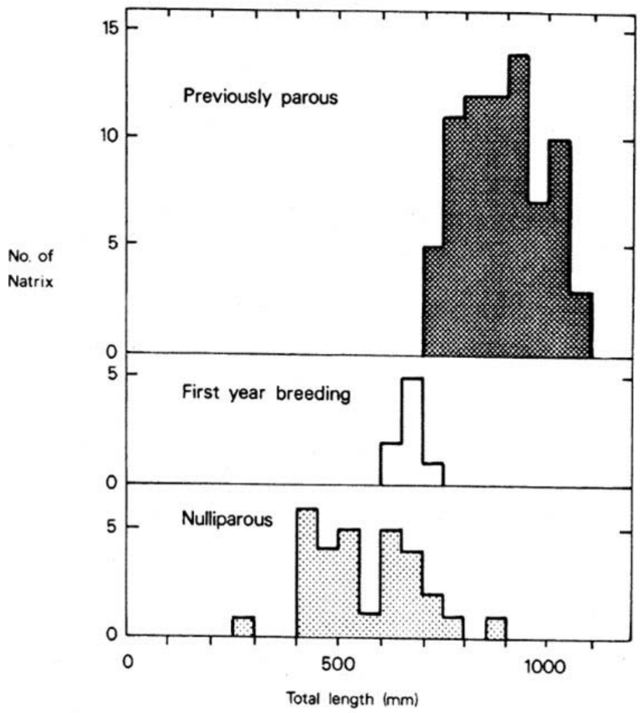

Figure 13. Size of breeding in female grass snakes determined from postmortem examinations. Figures show that all females over 700 mm length had laid eggs at least once (with the exception of one individual of over 850 mm).

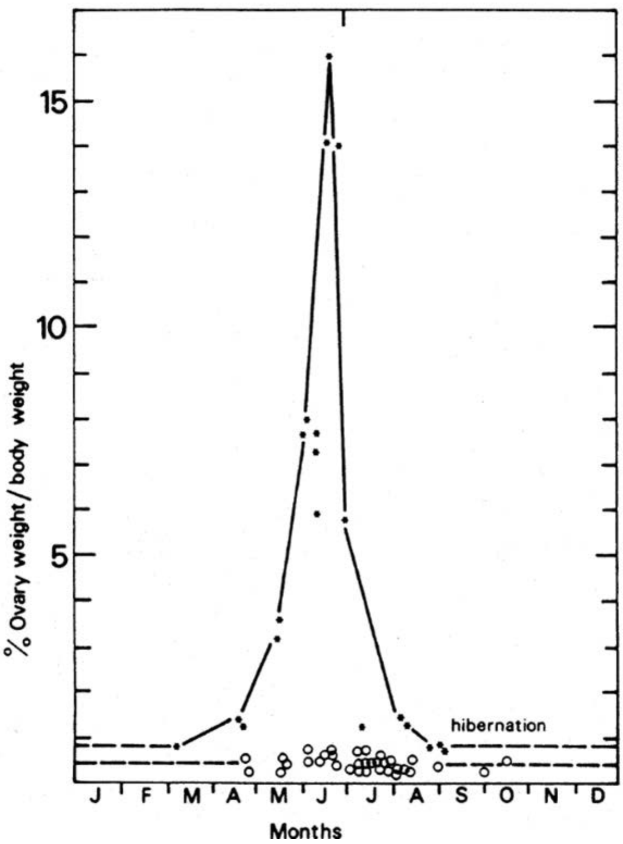

Figure 14. Results from postmortem examinations showing development of ovaries leading to egg laying. Immature females, O; parous females, *.

with large or developing ova yet having no scars or swelling in the oviducts were identified as being in their first year of breeding. As later reported by Beebee & Griffiths (2000), large, older females often had less distinct yellow collars (Fig. 12).

The results obtained (Fig. 13) indicate that snakes over 700 mm have almost always bred at least once, with four exceptions. One of 870 mm was apparently still an immature. Most snakes were found first breeding with body lengths between 600–700 mm. Examination of larger adult females suggested they probably bred every year. However, only eight females were confirmed as breeding in successive years: their first-year size was 745, 830, 880, 900, 940, 990, 1,000 and 1,040 mm and those animals grew in the second year respectively 55, 30, 20, 50, 70, 20, 50 and 60 mm. Figure 14 shows postmortem results of ovary mass indicating a rapid increase during May and June and a sudden drop after egg laying.

In Sweden, Madsen (1983) determined minimum size at sexual maturity based on the smallest individuals observed in copulation. He found the smallest sexually mature male measured 550 mm

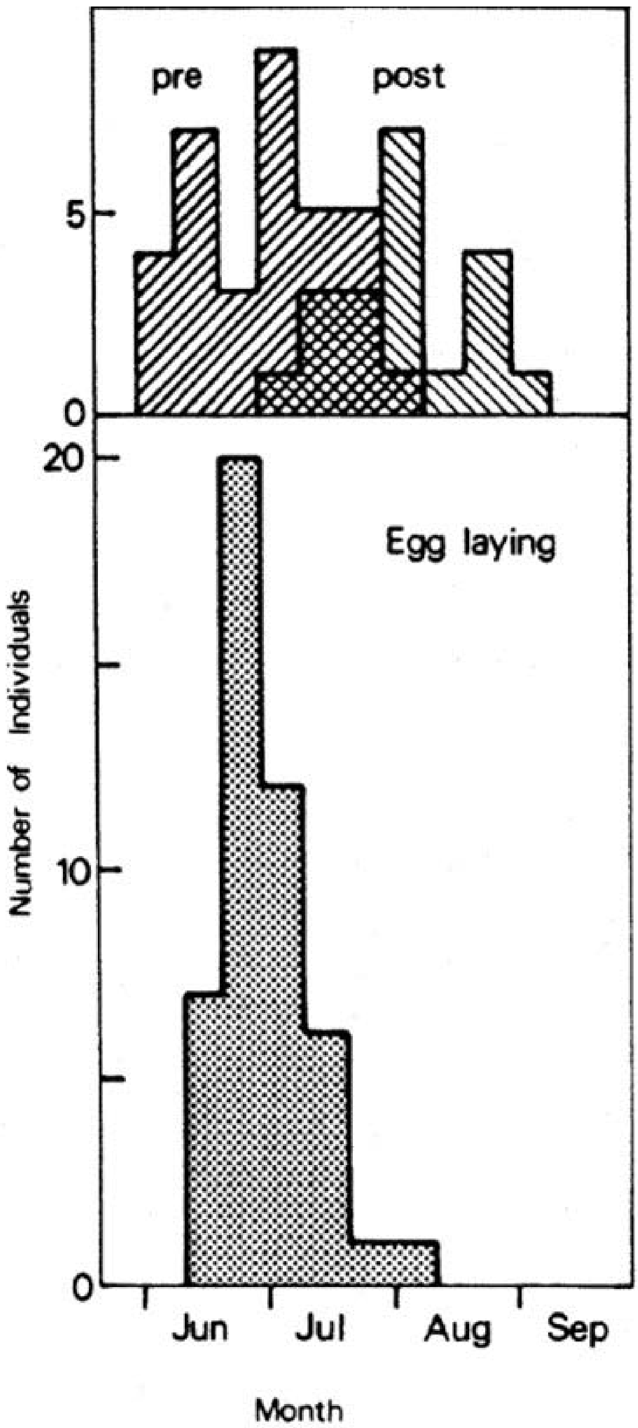

Figure 15. Dates of egg laying as found with before and after captures of individual female grass snakes, as well as those in process of laying.

and was 3 years old, while the smallest female laying eggs was 680 mm and was 4 years old. The snakes in Madsen's more northerly study area appear to be rather larger for a given age than those reported here and may have lived for 10 years or more. In Italy, Luiselli et al. (1997) observed that female grass snakes reached sexual maturity at 700 mm and an age of 6-8 years.

Egg laying. Female grass snakes were examined throughout the year and their breeding status recorded. Snakes caught away from the known egg laying site were recorded in the pre- or post-natal condition and enabled the approximate date of egg laying to be determined. Precise dates were obtained for animals caught while egg laying (Fig. 15).

Most captures of snakes laying eggs were in the last ten days of June. Some were found to retain a few eggs to the autumn and in one case to the following year. These individuals appeared to be unhealthy and possibly egg-bound. One individual laid 22 eggs (mass 146.7 g) but retained a further 7 eggs.

Throughout this study only a small number of eggs were found in locations which could be regarded as 'semi-natural'. Sixteen eggs were found in a stop-cock hole at Corfe Castle water-works laid on 10 August, and 15 were found beneath a stone on 5 August (Fig. 16). The only known egg laying places were sawdust, leaf compost and cattle manure heaps. At the Research Station where the gardener placed grass mowings and autumn leaves twelve batches of eggs were found laid in June and July 1961 and 1962. Only the large and historic sawdust heap at Creech (35 m^2) was used by many snakes each year. Fresh sawdust was added regularly from the adjacent sawmill. This heap had been present for at least 150 years. At the time of this study, old wet sawdust was covered with a layer of damp sawdust approximately 70 mm thick and topped with a 20 mm dry layer of fresh material. Much of the pile was covered with bramble (*Rubus* sp.) amongst which sloughed skins became entangled just before the egg laying.

Gravid females moved into the 1 m tall vegetation which encircled the sawdust, then after sunning for one to two days they sloughed before burrowing into the heap (Figs. 17 & 18). Holes excavated

Figure 16. Clutch of eggs found laid under a stone in the snake enclosure.

Figure 17. A large (1.1 m) gravid female grass snake photographed in 1962 and about to lay eggs in the large sawdust heap.

Figure 18. A large (1.01 m) female photographed while actively hunting on the edge of a Scots pine plantation. This individual was captured five times and quite docile – this photograph was taken by RES lying flat on the ground just half a metre from her nose. Two days later she had moved 1.1 km and was observed at the sawdust heap.

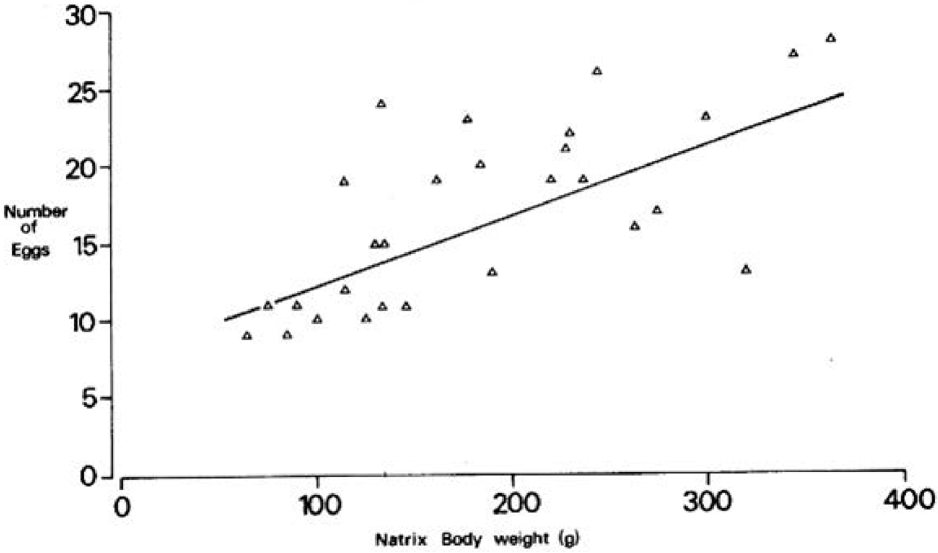

Figure 19. Relationship between body weight and number of eggs laid. The number of eggs were palpitated as the individuals arrived at the egg laying site; n = 28.

by small mammals were used sometimes but often the snakes used their snouts to push into the substrate. Once inside they penetrated to a depth of 200–500 mm which in hot weather could reach 35 °C. Some individuals created a chamber in which the eggs were deposited while others either doubled back on themselves creating a double 'snake-width' tube and a few laid their eggs in a single line. These observations were discovered by subsequent excavations when egg laying was complete.

The temperatures were recorded at various times in the egg laying period and subsequent days. There were higher temperatures with depth and the highest ones, up to 40 °C, being recorded in very hot weather. Temperatures were taken of the eggs nearest the surface and deepest in the heap on 3–4 August 1961 at 16:00 hrs GMT. Both days were hot and sunny with shade air temperatures of around 23 °C. On 3 August temperatures around the eggs ranged from 28.1–33.5 °C and on 4 August 32.3–36.8 °C. Since these temperatures were recorded after a period of warm weather it could be expected that much lower temperatures would be found in cool wet weather. Also, these high temperatures were recorded on the open south side of the heap most exposed to the sun and where many snakes chose to lay their eggs. But others laid on the shady north side which was covered in thick vegetation inevitably would be much cooler as so little of that surface received direct sun.

When the gravid females were at the egg laying site it was possible to palpate the number of eggs present and relate those to the total body mass (Fig. 19). For a given body mass there was a wide variation in the number of eggs to be laid. For example, two females of 135 g mass contained 11 and 24 eggs respectively.

A batch of 25 eggs laid by a 950 mm long snake ranged from 32 x 18 mm diameter (5.55 g) to 25 x 17 mm diameter (3.63 g) - mean 28.7 x 17.4 mm (4.54 g). A young animal 760 mm in length laid 14 eggs ranging from 28 x 18 mm (3.75g) to 24 x 15 mm (2.49 g) - mean 27.4 x 16.2 mm (3.0 g) (Table 5). Most females having laid eggs moved quickly away but a few remained at the sawdust heap throughout July.

Table 5. Number and mean weight of eggs from three females each laying late in season.

Field number	Length (mm)	Body mass post-laying (g)	No. of eggs	Mean mass of eggs (g)	Length/body mass	Date of egg laying
N388	970	168	29	6.7	5.77	19 July 1962
N373	950	137	25	4.5	6.86	5 August 1962
N415	760	77	14	3.0	10.0	7 August 1962

Figure 20. Hatchlings collected earlier in the day being released in the evening after processing in August 1962. Hatchlings were released into cover at dusk to protect them from predation by peafowl which went to roost at sundown.

Egg incubation. In July 1962 some incubation experiments were attempted. The precise date of egg laying was not often known for those collected, but eggs were transferred to a controlled temperature incubator where a variety of substrates were provided to maintain appropriate humidity. Three substrates were selected; decaying sawdust from the heap and around the laid eggs, sphagnum moss and filter paper saturated with water. The results suggest the substrate was not critical to hatching success providing high humidity was maintained. Many eggs placed in the incubator at 25 °C on 25 July died probably due to dehydration.

Six eggs from one female placed on sphagnum moss at 26 °C all hatched within 15 hours of each other. Two batches of 15 and 6 eggs kept on sawdust and filter paper at 33 °C hatched after 19 and 20 days respectively. However, the exact date of laying was not known but eggs were believed to have been laid within five days of the start of the experimental conditions.

These experimental results were similar to the field observations. The Creech sawdust heap was visited daily from mid-June to late August in 1961 and 1962. The earliest newly hatched snake was found on 23 July 1961 but first hatching period was from 1st and 2nd August. Most hatching occurred from 5–25 August and in the peak period from 8–17 August 1962, searches were made about every two hours throughout the day from dawn to dusk. All hatchlings were caught and removed for observations and measurements (Figs. 20 & 21). Few snakes were found in the morning but most were seen in mid to late afternoon when sawdust temperatures were highest. On cold and wet days few snakes were found. Unfortunately, it was not possible

Figure 21. Hatching of a grass snake in process. Note the white tip to the tongue which disappears within a few days of hatching.

to reliably quantify results because of severe predation by some 60+ domesticated peafowl, of which up to 25 at a time would stand on and around the sawdust heap. Clearly, they were eating the snakes as soon as they appeared.

The median date of egg laying was 27 June (n = 47) and the maximum numbers of young were encountered between 8–10 August some 42–44 days later. Hatching continued throughout August and probably well into September but observations could not be maintained. No adult was found on the sawdust heap when hatching was in progress.

The provision of artificial oviposition sites for grass snakes is increasingly being recommended as a measure to compensate for the loss of natural sites. The current study clearly shows that sawdust heaps are highly attractive as egg laying sites for female grass snakes. Recent research has shown that both the incubation medium and temperature profile have implications for hatchling grass snakes. Löwenborg et al. (2012) showed that hatching success was higher (71%) in eggs placed in manure heaps than compost heaps (43%). The temperatures of manure heaps were generally higher and more stable and resulted in earlier hatching. Equally, incubation temperature has been shown to influence size at hatching, colouration and behaviour of the hatchlings (Townson, 1990; Löwenborg et al., 2012; Hagman et al., 2015).

Although it is difficult to compare the temperatures measured in the sawdust heaps to those used in more experimental studies, the estimated hatching time of 42–44 days is similar to that observed by Townson (1990) under optimal temperatures of 27–28 °C. Temperatures higher or lower than this may result in reduced hatching success or hatchling fitness (Townson, 1990; Löwenborg et al., 2012). Likewise, in Italy most female grass snakes laid eggs in the second half of July and

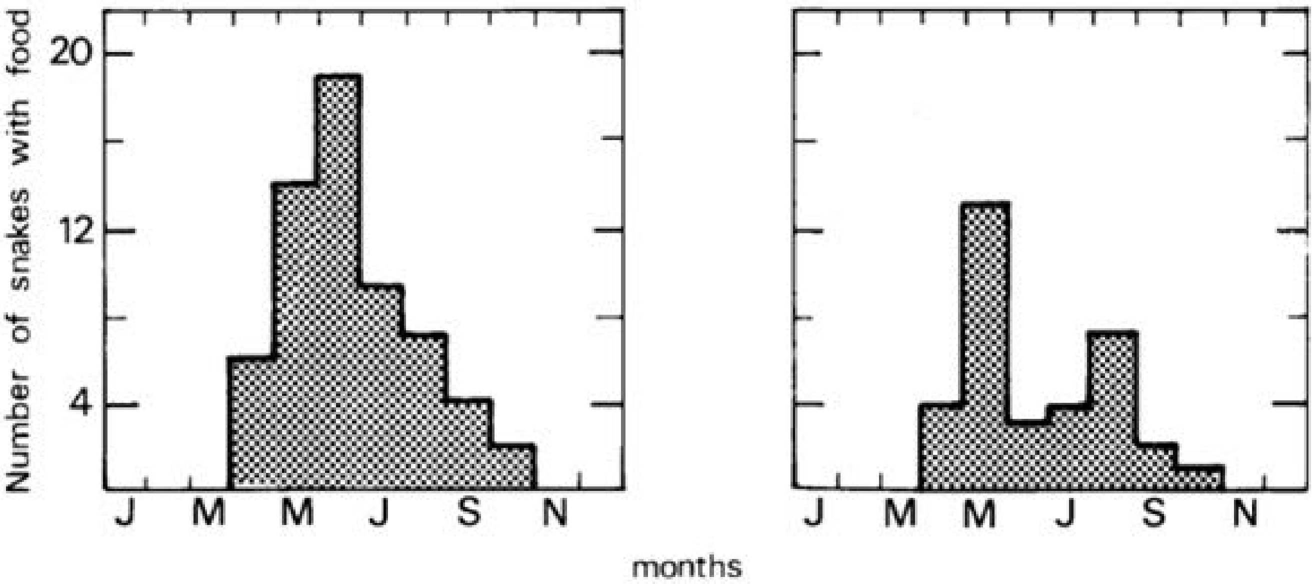

Figure 22. Feeding pattern in adult grass snakes. Number of individuals captured either actually feeding, by palpation or regurgitation. Females (left), n = 61; males (right) n = 43.

hatching occurred between 22 and 45 days later under natural temperatures (Luiselli et al., 1997).

Observations on eggs hatching. In August 1962 a batch of eggs was extracted from the sawdust heap and taken back to the laboratory so the process of hatching could be observed in detail. The eggs had been deposited in partially decaying sawdust at a depth of about 200 mm deep. They were placed on a 30 mm depth of sawdust in a glass aquarium about 450 x 300 x 300 mm high. A glass lid was provided to maintain humidity, the contents having been misted with water. The room had no window and the only light was placed beneath the bench so the room was at very low reflected lighting, just enough to observe progress. The room was maintained at about 28–30 °C. It was realised most hatching at the sawdust heap would occur in complete darkness.

A single batch of 23 eggs was introduced and initially observations were made at about three hourly intervals through the day and night. On the third day at around 18:00 hrs the first signs of hatching were seen. Two eggs had cuts through the parchment-like shells. At that point observations were made continuously for about 25 hours. The first signs of hatching were periodic slow movements within the shell. After varying times, the snake made sudden thrashing movements resulting in cuts through the shell made by its lip ‘egg tooth’. These violent movements were at intervals of between a few minutes and half an hour. Eventually a nose would be pushed through one slit often as far as the eye. Again, at widely varying intervals the snake would flick out its white-tipped tongue and pause. Then with no warning the snake emerged in a single sudden movement completely free of the egg in less than a second. Photographs were attempted using a non-reflex camera using PF1B magnesium flash bulbs, available from the 1950s and the original Kodachrome film ASA 10.

Table 6. Prey items eaten by grass snakes. Records from field observations (mostly resulting from regurgitation) and 112 postmortem dissections, 1958-1962. Common toads were abundant throughout the study areas but common frogs were very rare and confined to one pond after 1961.

Prey species	No. of snakes
Common toad (adult)	131
Common toad (toadlet)	7
Common toad (tadpoles)	7
Common frog (adult)	1
Common frog (4 froglets)	1
Palmate newt (adult)	7
Minnow (5-6 in 1 snake)	1
Goldfish (many in 1 snake)	1
Common roach	1
Unidentified shrew	1
Harvest mouse	1
Field vole	3
Nightingale (4 nestlings in 1 snake)	1
Unidentified bird (adult)	1
No discernible food	667

Feeding and fat bodies

Diet. Feeding occurred throughout the year from the beginning of April until October with most food items being taken in May (Fig. 22). Common toads *B. bufo*, which appeared to be the most abundant amphibian around the former clay extraction ponds, formed the most important element of the grass snake diet. Fish, bird and mammal prey were recorded on a few occasions suggesting grass snakes are opportunistic feeders on vertebrate prey (Table 6). No reptile prey was eaten despite the presence of all six native species living in the study area. Common frogs *Rana temporaria* were absent from the Creech area until their deliberate introduction by others in 1961. A batch of frog spawn was brought from the River Frome water meadows at Wareham. The adult bird appeared to be a finch and may have been eaten as carrion but the nightingale nestlings *Luscinia megarhynchos* were probably eaten out of the nest which is often on the ground (identification confirmed by A Bell and I Prestt). Some food was taken by adults of both sexes in April during the mating period but males ate rather less often. It appeared no food was consumed just prior to shedding or by gravid females which were about to shed and lay eggs. These gravid snakes were found to contain food and palpable eggs until 22 June, while still away from egg laying sites but from 22 June to 24 July a total of 48 females containing eggs were found on the sawdust heap, although none had detectable food. After egg deposition feeding commenced immediately.

Juvenile snakes less than 300 mm long were found feeding on tadpoles and metamorphosing toadlets in and around the edges of the ponds.

Snakes containing newly swallowed food found it difficult to move and escape capture, and when caught often they regurgitated the food. Because they are vulnerable at that time they lay out in as much sun as possible to help accelerate the rate of digestion. It was noticeable that when the body was distended by food the skin which shows between scales is matt black and hence helps absorb heat. One snake had a throat temperature of 31 °C while lying out in the sun with an air temperature around it of 18 °C. Observations suggested an adult toad took about one week to digest. A few snakes appeared to contain undigested food throughout hibernation, presumably because temperatures in winter were too low for digestion.

Fat body. The postmortem mean fat body mass results are shown in Figure. 23. In males, two

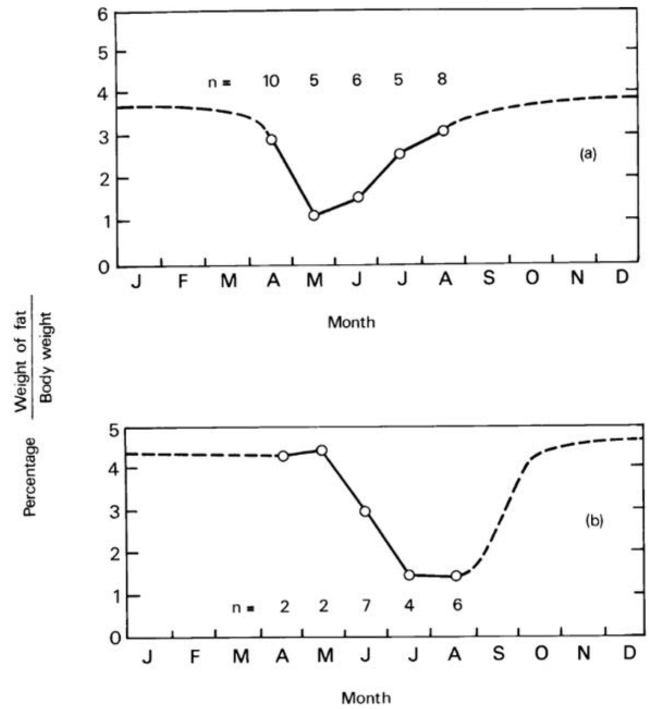

Figure 23. Fat body mass changes throughout the year from postmortem examinations; **(a)** adult males; **(b)** adult females. Dashed lines suggest patterns of change while in hibernation.

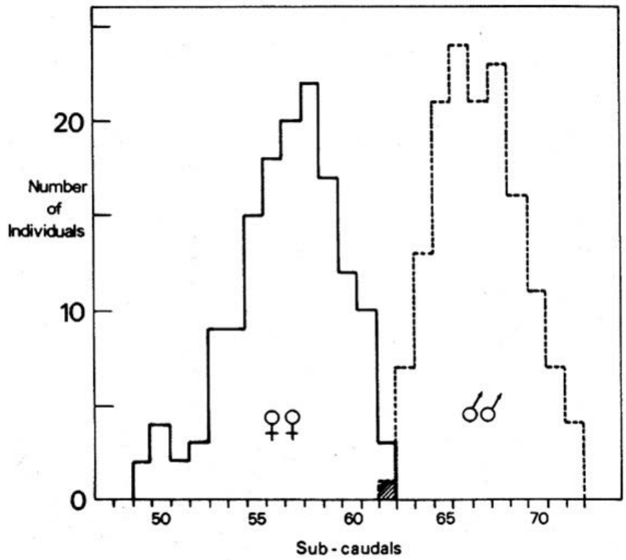

Figure 24. Identification of sex by counting subcaudal scales of adults (n = 390). Males also exhibit post-cloaca swelling due to hemipenes and females a post-cloaca tapering of the tail.

thirds of fat body mass is lost between April and May. This mass loss was probably due to mating activity when little food is taken. In the same period females showed little change. Males feed throughout the rest of the active season. Adult females, however, lost fat from May until July presumably due to conversion of fat to eggs. Although not recorded, it appeared rapid replenishment of fat must occur in August and September before hibernation because the females are ready again for breeding by the following spring. This was in contrast to the adders living in the similar area which generally took a year to recover after breeding (Prestt, 1971).

Three decades after the current study Reading & Davies (1996) observed that the diet of grass snakes at the same site was predominantly toads. Feeding mainly occurred between May and September with large toads eaten approximately every 20 days. In Kent, Gregory & Isaac (2004) also found that the diet of grass snakes was mainly anurans but primarily comprised non-native marsh frogs *Pelophylax ridibundus*. As observed here, Brown (1991) found that the activity of grass snakes is much reduced immediately following consumption of prey.

Population characteristics

Sex ratio. Field-caught adult grass snakes showed a bias towards females with 173 males to 217 females but examination of 292 hatchlings examined showed equal numbers, 148:144 males to females respectively. Sexing was based on the presence or absence of hemipenal swellings and by the number of subcaudal scales (Fig. 24). Two females exceptionally had counts of 63 and 65 but most were less than 62.

Population size and density. At Creech a total of 229 adult snakes (over 400 mm body length) were marked by the end of 1961. Of 174 adult snakes caught in 1962, 37 were already marked. This suggested an approximate population estimate of adult grass snakes of 1,076. These adults occurred in about 300 ha of the study area. This suggests an adult population density of about 3.6/ha. Because the sex ratio at hatching is equal there were an assumed 538 females and if each laid 17 eggs then a total of over 9,000 eggs being laid each year might have been expected.

Mortality. Grass snakes were killed accidentally and deliberately. Farm machinery, especially grass cutters and road vehicles caused the death of many snakes each year. All species of snake including grass snakes were often deliberately killed by people living in the area. In addition kestrels *Falco tinnunculus*, marsh harriers *Circus aeruginosus* and buzzards *Buteo buteo* consumed some annually, while the hatchlings emerging from the sawdust heap were eaten in large numbers by domestic peafowl.

Different methods can yield different estimates of population size and density, yet some comparisons with more recent studies are possible. Although the population estimate for Creech was about three times larger than that estimated by Mertens (1995) for a site in central Germany, the population densities quoted are remarkably similar (i.e. both 3.6 snakes/ha). Rather higher population densities of 4.8–52.4/ha were reported at a grass snake population in eastern England which was apparently growing in response to an increase in amphibians (Sewell et al., 2015). However, some density estimates may be misleading given that grass snakes are highly transient and may not take account of the total area over which they range. It is difficult to translate observations of predation into estimates of annual mortality, although the present study suggests high mortality of hatchlings by peafowl. In Sweden, Madsen (1987) suggested that the mortality rate of juveniles was lower than that of adults, while Sewell et al. (2015) modelled the mortality rate of adults as 0.44 per year. This estimate is similar to that modelled for another large population in the same region, although diseased snakes suffered much higher mortality (Allain, 2022).

Size and fecundity. Dissections of 27 gravid females showed there was a positive relationship between body mass and increasing clutch size, (Fig. 19). There was a similar correlation between the number of follicles and body mass.

Size at hatching. From 8–17 August 1962 hatchlings were caught and sexed from Creech sawdust heap and their tail and body lengths recorded. There was no significant difference in sex ratio as they emerged, but larger snakes tended to hatch earlier than small ones. This difference may be related to the more experienced females laying larger eggs earlier in the season or perhaps they lay their eggs in warmer conditions so the eggs develop quicker. Only three batches of eggs were weighed and measured from known individual females. Average mass of eggs from the largest female was more than twice that of the smallest snake. There was no significant difference between the mean size of males and females on hatching although males were up to 6 mm longer than females. Both sexes showed a

Table 7. Mean annual growth rates for grass snakes 1958–1962.

Initial body length (mm)	Males (mm)	Females (mm)
200–400	80 (n=1)	45 (n=2)
401–600	39 (n=6)	55 (n=6)
601–800	33 (n=10)	57 (n=11)
801–1000	21 (n=1)	36 (n=14)
1001–1200	/	40 (n=2)
Mean growth rate	37 mm/yr	47 mm/yr

wide variation in length, 137–183 mm for males (n = 186) and 140–177 mm for females (n = 204). Tail/body length ratio was not a reliable method for sexing grass snakes although males tend to have relatively longer tails.

Annual growth. Of 181 male grass snakes measured in the field only 18 were recaptured a year later. The average growth rate appeared to drop with increasing size and overall they grew 37 mm per year (Table 7). A total of 235 females provided just 35 growth rates when caught a year apart. Their overall growth rate of 47 mm per year was significantly faster than males, ($P < 0.05$) (Table 7). With these average growth rates, males would be 13.5 years old when they reach 700 mm in length but females would be 10.5 years old. These compare to estimates of snakes of 700 mm being about 7–8 years for males and 3–4 years for females in Madsen's (1983) study in Sweden. At the Cotness site there was a relatively enormous grass snake which evaded capture. It was estimated to be around 1,400 mm in length and of a considerable mass compared with the largest other specimens in that area. Grass snakes of similar size or larger had been caught in other places in England (Smith, 1951).

Growth rates appear to be slightly slower than those provided by Madsen (1983), although both studies show growth rate slowing with age. Comparisons of sizes of snakes between different studies is confounded by potential biases caused by sampling time and/or sampling method, as well as differences in the methods used to take measurements. Likewise, other long-term studies of grass snakes have also yielded differences in size trends over time. For example, an overall decline in body size accompanied by a shift in fewer females was observed over 40 years in Poland, while an increase in body size and fewer males was observed over 60 years in Switzerland (Palmeheden, 2022).

DISCUSSION

Grass snakes are secretive and flighty reptiles that are difficult to observe in nature. Consequently, methods for studying natural populations have developed over time with increasing emphasis on the use of Artificial Cover Objects (ACO) to detect individuals, and radiotelemetry to monitor movements. Such methods had not been widely developed at the time of the current study which relied on capturing free-ranging snakes and the use of snake traps. Nevertheless, the intensity of the sampling using these methods has resulted in some new insights into grass snake natural history. Although more recent studies have confirmed that the wide-ranging and highly seasonal movements of grass snakes observed here are fairly typical, we are unaware of any other studies that have documented movements of up to 4 km within four years.

The current study used scale-clipping as a method to identify individual snakes. This method was first described and applied to grass snakes by Carlström & Edelstam (1946), who also pioneered photographing the ventral pattern as an alternative and less invasive method. Madsen (1983) found that scale clips could result in rapid regeneration so advocated recording the ventral pattern instead, but scale clipping has continued to be used in some more recent studies (e.g. Mertens, 1995; Bury et al., 2022).

The timings of emergence and entry into hibernation, seasonal behaviour and egg-laying in 1958-1962 generally correspond to more recent observations of these activities suggesting that there have been no clear shifts in the face of climate change over the decades. Nevertheless, there may be climatic impacts on annual survival. Using a 68-yr dataset from Sweden, Elmberg et al. (2024) showed that milder winters with less insulating snow cover resulted in lower survival of grass snakes through hibernation. Although this was partly offset by increased survival during the summer months over the same period, overall annual survival decreased.

Two fundamental requirements for viable grass snake populations appear to be suitable egg laying sites and appropriate food resources. Although the sawdust mounds that clearly generated large numbers of hatchlings in 1958–1962 are no longer present, the water bodies still persist and local fishermen still report sightings of grass snakes (see below). Indeed, Reading & Davies (1996) reported the grass snakes feeding on toads

Figure 25. The study site in March 2025. Two views of large field (c.4.5 ha) 400 m north of former sawdust heap showing cattle grazed pasture and clumps of rushes.

Figure 26. Google Earth image showing the main pond and surrounding habitat today (c/f. Fig. 1).

at the same site three decades on from the present study, and the relationships between buoyant amphibian populations and grass snakes are well-described (e.g. Luiselli et al., 1997; Gregory et al., 2004; Sewell et al. 2015). Although there is a long history of records of grass snakes using anthropogenic oviposition sites - such as manure and compost heaps, and even warm ovens – identifying natural egg laying areas remains a challenge.

Population characteristics, such as sex ratio and size and age structure, are difficult to compare between populations because they depend on the methodology used to detect snakes. Different sizes and sex ratios may be observed at different times of the year. Likewise, the behaviour – and consequently the detectability – of snakes will vary according to size and age and may also be influenced by predation pressure and habitat structure.

THE STUDY SITE 60 YEARS LATER

A visit to the original main study area was made by RES on 3 March 2025 (Fig. 25). Although some areas could not be accessed, examination of recent aerial photographs helped interpret possible changes (Figs. 25 & 26). As would be expected, trees after over 60 years growth were generally much larger including some former hedgerows which are now belts of trees. Woodlands are generally of similar area but the conifer plantations have been removed and mixed scrubby woodland is developing.

The whole area of the former sawmill and other buildings in that area have been developed and the area once having the sawdust heap with brambles and rank vegetation is now a well-maintained formal garden. Former semi-derelict farm buildings have been rebuilt with development of large new agricultural barns.

Further afield about 12 former, mostly short, field boundaries have been removed and hedgerows better managed from an agricultural standpoint. Field boundaries have been tidied and ditch and hedges are now narrower, typical of agricultural 'improvements' of recent decades. Small rough grazed fields with sedges and rushes are now better maintained grass paddocks, mainly for ponies.

The three ponds remain but it was not possible to visit the central 'Lily Pond' which was the principal toad breeding site. Aerial photos suggest that pond is similar to its former area and vegetative cover (Fig. 26). The largest 'Breach Pond' appeared similar to its former condition. Two fishermen who both had fished there for just over 40 years said they see grass snakes swimming across at intervals and did not have a view as to whether the frequency had changed over the years. The big change has been the introduction of various fish species. Nothing is known of what might have been there 60 years ago, but since a fishing club obtained control perch, tench and carp as well as pike have been introduced deliberately or in the case of the latter, by someone to upset the fishing club! There used to be several species of water bird such as coot, moorhen and mallard but now cormorant are resident presumably feeding mostly on the fish as reported by the fishermen.

The heathlands to the north and west that surround the study area appear unchanged, but that to the east has been subject to more ball clay mining. Former heathland that was partly growing on former clay quarries and spoil, have been reclaimed as poor-quality grass fields.

In conclusion, it appears most of the habitat components of 60+ years ago remain in the area. Although the key habitat of the egg-laying site has gone it seems the amphibian breeding site remains. Although it appears that there is no systematic monitoring of the study area, according to Amphibian and Reptile Conservation there are scattered records of grass snakes across the study area over the past 30 years with a concentration in the north-west sector (although this concentration may represent a geographical recording bias). Although current egg laying sites in the area are unknown, the apparent persistence of a population after sixty years despite some habitat changes within the landscape is therefore encouraging.

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