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USE OF RADIOTELEMETRY ON SNAKES: A REVIEW

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Radiotelemetry is a useful technique for studying certain aspects of the life history and ecology of snakes. In the present paper a comprehensive overview is given of all the methodological experiences of herpetological radiotelemetry in the past 25 years. A useful guideline shows how to plan and carry out a study on snakes using this advanced method. Summaries and helpful comments are presented of almost every chapter of such a project; the possible aims of the study, the choice of the snake species in question, the selection of the study area and the different transmitters, attaching the transmitter to the snake's body, obtaining optimum results and the analysis of the results.

Separate chapters deal with the relevant technical aspects of radiotelemetry: type, size, lifespan and efficiency of the different transmitters and receivers; immobilisation of the snakes: anaesthesia and control during and after the implantation of the transmitter, cold immobilisation and local anaesthesia.

Results, which can be obtained by radiotelemetry are thoroughly discussed: location of the snakes with different techniques, details of behaviour, feeding, breeding, hibernation and habitat preference. Mathematical formulas for identifying and calculating home range size and movement are briefly referred. Concepts and solutions of biotelemetry as a useful aid for studying thermoregulation and the thermal biology of snakes is also described.

As an example, experiences from a project on a small European grassland viper (*Vipera ursinii rakosiensis*) are presented in order to illustrate problems and practical solutions when carrying out a radiotelemetric study.

Two tables on the radiotelemetric studies carried out on snakes further complement the review.

Key words: herpetological radiotelemetry, biotelemetry, anaesthesia, location, home range, thermoregulation, snakes, *Vipera ursinii rakosiensis*

INTRODUCTION

Until the beginning of the 70's only little information could be gathered about the biology, life history, thermal and territorial ecology, and behaviour of free living snakes. A revolutionary breakthrough was gained by the introduction of radiotelemetric techniques. The first such studies on snakes investigated the factors regulating their body temperature (MCGINNIS & MOORE 1969, OSGOOD 1970). Some months later FITCH and SHIER (1971) reported on radiotelemetric studies on 67 individuals of 8 species. The transmitters used were relatively heavy, with a short distance operation and lifespan. By continuously improving the technique it became possible to monitor the snakes' activity during a longer period. Even today, however, because of the large size of transmitters (relative to the animal's body), radiotelemetry is generally considered more useful for large species. Its efficiency, precision, low time and energy requirements, and the fact that it can produce results on species otherwise very difficult to study, makes the dispersion and further development of the method more justified. In North America, species of *Crotalus*, *Agkistrodon* and *Nerodia* (JACOB & PAINTER 1980, LANDRETH 1973, MOORE 1978, REINERT & CUNDALL 1982, REINERT & ZAPPALORTI 1988) have mostly been studied by radiotracking. In the genus *Sistrurus*, only a large species (*Sistrurus catenatus*) was studied by telemetry (REINERT & KODRICH 1982). In Japan, *Trimeresurus flavoviridis* (WADA *et al.* 1971); in Costa Rica, *Lachesis muta*; in Peru, *Bothrops atrox*; and in Europe, mainly *Natrix* (HUEY *et al.* 1989, MADSEN 1984, MERTENS 1994), *Coronella* (SPELLERBERG & PHELPS 1975) and *Vipera* species (NAULLEAU 1987*a, b*, 1989) were the objects of field investigations applying this technique. For a more detailed summary of radiotelemetric studies carried out on snakes, see Tables 1 and 2.

The present paper gives a comprehensive overview of all the methodological experiences of herpetological radiotelemetry in the past 25 years and, at the same time, tries to give a useful guidance on how to plan and carry out a study using this technique on snakes. It is built up according to the structure of an actual project; starting at the choice of the species to be studied, the possible aims, through the choice of the different transmitters and receivers, useful hints for the application of the method, to the evaluation of the results.

PLANNING A RADIOTELEMETRIC STUDY

Why radiotelemetry?

Radiotelemetry is a useful method to get a closer view on certain aspects of life history of cryptic animals like snakes. A number of factors, which cannot be studied with traditional observation, are possible to register and measure: seasonal and daily activity pattern, home range, microhabitat and substrate preference, etc. Recording temperature data, relation and regulation of the snake's body depending on the ambient temperature can be clarified. Thermoregulation and activity patterns might lead to intra- and interspecific niche-segregation (MOORE 1978). With the ability to follow snakes almost under any circumstances, data on feeding, digestion, shedding, mating, etc. can be gained, together with behavioural patterns of all these phenomena (REINERT *et al.* 1984).

Selection of the species

The choice of the species to be radiotracked and the method to be used depends on the purpose and the limitations of the study. If the purpose is not the monitoring of a particular species, but rather to test the method itself that we wish to apply, then it is best to select a common, large snake species. The larger the body size of the animal, the easier it is to get good results (BROWN & PARKER 1976, CIOFI & CHELAZZI 1991, MCGINNIS 1976, NAULLEAU 1973). On the other hand, if the species to be studied is already selected on other basis (e.g. taxonomic reasons, nature conservation projects, etc.), and it is relatively small, the availability of the appropriate equipment is necessary to be carefully considered.

Selection of the study area

Some of the physiology-related factors like feeding, digesting, mating, change of body temperature have mainly been studied in terraria or enclosures (FLEURY & NAULLEAU 1987, NAULLEAU 1973, 1979). Observing thermoregulation of snakes, however, can easily be realised under natural circumstances as well, provided that automatic data recording is available. Daily activity pattern of the animals can be recorded both in enclosures and in the field. Seasonal activity pattern, on the other hand, is best to record in natural circumstances, since it is effected by a number of factors, which are difficult to reproduce or forecast. There are studies dealing with the use of artificial hibernating and hiding places (FLEURY & NAULLEAU 1987). Special questions, such as orientation of snakes, should be answered with specially planned experiments (e.g. LANDRETH 1973).

Selection of the radiotelemetric equipment

What do we want to study? – The first thing that has to be decided is the aim of the study. Do we want to locate the movements of the snakes, measure their home range, daily activity pattern, or some physiological parameters, or maybe all together? In order to get data about the home range it is appropriate to select a simple, cheap and small transmitter, whereas physiological records can only be gained through the application of more complicated, heavier, advanced systems. If the purpose is to monitor body temperature, the type and the fixing of the transmitter is an important matter, influencing the nature of data.

If the aim of the study is just to follow the snake, a single-staged transmitter with triangle-shaped signal is good enough for this purpose. The length of the signal of these transmitters and the pause in-between cannot be identified precisely – so there is no possibility to code more information than location. A two-staged transmitter is recommended for the collection of biotelemetric data. This type of transmitters has a so-called quadratic signal, i. e. the length of the signal and the pause can be precisely identified. Additional information can be gained by measuring these time intervals. Depending on the physiological factors to be studied a transmitter with only two pause values (so-called digital transmitter) can also be used. The disadvantage of this type that it can only register two different states (e. g. "standing – laying", "motion – still", "live – dead" states). Its use on snakes due to their anatomy is quite limited. Only one study has found this transmitter type useful to define the habitat selection of the North American *Thamnophis elegans* (HUEY *et al.* 1989). When the animal was moving, the signal impulse was doubled, so movements and resting could be identified. Sensors (called digital mortality sensors) detecting long lasting pause in motion can be used to observe the beginning and the end of hibernation (FUISZ 1995).

Much more widespread are the so-called analogue transmitters, which have continuously changing signal parameters according to the factor they measure. Body temperature, heart rhythm, etc. of the snakes can easily be recorded in this way.

The size of the transmitter and of the snake – Most of the investigators recommend a transmitter that does not infer the normal mobility of the snake. A limit value of about 4–5% of the body mass is generally given (REINERT 1992, SECOR 1994, WEATHERHEAD & ANDERKA 1984), but in the case of smaller species length and width of the transmitter can also be important. For a small, slender snake the transmitter should be accordingly slender (WEATHERHEAD & ANDERKA 1984). Our experiences also show that even if the transmitter is less than 4% of the body mass, having a large diameter object under the skin can cause intolerable inconvenience to the snake.

It is suggested to apply as small transmitters as possible. Table 1 shows this relation in the past 25 years. Although a decrease in the relative transmitter size could have been expected, this is not the case undoubtedly due to unavoidable technical reasons.

The lifespan of the transmitter and the length of the study period – Because of the high price of the transmitters, the troubles caused by the implantation, and the life cycle of the snakes, every scientist would like to use the equipment they purchase as long as possible. Unfortunately, the smaller the transmitter (including batteries), the shorter is its lifespan. In the case of large snakes the size of the transmitter is a less important factor, but in small vipers it is difficult to find an appropriate transmitter, which gives signals safely and long enough. The lifespan of a transmitter – the amount of energy it uses – depends primarily on its type (whether single- or two-stage), the strength of the signal, and the pulse length and pulse frequency. One-stage transmitters need lesser power supply (1.3–1.5 V), and work for longer period, accordingly. A two-stage transmitter needs more than double amount of power (3–3.6 V), but its lifespan is considerably shorter. The stronger the signal we want, the bigger power is needed. In order to increase the lifespan of the batteries, a signalling combination of short impulse – long pause is favourable. A more advanced method is a transmitter with a miniature,

Table 1. Types and sizes of transmitters used on snake species.

Types	Weight [g]	Size [mm]	Frequency [MHz]	Transm. weight/ body weight [%]	Operational life [days]	Reception range [m]	Type	Manufacture	Authors
No type	11	13×35	26.87–26.94	7–11	40±10	–	–	–	BROWN & PARKER (1976)
SM1	2.5	25×9×8	148–149	0.9–1.0	40	150–500	–	AVM Instrument Company	CIOFI & CHELAZZI (1991)
No type	16	50×21×4	26.600–26.750	–	–	–	–	–	FITCH & SHIRER (1971)
SS–1	2.5	ca. 20	173.20–173.35	–	236	–	Simple	–	GENT & SPELLERBERG (1993)
Model T	–	–	–	–	14	–	Digital	Mini–Mitter Company	HUEY *et al.* (1989)
No type	17	60×22	27.555–27.615	12	–	–	–	Mini–Mitter Company	JACOB & PAINTER (1980)
No type	13.5	50×20	148	–	21	1500	Thermosensitive	–	LANDRETH (1973)
Short range	–	30×15	27.24	–	–	–	Thermosensitive	–	LILLYWHITE (1980)
Long range	–	–	27.24	–	–	–	Thermosensitive	–	LILLYWHITE (1980)
No type	3.5	17×12×7	27	5.4–0.9	90	50–100	Simple	–	MADSEN (1984)
Short range	–	6×16	–	–	4	–	Thermosensitive	–	MCGINNIS & MOORE (1969)
Long range	–	15×60	–	–	–	100	Thermosensitive	–	MCGINNIS & MOORE (1969)
Model SM–2	20	25×15	–	0.1	12	–	Thermosensitive	AVM Instrument Company	MONTGOMERY & RAND (1978)
No type	–	20×10	–	–	–	–	Thermosensitive	–	MOORE (1978)

Table 1 (continued)

Types	Weight [g]	Size [mm]	Frequency [MHz]	Transm. weight/ body weight [%]	Opera-tional life [days]	Reception range [m]	Type	Manufacture	Authors
BD–2GTI	1.95	19×8×6	152	1.3–3.0	133–197	600–700	Thermosensitive & simple	Holohil Systems Inc. Ltd.	NAGY & KORSÓS (1999)
No type	15	60×15.5	108	–	53	–	Thermosensitive	CEBAS*	NAULLEAU (1979)
AVM	15–20	50×15	150	4–8	28–70	–	Thermosensitive	–	NAULLEAU (1987)
No type	16–20	–	–	5.7	180–120–90[a]	200	Thermosensitive	–	NAULLEAU (1989)
No type	12–15	60×15.5	88–108	–	53	–	Thermosensitive	CEBAS	NAULLEAU & MARQUES (1973)
Long–range	12	40×15	27	2.4	–	100	Thermosensitive & simple	–	OSGOOD (1970)
Short–range	6	20×10	0.5–1.6	1.2	–	0.5[b]	Thermosensitive	–	
Model T	4–5	30×12	–	2–9	30	5–100	Thermosensitive	Mini–Mitter Company	PETERSON (1987)
CHP–2P	6.1	32×14.7×9.2	–	5	150–270	250–600	–	Telonics Inc.	PLUMMER & CONGDON (1994)
SB 2–IV	3–12	–	–	1.8–4	120–300	200–500[c] 1000–1500[d] 2300[d]	Simple	AVM Instrument Company	REINERT & CUNDALL (1982)
SM1	12–15	–	–	–	60	500	–	AVM Instrument Company	REINERT & ZAPPALORTI (1988)
CHP–2P	6.1	32×14.7×9.2	–	4.7	150–270	250–600	Thermosensitive	Telonics Inc.	SECOR (1994)

Table 1 (continued)

Types	Weight [g]	Size [mm]	Frequency [MHz]	Transm. weight/ body weight [%]	Opera- tional life [days]	Reception range [m]	Type	Manufacture	Authors
TT–IU–080	20	50×20	150–153	<4	–	200–500	Thermosensitive	G. Stuart Enterprises	SHINE & LAMBECK (1985)
AVM	20	70×12	–	–	70	–	Simple	AVM Instrument Company	TIEBOUT & CARY (1987)
Long–range	11	13×35	26.87–26.94	–	15	100	–	Made by the authors after OSGOOD (1970)	TOMKO (1972)
BD–2GT	2	16×9	152	4	–	500–700	–	Holohil Systems Ltd.	ÚJVÁRI & KORSÓS (1997)
No type	38	10×6×8	700	–	–	100	Simple	Institute for Medical Electronics	WADA *et al.* (1971)
No type	15	52×12.5	172	4	–	150–300	–	Made by the authors	WEATHERHEAD & ANDERKA (1984)

a – 6 months at 10°C, 4 months at 20°C, 3 months at 30°C
b – with an expensive antenna, 1.0×1.2×4.0 m enclosure area
c – mountainous, heavily wooded terrain
d – in flat, less wooded terrain
e – from the top of a fire tower in mountaineous country

*CEBAS Centre d'Études Biologiques des Animaux Sauvages (recent name: Centre d'Études Biologiques de Chizé – Centre National de la Recherche Scientifique).

built-in magnetic switch, and in the last few years programmable transmitters have also been introduced to the market (SZEMETHY 1995). In latter, the transmitting period of a transmitter can be pre-set with a computer according to the active life periods of the animal (i. e. it can be switched off during the longer resting period, hibernation, aestivation, etc.). For the time being, unfortunately, the precision of this type of transmitters is largely depending on the ambient temperature (about 20% deviation from the pre-set time schedule), which makes the accurate programming more difficult, and ultimately the animal could be lost. The maximal lifespan of the radio transmitters for small reptiles today are around 6–8 months (on 25°C), and this is not enough to cover a whole year life cycle. Maybe with the programmable transmitters this period can be extended, but we have not found yet any references mentioning their use on snakes.

The lifespan of the temperature sensitive transmitters highly depends on the ambient temperature (NAULLEAU 1989). In high ambient temperature these transmitters give impulses at a higher rate, requiring more power, which decreases their lifespan. A transmitter that works for 6 months at 10°C will shorten its activity to 4 months at 20°C and to 3 months at 30°C, respectively. We have experienced similar results in our study: the manufacturer gave 7–8 months as an expected lifespan at 25°C, whereas the transmitters stopped signalling after about 5 months. The only possible explanation is that during the summer at a body temperature of 30–35°C the transmitters needed much higher energy than expected (ÚJVÁRI & KORSÓS 1997).

The transmission range and the size of the study area – During a radiotelemetric study our primary aim is to find the animal with certainty, but this depends on field conditions and the behaviour of the snakes as well. In a relatively flat field, without major shading and disturbing objects, a small transmitter can produce a signal detectable from large distances. In a forest or a rocky area, however, where the signal can be reflected or absorbed by the complex structure of the habitat, it is better to use a transmitter with relatively stronger signals.

The performance of the transmitter can be improved with the appropriate length of its antenna, and the range of receiving the signals can be enlarged by using a more sensitive receiver and antenna system. With increased performance of the receiver, the effective transmission distance can be extended. A transmitter with a usual 0.5 meter transmission distance can eventually be used in an area of 1.0×1.2×4.0 m (OSGOOD 1970). The effective distance, however, depends also on the position of the animal (for more details see e.g. FUISZ 1995, MADSEN 1984, WADA *et al.* 1971).

THE RADIOTELEMETRY: TECHNICAL BASES

The receiver

A receiver of the best choice makes the work easier, the time of the localisation shorter, hence the efficiency of the transmitters bigger. It should be small, lightweight, compact, withstand water, shock and rough environmental conditions. Walkie-talkies used in early works enabled only tracking of moving animals (OSGOOD 1970). More novel instruments have a gain control to increase sensitivity, a noise filter to reduce interference, fine tuning, channel selection, etc. In some cases automatic or programmable data processing is also available. Some receivers have prefixed frequency range in which they can track a transmitter, usually burned into the memory by the manufacturing company. Frequency range was usually wide in the early receivers, meaning they had high noise ratio. New equipments, like the Telonics (Arizona, USA, type: TR-4 for 150–154 MHz) used by us have a selectable radio band width of 10 kHz, but there are also receivers with 1–2 kHz selectivity.

For biotelemetric purposes a receiver able to measure the length of and pauses between signals has to be purchased. A simple basic equipment can also be upgraded to this level by appropriate accessories. NAULLEAU (1989) for instance, used an A.V.M. LA 12 v. Custom RB 4/6 receiver with automatic data recorder to monitor body temperature. It had a limited receiving range of about 30 m radius (without adjusting the antenna). Several similar data processors (signal indicators, etc.) can be attached to the Telonics receivers as well. These assemblies are generally less expensive, and can be gradually developed to more advanced systems. When investigating home range, or simply starting a new study, it is usually enough to invest into a basic equipment, and then adopt and complete it to the special conditions of the given species. In our opinion complex receiving instruments are less exploitable for radiotelemetric research on snakes, because the specific conditions make inevitable the individual modifications.

The receiving antenna

An appropriate antenna should be selected according to the measuring methods. For tracking purposes directional H-type and Yagi antennas are a good choice. In the case of species with relatively small home ranges, there are folding or assembling models, which need little space to carry. Yagi antennas are efficient for bigger distances as well, depending on their size and the number of elements. For exact identification of the location of the animals short-distance loop antennas do their job. They are absolutely necessary if one is to follow the animal's movement precisely. We could track a burrowing viper under the ground by the Telonics RX loop antenna almost centimetre by centimetre.

In biotelemetric studies Yagi and H-type antennas are also useful if combined with direction identification. A method invented by NAULLEAU (1979, 1989) and GILMER *et al.* (1971) was an automatic data recorder attached to a Yagi antenna in the field. The original range was 200 meters, but due to the shadowing effects of field objects it decreased to 30 meters, still enough for their study.

When the purpose is definitely to collect only physiological parameters, and direction identification is not necessary, the omnidirectional whip antenna can detect a signal from a greater area. Its advantage in not disturbing the animals from a close distance is obvious (GENT & SPELLENBERG 1993, MERTENS 1994, SZEMETHY 1995). In enclosures a combination of several whip antennas can cover the whole area, depending on the performance of the transmitters. Data collection is, however, more efficient if the ground area is equipped with a loop antenna system (MCGINNIS & MOORE 1969, MOORE 1978).

When using a receiving antenna, the fact should be taken into consideration that the transmitting antenna in the snake has a horizontal position (snakes move usually along the soil surface) whereas the signal given is polarised vertically (SZEMETHY 1995). It is important to orientate the receiving antenna according to this and also to the shadowing or mirroring effect of the field objects. The wave length of the signal (calculated from the transmitting frequency, see below) gives a hint during this process. On open, plain terrain with smaller field objects than the wave length, the receiving antenna should be held in a vertical position because the objects cannot shadow or disturb the signal. In a forest, or in the field with objects of a comparatively large size, horizontal position is more appropriate to measure the horizontally polarised component of the signal (SZEMETHY 1995). WADA *et al.* (1971) used a simple television antenna which could not receive any signal in the extreme case when the animal supplied with the transmitter moved into a hole.

The transmitter

The transmitter has three main components: the signalling electric circuit, the power supply, and the transmitting antenna. The majority of its mass (60–70%) is given by the battery, the rest includes the circuit to which the short whip antenna is attached, and the plastic cover. Description of the circuit is given in various articles (IKEDA & OSHIMA 1971, NAULLEAU & MARQUES 1973, OLDERS *et al.* 1985, STEBBINS & BARWICK 1968). Different manufacturers apply various battery types. Mercury cells with 1.4 or 2.8 Voltage are widely accepted because of their high specific performance (GENT & SPELLERBERG 1993, HUEY *et al.* 1989, NAULLEAU & MARQUES 1973, REINERT & CUNDALL 1982, REINERT & ZAPPALORTI 1988). In temperature sensitive transmitters usually two pieces of 1.5 V silveroxyd batteries are built in (OLDERS *et al.* 1985, PETERSON 1987). Despite their high temperature tolerance and performance capacity lithium thionyl chloride batteries are only rarely used (3.5 V, 290 mAh, see NAULLEAU 1989, WEATHERHEAD & ANDERKA 1984), perhaps due to their price and availability.

Signalling – The transmitting circuit itself is simply an oscillator giving impulse at a certain rate on a certain frequency. Frequency stability is achieved by a quartz crystal, and defined by its geometrics. The first transmitters signalled at AM 530–1600 kHz and FM 88–108 MHz. Their drawback was the small transmitting distance, less than 1 meter. Other rarely used frequency bands were CB 27 MHz and VHF 138–174 MHz (OSGOOD 1970), having the advantage of a cheap receiver ("Walkie-Talkie"). They soon went out of fashion because these overcrowded bands have many disturbing signals, and the transmitters had a short life span. Nowadays frequencies around 150 MHz are the most widespread in the field of radiotelemetry.

To produce signals in the 100–170 MHz a very thin quartz crystal is necessary, which is vulnerable and has a weak temperature stability. To achieve higher frequency a thicker crystal is used which resonates at 49–50 MHz, and is tuned up to three times of its base frequency. Direction measuring is better on high frequencies, but penetrating through field objects is weaker. In water, on the other hand, signals at lower frequencies disperse more effectively, and 40–49 MHz is more appropriate (FUISZ 1995). WADA *et al.* (1971) in their paper published the first report about a transmitter of 700 MHz, which they could hardly follow when the snake moved into water. SHINE and LAMBECK (1985), however, had good results with a transmitter of 150–153 MHz in *Acrochordus arafurae* living in water, too.

The transmitting antenna – The length of the transmitting antenna is scaled according to the frequency of the oscillator. It should be compared to the wavelength: the closer to it the higher its performance, and the greater the transmitting distance. The formula by REINERT (1992) expresses the relation between the wavelength and the frequency of the transmitting oscillator:

Wavelength (m)= Velocity of light (300,000,000 m/s)/Frequency (in Hertz)

For example, in the case of the most frequently used 150 MHz (= 150,000,000 Hz) an antenna length of 2 meters would be ideal. This is obviously impossible (in a snake), so usually 1/4, 1/6 or 1/8 λ are chosen. This gives a more acceptable 25–50 cm antenna size, which is readily applicable in bigger species (REINET 1992, REINERT & CUNDALL 1982, SZEMETHY 1995, ZAPPALORTI & REINERT 1988).

The transmitting antennas are almost exclusively omnidirectional, flexible, teflon or plastic coated whip antennas. They are implantable into the body cavity of the snake, sometimes in the intestinal tract, when the antenna is coiled around the transmitter. Even so, an antenna in the alimentary canal disturbs very much the normal digesting process, causing vomiting or starving. The transmitter or its antenna, on the other hand, can also be damaged by the digestive enzymes (REINERT 1992). The size of the antenna implanted into the snake depends also on environmental conditions: in diverse, rocky habitats, for instance, it is recommended to use a longer transmitting antenna in order to increase the output performance. The limit is, of course, the size of the given snake species. In our case with the meadow viper of an average body size of 40 cm, the maximum antenna length with the transmitter on 151 MHz could not exceed 8–9 cm (about 20% of body length). The transmitting distance was accordingly short, although the manufacturer gave a reference to 1000 m, good quality signals could generally be received only from 200 meters. Considering the relatively small home range of this insectivorous viper, this was still sufficient for our study, however the whip antenna caused some problem for us. The antenna of the transmitter is usually a flexible plastic coated copper wire, which is put under the skin of the snake (ventral side), directed towards the head, parallel to the vertebral column. In our study about 7 weeks after the implantation, studied snakes were found in the field having pierced their skin by the blue coated antenna wires. The wire pierced the skin at about the half length of the animal, on the side of the belly, and cca. 2–3 cm length of the antenna was sticking out of the body. The snakes were otherwise healthy, with normal defending behaviour and good condition. We put the antenna back under the skin and fixed the wound with an adhesive surgical band. We think that the antenna wasn't sufficiently flexible and softly coated, this may have been the reason for the unconvenient injury of the snakes.

The cover – The cover of the transmitter should fulfil several criteria. The original material must be water resistant, strong but easy to shape, removable (in the case of battery replacement), and protective (to encapsulate the vulnerable parts of the transmitter). It is important to withstand the digestives and other body fluids in the case of intragastric and intraperitoneal insertion, and also should not cause inflammation or irritation. McGINNIS (1967) potted his transmitter in epoxy and coated with beewax film to prevent reaction of the epoxy with body fluids. OSGOOD (1970) used silicone rubber. Pure silicon and epoxy are too rigid, hard to shape, so they are often mixed with paraffin (MADSEN 1984, PETERSON 1987). This is important when one wants to replace the batteries. Some transmitters were coated with Dupont Elvax 260 vinyl acetate copolymer and paraffin (ratio 1:5 or 3:7) (GOODMAN & GIBSON 1970, NAULLEAU 1987, 1989, WEATHERHEAD & ANDERKA 1984). More recently 1:1 or 3:1 mixture of paraffin and beeswax are most widespread (REINERT 1992, REINERT & CUNDALL 1982, SHINE & LAMBECK 1985, ZAPPALORTI & REINERT 1988). Beeswax is a soft, water resistant, gentle to tissues, easy to shape, smooth material, ideal for transmitter coating. The paraffin component increases its resistance and strength.

ATTACHING A TRANSMITTER

There are several methods of attaching a radio transmitter to a snake's body (Table 2). The method to be used depends on the aim of the study, whether we only want to observe the movements of the animal, or collect physiological data as well. In the first case the transmitter can simply be attached to the skin surface, whereas in the other case the transmitter should be placed inside the body of the snake. In the following chapters the different methods are shortly described, then it continues with the problems of implantation, including immobilisation, anaesthesia, operation and post-operational control.

Apart from attaching the transmitter to the body surface, there are three different methods of "implantation" widely used in the literature: force-feeding into the stomach or gut (NAULLEAU 1979, NAULLEAU & MARQUES 1973, REINERT 1992), implantation into the coelomic or abdominal cavity (REINERT 1992, REINERT & CUNDALL 1982), and subcutaneous implantation (NAULLEAU 1987, 1989, PLUMMER & CONGDON 1994).

Table 2. Attachment and anesthesia methods during the radiotelemetric studies of different snake species.

Authors	Species	Attachment	Anaesthesia
BROWN & PARKER (1976)	*Coluber constrictor*	Palpated in the stomach + thin nylon	–
CIOFI & CHELAZZI (1991)	*Coluber viridiflavus*	Externally	5 °C refrigerator for 15 min
FITCH & SHIRER (1971)	*Elaphe obsolata* *Pituophis melanoleucus* *Coluber constrictor* *Agkistrodon contortrix* *Lampropeltis calligaster* *Thamnophis sirtalis* *Natrix sipedon* *Crotalus horridus*	Force feeding + abdominal implantation	–
GENT & SPELLERBERG (1993)	*Coronella austriaca*	Externally	–
HUEY *et al.* (1989)	*Thamnophis elegans*	–	Brevital sodium
JACOB & PAINTER (1980)	*Crotalus viridis*	Surgical implantation Force feeding	Fluothane
LANDRETH (1973)	*Crotalus atrox*	Force feeding	–
LILLYWHITE (1980)	*Acanthophis antarcticus* *Austrelaps superbus* *Notechis scutatus* *Pseudechis porphyriacus* *Pseudonaja nuchalis* *P. textilis* *Unechis flagellum*	Force feeding	–
MADSEN (1984)	*Natrix natrix*	Intrapleuro–peritoneal & subcutaeously	Ketalar, Rompun, Xylocaine
MCGINNIS & MOORE (1969)	*Boa constrictor*	Force feeding	–
MONTGOMERY & Rand (1978)	*Boa constrictor*	Force feeding	–
MOORE (1978)	*Crotalus mitchelli pyrrhus* *Crotalus cerastes laterorepens*	Orally inserted	–
NAGY & KORSÓS (1999)	*Natrix natrix*	Subcutaneously	Fluothane (4%), SBH–Ketamin
NAULLEAU (1979)	*Vipera aspis*	Force feed with mouse	–

Authors	Species	Attachment	Anaesthesia
NAULLEAU (1987, 1989)	*Elaphe longissima*	Subcutaneously	5°C refrigerator for one hour & local anesthetized by Hostacin or Laocaine
OSGOOD (1970)	*Natrix taxispilota*	Force feeding	–
PETERSON (1987)	*Thamnophis elegans*	Subcutaneously	Crushed–ice for 3–4 h
PLUMMER & CONGDON (1994)	*Coluber constrictor*	Surgically implanted in the body cavity	MS 222 + Halothane
REINERT & CUNDALL (1982)	*Crotalus horridus* *Agkistrodon contortrix*	Surgically implanted in the body cavity	MS 222 + Halothane
REINERT & ZAPPALORTI (1988)	*Crotalus horridus*	Surgically implanted in the body cavity	MS 222 + Halothane
SECOR (1994)	*Crotalus cerastes*	Surgically implanted in the body cavity	MS 222 + Halothane
SHINE & LAMBECK (1985)	*Acrochordus arafurae*	Force feeding	–
TIEBOUT & CARY (1987)	*Nerodia sipedon*	Surgically implanted in the body cavity	–
TOMKO (1972)	*Masticophis t. taeniatus*	Palpated in the stomach + thin nylon string	–
ÚJVÁRI & KORSÓS (1997, 1999)	*Vipera ursinii rakosiensis*	Subcutaneously	Ketamin, Halothane
WADA *et al.* (1971)	*Trimeresurus flavoviridis*	Subcutaneously	–
WEATHERHEAD & ANDERKA (1984)	*Elaphe obsolata*	Subcutaneously	–

On the skin

A radio transmitter attached to the snake's body surface may prove to be useful in few cases and for short study periods only. GENT and SPELLERBERG (1993) turned to this method prompted by the strict nature conservation regulations in Great Britain and the endangered situation of their study object, the smooth snake (*Coronella austriaca*). The transmitter was placed on the snake behind the cloaca at the first section of the tail and fixed by glue and medical tape. This method could fix the transmitter for a period between 0.07–9.71 days. During the three-year study of GENT and SPELLERBERG from the 39 marked specimens 6 lost the transmitter and 7 got caught in the vegetation due to the "package" on the tail. The conclusion is that this method can be recommended only in the case of very short term observations and when the implantation represents a high risk of loosing even one single specimen. With an externally fixed transmitter, almost permanent monitoring is necessary to prevent any problem arising from the movement difficulties. This, on the other hand, can cause heavy disturbances and likely changes the natural behaviour of the study animal.

Another method of attaching externally the transmitter is protected at least against the loss of it. A thin nylon thread led subcutaneously through two incisions on the subcaudal plates behind the cloaca can fix the transmitter to the vertebral column (CIOFI & CHELAZZI 1991). The subcaudal diameter of the snakes is smaller than the maximal body diameter, so a transmitter small enough less disturbs their movement. The method has a great advantage due to the following reasons: for the replacement of the transmitter (or the batteries) there is no need of surgical treatment. According to the authors, it can also be used in smaller species.

In the stomach

The simplest method to supply a snake with a radio transmitter and which is already used for a long time is to force-feed the device into the stomach (OSGOOD 1970). JACOB and PAINTER (1980) have put the transmitter in mineral oil to promote the swallowing. In the beginning of the era of telemetry, transmitters were implanted into mice then force feed by the snakes (FITCH & SHIRER 1971, NAULLEAU 1979, NAULLEAU & MARQUES 1973). The transmitter takes soon a fix position in the snake and stays there for a period of several days to several months. The animal continues normal feeding and digesting, the alien body in the stomach seems to disturb it only slightly. According to different authors, the force-fed transmitter has no effect on the feeding, digesting and voiding of the snakes, neither on their body temperature (NAULLEAU 1979, SHINE & LAMBECK 1985). However, force-feeding is not an appropriate method for long term studies, because the transmitter in the stomach may disturb the natural behaviour of the snakes (FITCH & SHIRER 1971), and sooner or later they vomit the device (NAULLEAU 1979, NAULLEAU & MARQUES 1973). Besides, the lack of antenna has a consequence of relatively short effective transmitting radius. Putting a constricting tape around the body may prevent vomiting the snake (BROWN & PARKER 1976, FITCH 1987, FITCH & SHIRER 1971, JACOB & PAINTER 1980), but this obviously causes further problems with the movement. According to the study of LUTTERSCHMIDT and REINERT (1990) the transmitter in the stomach has a similar effect to the snake's behaviour than that of a swallowed prey. Force-fed snakes have also chosen a substrate with slightly higher temperature in contrast to those without food. Their normal feeding behaviour, however, was out of cycle and they spent more time without food, lying on the sun. Some observations showed that the transmitter in the stomach can alter (usually rise) the body temperature (FITCH & SHIRER 1971, KITCHELL 1969, LUTTERSCHMIDT & REINERT 1990, LYSENKO & GILLIS 1980, NAULLEAU 1983, REGAL 1966, SAINT GIRONS 1975). JACOB & PAINTER (1980) suggested that the fact that rattlesnakes came out and started sunbathing after the beginning of hibernation may also be due to the effect of transmitters. A too small transmitter, however, can easily go through the whole intestine, and eventually leave the snake with the excrement (MCGINNIS & MOORE 1969).

In the coelomic cavity

REINERT and CUNDALL (1982) reported a complex implantation method, in which the transmitter was placed in the abdominal cavity in front of the sexual organs, and the antenna was led subcutaneously toward the head of the rattlesnake. The placement of the antenna was carried out with the help of a 20 cm long injection needle. The wire was thread with the needle section by section through the skin. The method was adopted in several other studies (PLUMMER & COGDON 1994, REINERT & ZAPPALORTI 1988, SECOR 1994). It was successfully used on more than 100 specimens of 8 species. No problem with feeding, growing, or breeding was experienced. There are examples of snakes carrying radio transmitter in the coelomic cavity for 9 years without disturbance (REINERT 1992). SHINE and LAMBECK (1985), however, oppose the surgical implantation. In four out of five cases they have reported an incomplete recovery after the operation, and wounds were reopened. They support force-feeding instead.

Subcutaneously

When implanting the transmitter under the skin, a several millimetre long longitudinal incision is usually made dorsolaterally at the lower third of the snake, then the device is placed caudally and the antenna threaded in anterior direction without cutting tissues (MADSEN 1984, NAULLEAU 1987, 1989, PETERSON 1987, ÚJVÁRI & KORSÓS 1997). There are very weak connective tissues between the skin and the lateral muscles of snakes. For the antenna, WEATHERHEAD and ANDERKA (1984) used a brass threading needle 25 cm long and 1.5 mm in diameter. It was drawn under the skin with the antenna wire in its cavity, then removed with a new incision on the skin at the end of the length of the antenna. The snake has to be completely unconscious during the operation. (For the immobilisation methods, see the following section.) First we used a similar technique in our study (ÚJVÁRI & KORSÓS 1997) with a steel needle of 8 cm length, but the relatively rigid antenna (type Holohil BD-2GT) could not be placed smoothly and the remaining loop later pierced the skin of the snake. Using a flexible plastic catheter the problem was avoided and only two incisions were needed at the beginning and the end of the antenna wire (ÚJVÁRI *et al.* 1999).

During the implantation the usual veterinary hygiene should be applied (disinfecting by ethanol, Betadine, or Pulsaureo powder (= 2% chlortetracycline-hydrochloride), (NAULLEAU 1987). The wound should be covered with surgical tape or plastic wound spray (e. g. Nobecutane = etoxy metacryl polymer plastic wound spray (MADSEN 1984), or Topozone furazolidone spray (PETERSON 1987). Sewing up the wound with one or two suture could also be recommended. Implantation carried out just before shedding is not recommended, since the peeling skin can remove the surgical cover and hence reopen the wound (WEATHERHEAD & ANDERKA 1984). Even 1.5 months after the operation, shedding difficulties may appear around the wound. Transmitters remaining longer in the snake may be encapsulated in tissues, but removal does not seem problematic (WEATHERHEAD & ANDERKA 1984). Although it seems that the most effective method for attaching the radio transmitter to the snake is the subcutaneous implantation, with small body size it still can cause troubles during the movement or alter the behaviour of the animal.

METHODS OF IMMOBILISATION

Anaesthesia of snakes

To implant a transmitter under the skin the snake has to be immobilised. The anaesthesia of snakes needs special training since these animals have a number of specialities with regards to their breathing. The trachea is narrow and long, making up to one-fifth of the length of the body (GANS 1976), its opening is situated at the front of the mouth and is freely movable from one side to the other. Another special anatomical feature is that only the right lobe of the lung is developed to the two-fifth of the total body length, whereas the left lobe is almost missing. Snakes have no diaphragm; their cerebral regulation is weak. Spinal neuroregulation has more influence; metabolism is generally low and depends in a great extent upon the environmental temperature.

During the anaesthesia of snakes all these anatomical features must be taken into consideration. Due to the low metabolism the influence of the anaesthetics builds up slowly, and the awakening may be delayed as well. In order to achieve total immobilisation of the snake the spinal reflex must be inhibited, but this – especially in the case of a largely vegetatively neuroregulated animal –

may cause death in extreme cases. Anaesthesia may block the muscles between the ribs, and because snakes have no diaphragm it might stop the respiration completely (BETZ 1962).

Inhalation agents – The first reports on anaesthesia of snakes were published at the end of the 1930s. They were all connected to research on the venom glands and venom production of poisonous snakes (CLARK 1937, KELLAWAY 1937, TAIT 1938). In these experiments mainly chloroform, and later a mixture of ether and air were used as an inhalation anaesthetic agents, which made the animal motionless during the operation of the venom gland. Ten years later a new inhalation agent called Fluothane or Halothane (= $C_2HBrClF_3$; 2-bromo-2-chloro-1, 1, 1-trifluoroethane) appeared on the market. This volatile fluid has five times higher influence than ether, it is not inflammable, and does not irritate the respiratory tracks (HACKENBROCK & FINSTER 1963). It is heavier than the air which needs to be considered when applying and hence it is important to prevent the snake lifting its head out of the gas. For a short anaesthesia (5–20 minutes) of big rattle snakes about 5 cm^3 Fluothane proved to be enough, and awakening did not take more than 10 minutes. REINERT and CUNDALL (1982) invented a simple technique for anaesthesia of snakes. A small piece of textile saturated with Halothane, Methoxyflurane or Isoflurane is placed together with the animal into a glass tank, and when the snake is sleeping, it is pulled into a plastic tube which is plugged at one end by a cotton with anaesthetics. Inhalation during the operation can be controlled simply by removing the cotton plug when necessary.

For implantation of the radio transmitter we have also successfully used Halothane as an inhalation agent. In our experiments (ÚJVÁRI & KORSÓS 1997, ÚJVÁRI *et al.* 1999) we used a proper anaesthetic equipment appeared in human and veterinary medical treatment. It was a little bit modified for snakes, i. e. instead of the inhalation mask used for large mammals, a thin rubber membrane was placed at the end of the inhalation pipe with a narrow hole in it. The head of the small sized Meadow viper (*Vipera ursinii rakosiensis*) was placed here until anaesthesia took effect. At the beginning of the operation pure Halothane, later a mixture of Halothane and oxygen was given, the ratio depending on the status of the animal. The inhalation pipe was transparent for the continuous control of the snake. The operation (implantation of a radio transmitter) lasted about 20 minutes, and following the fixation of the wound the snake woke up almost immediately due to the pure oxygen given. The technique also worked well with the common Grass snake (*Natrix natrix*) (NAGY & KORSÓS 1999).

Injectable agents – The cumbrous application of ether and chloroform in the 1950s was replaced by three other injectable agents Pentothal sodium, Nembutal and MS-222 (KARLSTROM & SHERBURNE 1955). They were introduced into the organism in exact doses, and all three were found to be uniformly effective in 26 individuals of 7 snake species. BETZ (1962) tested two agents (Nembutal and Surital) in 18 specimens of *Natrix rhombifera* and found them to be equally effective, although the heartbeat rhythm of the animals in anaesthesia with Surital was a little lower. REINERT and CUNDALL (1982) reported that in their experiments when using only MS-222 they found 7–17% mortality due to the stop of heart after the injection of the agent.

Inhalation + injectable agents – HACKENBROCK and FINSTER (1963) were the first to recommend that Fluothane can be used as a preparative anaesthetics for longer anaesthesia with Nembutal or other agent. REINERT and CUNDALL (1982) used the combination of 125–300 mg/kg M. S. 222 intraperitoneal injection and inhalation of Halothane to immobilise *Crotalus horridus* and *Agkistrodon contortrix*. The method was tried in 55 cases on 38 specimens of snakes without a single case of mortality.

Cold immobilisation and local anaesthesia – It is a widespread method to cool the snakes before anaesthesia, because it makes the handling of animals easier. WEATHERHEAD and ANDERKA (1984) put the snakes into a refrigerator of 5°C for 45 minutes before injecting the agent (80 mg/kg Ketaset) intramuscularly in four different parts of the body. When anaesthesia took effect they placed the snakes back into the fridge for another 15 minutes just before the operation. NAULLEAU (1987) also placed his animals (Aesculapian snakes, *Elaphe longissima*) into 5°C refrigerator for one hour before injecting the local anaesthetics (2% Hostacin or Laocaine S2). After 15–20 minutes the operation was started. MADSEN (1984), however, reported unsuccessful cooling in Grass snakes (*Natrix natrix*), which reacted vividly even at +1°C to the pinprick. Thirty minutes before the operation (implantation of a radio transmitter) he used the intrapleuroperitoneal injection of Ketalar (100 mg/kg) and Rompun (20 mg/kg), then Xylocaine (lidocaine chloride) as local anaesthetics (16 mg/kg) during the operation.

Control of anaesthesia and summary – The work of BETZ (1962) initiated a new period in the anaesthesia of reptiles. He gave a comprehensive summary of the effects of the different agents, and also evaluated for the first time the behavioural criteria of the control of anaesthesia. It was already known by earlier authors (BRAZENOR & KAYE 1953, KAPLAN & TAYLOR 1957, KARLSTROM & COOK 1955, TAIT 1938) that the lack of certain spontane movements, like the tongue reflex, or of the reaction to external stimuli, like the tail reflex, are signs of deep anaesthesia. During inhalation of ether, spinal reflexes were used for control, but this has its disadvantages as mentioned earlier. According to BETZ (1962) it is enough to get an anaesthesia until the tail reflex disappear, the lack of tongue movements is a sign of a deeper influence, which is not necessary. MADSEN (1984) had an opposite opinion: he immobilised the snakes with the injection of Ketalar (100 mg/kg) and Rompun (20 mg/kg), when the tongue reflex had already disappeared the tail reflex was still present. In order to avoid overdosis later he only used local anaesthetics (Xylocaine 16 mg/kg).

Among the inhalable anaesthetics ether is inflammable, chloroform is cardiotoxic and inhibits liver and bile function. It proved to be carcinogen in human medicine, too. Halothane and Methoxyflurane are four to eight times more effective than chloroform and ether, and furthermore, they do not irritate the respiratory system. They are the most recommended agents in herpetological anaesthesia (AIRD 1978). There is a good summary on reptile anaesthesia by MCDONALD (1976).

During the implantation of transmitters into snakes we recommend the application of Halothane as an inhalable agent and the use of a proper anaesthetic equipment. It has the disadvantage of being bound to a veterinary hospital, but the possibility of the control during the whole operation puts it in balance. You have to keep in mind, however, that all the anaesthetic agents have the danger that in case of overdosis there is no antidote against them (BETZ 1962).

Control following implantation

It is necessary to devote a several day observation period to study the animal after the surgical operation. The length of the period depends on the implantation and immobilisation technique used, but it should last at least 1–2 days to establish safely the recovery of the specimen. It is recommended to monitor continuously the snake's behaviour in a terrarium, give warmth and drink as necessary. It may take as long as two days to recover from the deep unconsciousness for a surgically operated snake (MADSEN 1984). In the case of animals force-fed with radio transmitters, release and data collection can follow immediately the intervention.

LOCATION AND OTHER RESULTS

The snakes, depending on the type of the habitat, can be radio tracked by walking or from a boat, in the case of aquatic species (SHINE & LAMBECK 1985, TIEBOUT & CARY 1987). Car and aerial tracking is usually out of question, even in the case of large snakes, since their movement rarely reaches the magnitude of kilometres, which is still easily covered by walking. In most studies the relative undisturbance of the animals is a primary consideration, which can be tested against sudden movement (escaping), or long hiding. Ideally, the purpose is to locate the snake's position without its perception. This, of course, can change by species and environmental conditions. In a study by TIEBOUT and CARY (1987), the position could be identified by 0.5 metre precision from a distance of 3–6 metres without actually seeing the animal.

Direct tracking

In this case the observer follows the strongest radio signal until the animal eventually can be seen and found. This technique is primarily used when the habitat terrain does not allow remote sensing and the researcher has no idea where to search for the snake and hence location starts from a large distance. Direct tracking can support detailed visual behavioural and/or ecological observations, when the disturbance of the animal is not so important.

Triangulation

Triangulation is based on signal search from two or three more-or-less rectangular directions. First the exact direction of the strongest signal is determined and then the point of intersection gives the locality of the transmitting animal. Since handhold antennas used for radiotracking snakes have an accuracy of ca 5 degrees, the estimated locality of the animal is actually not a point but a small area identified by the overlap of the sensing strips (error polygon). TIEBOUT and CARY (1987) recorded the localities with 0.5 metre bias and calculated the size of activity range later from the map. Movement between two consecutive measurements was compared to the side of the error polygon: if the first was smaller, then the movement was considered zero, because it could not be decided whether it actually happened or it was the error of the method. With this concept, unfortunately, the relatively small daily movements are almost impossible to track.

Actual location of a snake with a radio transmitter is usually the result of the combination of the two methods: direct tracking and triangulation. Search is started far away with a handhold Yagi antenna, where triangulation is usually inapplicable because of the large distance and the shadow effects of the terrain. The error polygon would also be too large and even two rectangular measuring points are too remote from each other to walk. Exact direction determination is difficult. Approaching to the locality the signal is strengthening, and the triangulation method becomes easier. From a closer distance the Yagi antenna becomes clumsy, and precise location is impossible because the signal comes from everywhere with the same strength. A small loop antenna can help in this case, and the snake with the transmitter can be found step by step, almost centimetre by centimetre. If so exact location is not necessary, the square metre that the snake occupies is easily determined without disturbing the animal (LANDRETH 1973, ÚJVÁRI & KORSÓS 1997).

Frequency of observations is adjusted to the aim of the study, and the seasonal and daily activity dynamics of the snake in focus. Data should cover the whole study period and also should be frequent enough to describe the movements of the animals, taken densely and in relatively equal intervals. Examples show measurements in every 48 hours, week, or two weeks (REINERT *et al.* 1984). Daily activity can be sampled by every hour, two or six hours, or continuously 24 hours long. Locations in every hour are, in our opinion, extremely disturbing and hence to be avoided, since this could result in permanent escape or shelter of the snakes. Vipers need at least two hours after disturbance to retain their original behaviour (ÚJVÁRI & KORSÓS 1997). The shorter the interval between two locations, the more likely the subsequent one is influenced by the previous one. Frequency of the observations should therefore be selected according to the independence of data. Several formulae were developed in order to test independence of data (see WHITE & GARROTT 1992 for more details).

Movements and home range

Development of research technology in radiotelemetry of snakes was accompanied by forming a conceptual system for the description of their activity. There are numerous definitions in the literature describing the range of animal movements. MOHR and STUMPF (1966) considered the terms home region, home range, home area to be synonymous when individuals remain around, and use a home more than 24 hours. In their opinion the territories make part of the home range, some apparently fill out the entire home range and others consist of small areas within the home range. The home range of snakes and movements within it were first reported by BROWN and PARKER (1976). Snake movements perceived as seasonal pulses away from hibernaculum each spring and toward it each fall (TIEBOUT & CARY 1987) was given the term total range (HAMILTON *et al.* 1967, HIRTH *et al.* 1969, TIEBOUT & CARY 1987). ROSE (1982) in her review of lizard home ranges extended the term to the whole area where an individual occurred. HAYNE (1949) differentiated the points with the highest activity as the home site. MOORE (1978) introduces the term core area for practically the same concept. DIXON and CHAPMAN (1980) defined the centre of activity as the geographical location within the home range which has the points of greatest activity.

The background of the movements between two consecutive locations (reasons, dynamics, etc.), i.e. the pattern of activity was first dealt by TIEBOUT and CARY (1987). Radiotelemetry is a useful tool to identify other information than movements of snakes: habitat and substrate preference, hibernation sites, movement frequencies, and reasons for moving. When identifying an exact place where a particular snake specimen is staying, plenty of other ecological and behavioural observations can be gained.

Behaviour, prey utilisation

Especially with direct tracking, radiotelemetry gives an opportunity to observe the behaviour of the snake. Details of feeding, such as sit and wait or active foraging strategies, sheltering, shedding, courting, copulation, etc. can be collected. The food of the snakes can be identified by excrement analysis during the active intervention (transmitter implantation, battery change) or in the field, based on insect chitin cuticle, mammal hair or bone remnants (REINERT *et al.* 1984). There are a number of peculiar environmental conditions, when the behavioural aspects of the given species can hardly be studied in any other way than radiotelemetry. For example the investigation of the behaviour of the aquatic arafura filesnake (*Acrochordus arafurae*) was almost impossible because of the muddy water full with crocodiles. Its daily activity, including temperature regulation, was only available for study by the technique of radiotelemetry (SHINE & LAMBECK 1985).

Orientation

Although radiotelemetry could be a useful tool in the study of orientation of snakes, relatively few research has been devoted to it. BROWN and PARKER (1976), for instance, have observed that specimens of *Coluber constrictor*, when returning to their hibernation site, have used the same route every year in the two-third of their journey. LANDRETH (1973) built a large outdoor test arena and found that rattlesnakes (*Crotalus atrox*) use the solar cues in orientation.

Habitat preference

Radio tracking of snakes can be useful in determining their habitat and substrate choice, which is an important factor in their ecology. TIEBOUT and CARY (1987) suggest two different statistical methods for calculation: proportional similarity index (PSI) and the well-known Chi-square test.

Hibernation

There are several examples showing that snakes frequently use a common hibernation site, sometimes years after years (ALEKSIUK 1976, BURGER *et al.* 1988, JACOB & PAINTER 1980). If tracking a specimen supplied with radio transmitter is successful until it finds the hibernation site, actually the wintering den of the whole population can be found. CIOFI and CHELAZZI (1991) found that specimens of *Coluber viridiflavus* are faithful to their hibernation sites and return to it not only every autumn, but also for hiding in their active period.

BIOTELEMETRY

Biotelemetric studies are aimed at studying various physiological, ecological and behavioural parameters. In the first period of using biotelemetry, implanted radio transmitters provided data on the temperature relationship of the digestion of snakes. NAULLEAU (1979) gave a good summary on the beginning and development of the investigation of temperature regulation. Before the advent of radiotelemetry, quick-recording mercury thermometers were put into the cloaca of snakes and the body temperature of snakes was measured during different activities (KITCHELL 1969). In this way continuous temperature regulation is difficult to follow, since measurements are interrupted and always go together with the disturbance of the behaviour. Later the thermosonda (telethermometer) was invented but it considerably restricts the animal's activity, too (REGAL 1966, SPELLERBERG & PHELPS 1975).

Invention of radiotelemetry made possible for the first time to monitor the animals without actually disturbing them. The technique was introduced by MCGINNIS (1967) in the USA, and was later widely applied to turtle, lizard and snake species around the world. The first biotelemetric transmitters were force-fed together with the food or on its own, hence placed in the intestinal system (MCGINNIS & MOORE 1969, NAULLEAU 1979, NAULLEAU & MARQUES 1973). Later the position of the implantation was influenced by the study purpose: whether to measure temperature dynamics of digestion, hibernation or environmental effects.

Planning a biotelemetric study

Measuring can be done in several different ways. In laboratory a short range receiver is enough, and measurements can be taken automatically or by hand at regular intervals. In the field usually long distance receivers are needed, and automatic data collection is more costly. If finances or safety conditions do not allow automatic data processing, an omnidirectional whip antenna or a hand-held Yagi antenna can do a good service for manual signal recording. In both cases the main purpose is to not disturb the animals' natural activity.

The principle of most temperature sensitive transmitters is to give signals at different pulse rates according to the change of temperature. A calibration diagram is usually provided by the manufacturer to identify the proper temperature from the regular time length (in milliseconds) between the individual signals. The degree of deviation is generally not more than 2°C. A simple receiver cannot directly show the intersignal period, in this case counting the number of signals during a certain time interval (e. g. 10 seconds) can help to calculate it. Modern transmitters display the intersignal period in milliseconds. To understand the body temperature changes of the snake, it is recommended to monitor continuously the ambient environmental factors like soil, air and vegetation temperature, light or radiation intensity, wind speed, etc.).

Frequency of recording is usually determined by the environmental factors and the study conditions. NAULLEAU and MARQUES (1973) e. g. made notes in every 5 minutes when the temperature change was faster and in every 15 minutes if it slowed down. LILLYWHITE (1980) adjusted the measuring intervals to an average of 20 minutes, but sometimes faster or slower, according to the daily activities of five Australian snake species. We have found that a measurement in every hour during a 24 hours period is quite appropriate to record the activity pattern of a temperate species. Automatic systems can be adjusted to any desired recording interval. Data processors built into the receiver can record temperature measurements for a long time (depending on battery life) and data may be transmitted into a computer weekly.

Terminology

Parallel with the development of biotelemetry a set of special expressions became also widespread among researchers. NAULLEAU (1987*a*) proposed six values of body temperature which are effected by the ambient temperature: (1) lethal minimum is the temperature when a snake dies, (2) critical minimum when its movement is blocked, (3) temporarily tolerable minimum induces the snake to stay in its shelter, (4) preferred temperature is what the snake actively chooses to regulate its own body, (5) temporarily tolerable maximum can be tolerated for a short time, but the snake searches for another place if it is possible, (6) critical maximum which is too hot to tolerate even for short period and the snake is paralysed, unable to move, and dies soon. LILLYWHITE (1980) suggested two factors to identify critical minimum temperature: (1) inability of the animal to right itself or to twist the body when turned ventral side up, and (2) the cessation of tongue flicks. The snakes were put on ice rocks and kept cool as long as both criteria fulfilled.

MOORE (1978) determined the temperature categories on the basis of the snakes' daily activity pattern. Preferred temperature (PT) was defined as the mean of all body temperatures recorded within the normal activity period, it represents the mean voluntary temperature of an active individual. Voluntary minimum (Vmin) was defined as the lowest body temperature recorded in an active individual; whereas voluntary maximum (Vmax) was the same at the higher end. Hence the relationship between the three is obvious: normal activity range (NAR) is the range of body temperatures of active individuals from voluntary minimum to voluntary maximum temperatures.

Biotelemetry is often connected to the observations on movements, home ranges, territories or hibernation sites of the snakes. However, with biotelemetry temperature sensing is always in focus, which can give hints on the mobility as well. Night movements, for example, are sometimes indicated by temperature change, and activity at night can be determined by the varying strength of the transmitter signal being received as the snakes crawled from one place to another (MOORE 1978).

DATA EVALUATION AND ANALYSIS

To determine the home range or range of activity of a snake many factors should be taken into consideration already at the planning stage of a study. The first and perhaps the most important is the sampling frequency. It is extremely important to gain even information from the different activity periods of the animal, selecting an appropriate sampling interval can be crucial to the success of the investigation. There is a conflict between the number of individual observations, which should be as dense and as many as possible, and the disturbance of the snake's behaviour, which should be, on the other hand, as low as possible. The length of a sampling procedure should be relatively short, but enough to collect the maximum information about the given locality. With the increasing number of observations the size of the home range and the accuracy of its estimation is generally increasing, too. Sampling frequency should differ in the breeding period, before, after and during hibernation and in other relatively passive periods. Range of activity is a function of the size, age and sex of the specimen as well as of its feeding, shedding and other behavioural or social habits. Individual movements of males are usually larger than that of the females, and in copulation time it can even exceed their energetic requirements. Juvenile snakes have usually smaller home ranges than the adults, which is the result of the sexual and intraspecific interactions of the latter. It was observed in the case of lizards (ROSE 1982), that males have extended their home ranges after sexual maturity to meet more females, which, on the other hand, occupy overlapping areas. The size of the home range may also depend on the density of the population, as an antagonistic relation. Home range size should be regarded also dynamically, a given individual can change its range of activity according to the presence or absence of conspecific competitors, lack of food, changing environmental conditions, etc.

It is important to make a difference between the error of measurement and the real movement of the animal. WHITE and GARROTT (1990) considered only differences larger than 5 metres as sign of activity. Sampling frequency depends on species and habitats, so it should be defined a priori by the researcher. As a starting point, one could consult the work of MACCARTNEY *et al.* (1988), who published home range measurement methods of 40 snake species beginning from the fifties.

Trackogram

This is the simplest and most recommended method in the case of relatively few data collected at constant frequency during a short period. Estimation of exact home range size is difficult, but daily movements and activity pattern is easy to follow. The technique is made up of putting the different locations on the map and simply connecting them in time sequence (FUISZ 1995, SZEMETHY 1995).

Polygon methods

Convex polygon – This method is based on the work by JENNRICH and TURNER (1969) who drew the smallest convex polygon containing all of the capture points. Locations are described in a two-dimensional co-ordinate system, in which the convex polygon also appears when connecting all the outermost points (ROSE 1982). The disadvantage of the method is that it takes into consideration all locations regardless their possible biological meanings, and that it does not differentiate between points with various capture probabilities. The area of the polygon is an estimate for the home range size, and can be calculated with co-ordinate geometrical formula (see WHITE & GARROTT, 1990), or manually by dissecting into triangles.

The advantage of the convex polygon technique is that it has historical prominence, graphical simplicity, and exhibits reasonably good statistical stability (JENNRICH & TURNER 1969). WHITE and GARROTT (1990) added flexibility of shape as an advantage, too. There are relatively many drawbacks, on the other hand, brought up in the literature. In addition to the two mentioned above, the main problem is that the estimated size of the polygon depends largely on the number of observations. Increasing sampling frequency extends the home range size, which is not in accordance with the biological meaning. Estimation does not only consider regular movements, but the whole area covered by locations, so the polygon includes areas that were actually not visited by the animal. Reasons why certain points are far from the "core" area cannot be revealed with this method.

To decrease bias resulting from the number of superfluous observations the 95% convex polygon method was introduced, which simply means that locations contributing mostly to the undesired increase of the area are left out from the calculation. The limit is drawn at 5% of all the capture points. Knowledge on the ecology of the given species can also support certain type of selections when the estimating the home range of the aquatic *Acrochordus arafurae* by the convex polygon method, terrestrial habitats inside the polygon were left out for the snake never goes onto the dryland (SHINE & LAMBECK 1985).

MADSEN (1984) calculated home ranges by two different ways using convex polygons. Total home range was defined by summarising all locations during the tracking period, while combined home range was got by adding the areas observed during the activity periods in each month.

Minimum polygon – Minimum polygon or minimum area method differs from convex polygon by restricting the connection of capture points to the more frequently repeated observations. Rarely (once) used points of occurrence are excluded from the polygon and hence the estimated area is much smaller than in the case of convex polygon. The advantage of this method that it is less dependent on the number of locations. Graphical evaluation is also easier, since it becomes geometrically difficult as the number of capture points increases. Algebraic evaluation is simple (JENNRICH & TURNER 1969). A drawback of the technique that the area drawn is less accurate and its shape is largely affected by the sequence of the observations (ROSE 1982). With a great number of locations several different minimum polygons can be figured (JENNRICH & TURNER 1969). Statistical stability of the method is weak, and, according to JENNRICH and TURNER (1969), it was not described precisely originally. The technique was adopted by FITCH and SHIRER (1971) and CIOFI and CHELAZZI (1991), among others.

Parametric statistic estimates

This family of methods uses the probability density function, which calculates statistical parameters of an assumed distribution of the actual observations (ROSE 1982). Home range size estimation depends on the statistical methods applied.

Recapture radius – The distribution of the locations is approximated by the normal (Gauss) distribution. First the geometric centre is defined by averaging all point co-ordinates, then the distance of every point from the centre is calculated. The average of these distances is taken as a radius of the estimated home range. The recapture radius method gives usually slightly bigger area than the convex polygon method. Estimations can disperse very much if the shape of the actual home range is far from a circle. Individual variations may also destroy the accuracy of the radius method. Several authors recommend the determinant method instead (JENNRICH & TURNER 1969, ROSE 1982).

Bivariate normal models – It is true for all of the home range estimation methods that the randomness of observations is assumed. It is also true in the majority of cases, that the capture probability of the specimen in the geographical middle of its activity range is supposed to be higher than in the peripheries.

In order to avoid the bias of the previous methods JENNRICH and TURNER (1969) invented the determinant estimator which is based on the radius method but using covariant matrix. The method is also called JENNRICH-TURNER estimator (WHITE & GARROTT 1990), or confidence ellipse method (REINERT 1992). It operates with a bivariate normal distribution and allows an elliptic home range shape, too. The size of the activity range is determined by a certain confidence interval, within which the occurrence of the animal has a high probability value. For the ultimate calculations see JENNRICH and TURNER (1969) or WHITE and GARROTT (1990). The main advantage of the method that it does not depend on the sample size, so different results can easily be compared. Its drawback, however, that for a reliable estimation relatively high number of observations is needed. At 20% covariance level the minimum is 100 samples (WHITE & GARROTT 1990).

The weighted bivariate normal estimator is an improved JENNRICH-TURNER estimator. The difference lies in the weighting procedure of all data by the distance from the average centre.

Non-parametric approaches – Grid methods

With the non-parametric methods the normal distribution of data is not a condition and they do not have a demand for minimal data set. Apart from the following two, there are several other parametric and non-parametric methods such as multiple ellipses, Dunn estimator, Fourier series smoothing, etc. (WHITE & GARROTT 1990), but because of their rare applications we do not go into details with these procedures.

Grid cell – The size of the activity range is determined with the help of a grid covering the observed area. Grid cell size is calculated with the average distance between consecutive locations, sometimes adjusted by the size of the study area. Home range estimation is made by including cells that have at least one occurrence. The area obtained may be a concave polygon, but it may also consist of several disjunct forms. If relative frequencies of the occurrences are also considered, the use of the different parts of the home range can also be estimated ("core areas"). The overlap in time and space between different individuals of the same population is easy to follow and depict. Using background information, such as vegetation maps habitat preferences can also be investigated.

Harmonic mean – The method was invented by DIXON and CHAPMAN (1980). In herpetology, it is perhaps the most widespread for estimating the area used by reptiles (REINERT & ZAPPALORTI 1988, SECOR 1994, TIEBOUT & CARY 1987). The calculation starts again with fitting a grid to the study area. Distances of every localities from all grid corners are measured, then the localities are categorised according to the harmonic mean values of these distances. Points in the same category are connected and form an isopleth. The isopleths delimit areas used with equal probabilities by the animal (REINERT & ZAPPALORTI 1988).

Summary of data evaluation

Summarising the different home range size estimation methods described above, the convex polygon can be recommended in most cases where sample size is reasonably high (ROSE 1982). Its main disadvantage is that the size of the estimated area increases with the sample size. From the statistical methods grid cell and harmonic mean are the most widespread (REINERT *et al.* 1984). The advantage of the grid cell method is that it gives information on the locations that are the result of accidental movements and occupy peripheral places. It is also suitable for analysing overlapping patterns and habitat preferences. Its drawback lies in the dependence on the realisation. Harmonic mean calculates only with the areas really occupied by the animal and can represent home ranges of any kind of shape. The areas limited by the isopleths are determined by the intensity of the activity. Selecting the different isopleths, different home range parts can be defined: 95% isopleths to represent total home range or total activity range, 50% isopleths to represent a core area, or area of most intense use, 75% intermediate range can be calculated for comparative purposes. The core areas represent on average only about 7.7–9% of the total home range size (REINERT & CUNDALL 1982, REINERT & ZAPPALORTI 1988, SECOR 1994, TIEBOUT & CARY 1987). The harmonic mean is also well-suited to time-series analysis used to detect shifts in activity centres (TIEBOUT & CARY 1987). SECOR (1994) compared convex polygon and harmonic mean methods and has found several hectares difference to the advantage of the former.

With the development of computer programs a PC software package was made for estimating home range sizes with minimum convex polygon and harmonic mean methods (Micro-computer Programs for the Analysis of Animal Locations – McPAAL Ver. 1.21, Michael Stuwe, National Zoological Park of the Smithsonian Institution, Front Royal, Virginia).

RADIOTELEMETRY OF VIPERA URSINII RAKOSIENSIS: A CASE-STUDY

The main problem with radiotracking small sized vipers is to select an appropriate transmitter. If temperature sensing is a demand (as usual) then a transmitter with reasonably long lifespan (13–20 weeks) weights 2–2.2 g and measures 15–18 × 6–9 mm. Transmitters smaller than this have short (11 weeks) or very short (3 weeks) lifespan that makes them less useful for ecological studies. The conflict between the transmitter size and the length of the observation often ends in a compromise to decrease the study period.

Force-fed transmitter is not an option in the case of the small grassland vipers since they feed mainly on insects. CIOFI and CHELAZZI (1991) recommend their external attaching method, which is good when one has to replace the battery or repair the transmitter, but we have reservations with the drastic way of fixing the device to the vertebral column with a plastic thread. Even if it is only on the tail, it can cause serious troubles to the snake when moving between the dense tussocks in the grass and stays open to infection due to the permanent movement.

In our opinion the best method to attach a transmitter is the subcutaneous implantation. For immobilisation during surgery we recommend halothane anaesthesia using a professional respiration machine. With the machine respiration can be regulated and anaesthesia maintained at the edge of cessation of tongue flicks. With the proper dose of the narcotic and the oxygen the risk can be minimised and awakening shortened only to several minutes. Despite this, indoor control of the vipers in the following one or two days is always necessary.

Before selecting a transmitter for implantation it is wise to ask information about the size, lifespan, and effective range from the manufacturers on the market. Although companies can come and go, a useful selection of present manufacturers can be found in Table 1 of this paper. If it is possible, a trial of a sample transmitter could also be extremely beneficial in the choice of the different trademarks.

In our study we selected the transmitters produced by Holohil Systems Ltd. Ontario, Canada (type BD-2GT) to study the movements and temperature relationships of the Hungarian Meadow viper (*Vipera ursinii rakosiensis*) (ÚJVÁRI & KORSÓS 1997, 1999, ÚJVÁRI *et al.* 1999). The temperature sensitive transmitters weighted 2 g, with a length of 16 mm, width of 9 mm, emitting frequency around 152 MHz. Their life span was announced to be around 7–8 months, depending on the environmental temperature. Average body mass of the vipers is about 40 g, length 35–40 cm. A transmitter which was implanted subcutaneously made up to 4% of the body mass of the snake.

About one month after the implantation, the antenna wires of the transmitters pierced the skin of the snakes. In one specimen a loop came out where the wire was originally threaded, in the other the end of the wire pierced the cuticle. The antennas were put back into the animals and the openings were fixed with surgical tapes. Another one month later the animals were in proper conditions regarding the implanted transmitters. Later one transmitter was found on its own on the ground (it was probably pushed out of the animal). The other gave normal signals 4.5 months after the implantation, but then suddenly indicated unbelievable high body temperatures and stopped to function in the next week. We have lost both the animals and the transmitter inside. Another female viper received a switchable transmitter from the same set ordered from Holohil in 1995, but stopped to function in only 1.5 month. Our inquiries both about the wire rigidity and the expected lifespan remain unresponded by the manufacturer.

The signals of the transmitters in the field were received by a two- or three-element Yagi antenna, a handy loop antenna and a simple radio receiver apparatus. For biotelemetric purposes more advanced receivers (with built-in data processor) and an omnidirectional whip antenna can also be useful. Small grassland vipers are sit and wait predators (FARRELL *et al.* 1995) and have a relatively small activity range. They usually spend a lot of time in or near a rodent hole or a grass tussock. Their regular movements hardly exceeds several metres at once, but time to time they may move a larger distance (a couple of hundred metres) to find another suitable hunting area and shelter (CIOFI & CHELAZZI 1991, NAULLEAU 1989, ÚJVÁRI & KORSÓS 1997). A Yagi antenna for the remote search and a loop for more accurate location seem to be satisfactory for a simple preliminary study.

It is very much recommended to compile a good map on the study area or even combine it with a vegetation map with precise borders of the different plant associations (grasslands may have extremely important vegetation microstructure which is hard to identify and describe without the help of a botanist!). With the aid of a good map we can immediately determine our position (and that of the viper) in our co-ordinate (or other reference) system.

Measurements (locations) can be more frequent (say every second day) in the higher activity periods (after and before hibernation, during copulation, birth, etc.), and relatively scarce (once every week) in the more passive periods (summer "aestivation", shedding, digestion, etc.). The habitat of the Hungarian meadow viper is altogether only several hectares, so locations were taken every week not to disturb the animals. Successful locations were marked with a pole and next time search could be started from that point. To record their daily activity and temperature regulation, we conducted several 24–hour long continuous monitoring, when locations were omitted, only body temperatures by remote sensing were collected in every hour. During fast changes (early morning and late afternoon) half an hour or even more frequent recordings are recommended. During the day or especially at night, on the other hand, the temperature of the vipers is relatively stable or only oscillates around a certain point, so two hours recording intervals may prove to be adequate. Sudden but in their extent small temperature changes, however, can indicate movements like sheltering in a hole, so "stability" should always be handled carefully.

Evaluation of the data collected depends on the sample size, observation frequency and the aim of the study. In a poorly known species even few data and the compilation of a simple trackogram can provide many useful and new information (see more details: ÚJVÁRI & KORSÓS 1997, 1999, ÚJVÁRI *et al.* 1999). For home range analysis with more locations we recommend the harmonic mean method. Biotelemetric data (i. e. temperature regulation) should be evaluated in connection with the environmental factors.

Summarising all the information available for us from the literature and from our own experiences, we can conclude that radiotelemetry is an extremely useful method in the ecological study of snakes. In the case of large species it is very useful to follow their movements, to describe the seasonal and daily activity patterns, estimating home range dynamics, and many other ecological and behavioural aspects. In small snakes its applicability is limited to a certain degree by the size of the transmitter, but the method can still provide extremely useful and missing information on the biology of the animals, which otherwise would almost be impossible to study.

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REFERENCES

AIRD, S. D. (1986) Methoxyflurane anesthesia in Crotalus: comparisons with other gas anesthetics. *Herpetological Review* **17**(4): 82–84.

ALEKSIUK, M. (1976) Reptilian hibernation: evidence of adaptive strategies in Thamnophis sirtalis parietalis. *Copeia* **1976**(1): 170–178.

AUDET, D. & THOMAS, D. W. (1996) Evaluation of the accuracy of body temperature measurement using external radio transmitters. *Can. J. Zool.* **74**: 1778–1781.

BETZ, T. W. (1962) Surgical anesthesia in reptiles, with special reference to the water snake, Natrix rhombifera. *Copeia* **1962**(2): 284–287.

BRAZENOR, C. W. & KAYE, G. (1953) Anesthesia for reptiles. *Copeia* **1953**(3): 165–170.

BROWN, W. S. & PARKER, W. S. (1976) Movement ecology of Coluber constrictor near communal hibernacula. *Copeia* **1976**(2): 225–242.

CAFFREY, M., DOIG, V., GARBER, S. D., LAURO, B., MIKOVSKY, M., SAFINA, C. & SALIVA, J. (1988) Hibernacula and summer den sites of pine snakes (Pituophis melanoleucus) in the New Jersey Pine Barrens. *J. Herpetology* **22**(4): 425–433.

CIOFI, C. & CHELAZZI, G. (1991) Radiotracking of Coluber viridiflavus using external transmitters. *J. Herpetology* **25**(1): 37–40.

CLARK, H. (1937) Embryonic series in snakes. *Science* **85**: 569–570.

DIXON, K. R. & CHAPMAN, J. A. (1980) Harmonic mean measures of animal activity areas. *Ecology* **61**(5): 1040–1044.

FARRELL, T. M., MAY, P. G. & PILGRIM, M. A. (1995) Reproduction in the rattlesnake, Sistrurus miliarius barbouri, in Central Florida. *J. Herpetology* **29**(1): 21–27.

FITCH, H. S. & SHIRER, H. W.(1971) A radiotelemetric study of spatial relationships in some common snakes. *Copeia* **1971**(1): 118–128.

FLEURY, F. & NAULLEAU, G. (1987) Activité locomotrice de Vipera aspis L. (Reptilia, Viperidae) soumis a différentes thermopériodiques durant l'hivernage. *C. R. Acad. Sc., Paris* **3**(1): 304.

FUISZ, T. I. (1995) Rádiós nyomkövetés és biotelemetria használata az ornitológiában. [The use of radiotracking and radiotelemetry in ornithology.] *Ornis Hungarica* **5**: 33–64. [In Hungarian with English abstract]

GANS, C. (ed.) (1976) *Biology of the Reptilia, Vol. 5, Physiology A.* Academic Press, London, N.Y., San Francisco, pp. 43–53.

GENT, A. H. & SPELLERBERG, I. F. (1993) Movement rates of the smooth snake Coronella austriaca (Colubridae): A radio-telemetric study. *Herpetological Journal* **3**: 140–146.

GILMER, D. S., KUECHLE, V. B. & BALL, I. J., Jr. (1971) A device for monitoring radio-marked animals. *J. Wildlife Managment* **35**(4): 829–832.

HACKENBROCK, C. R. & FINSTER, M. (1963) Fluothane: a rapid and safe inhalation anesthetic for poisonous snakes. *Copeia* **1963**(2): 440–441.

HUEY, R. B., PETERSON, C. R., ARNOLD, S. J. & PORTER, W. P. (1989) Hot rocks and not-so-hot rocks: retreat-site selection by garter snakes and its thermal consequences. *Ecology* **70**(4): 931–944.

IKEDA, K. & OSHIMA, M. (1971) A wireless tracking system for behavioral studies of snakes. *The Snake* **3**:14–19. [In Japanese with English summary]

JACOB, J. S. & PAINTER, C. W. (1980) Overwinter thermal ecology of Crotalus viridis in the North-central Plains of New Mexico. *Copeia* **1980**(4): 799–805.

JENNRICH, R. I. & TURNER, F. B. (1969) Measurement of non-circular home ranges. *J. Theor. Biol.* **22**: 227–237.

KAPLAN, H. M. & TAYLOR, R. (1957) Anesthesia in turtles. *Herpetologia* **13**: 43–58.

KARLSTROM, E. L. & COOK, S. F. Jr. (1955) Notes on snake anesthesia. *Copeia* **1955** (1): 57–58.

KELLAWAY, C. H. (1937) The results of the excision of the venom glands of the Australian tiger snake (Notechis scutus). *Austr. Jour. Exper. Biol. & Med. Sci.* **15**: 212–230.

KEPHART, D. G. (1980) Inexpensive telemetry techniques for reptiles. *J. Herpetology* **14**(3): 285–290.

KITCHELL, J. F. (1969) Thermophilic and thermophobic responses of snakes in a thermal gradient. *Copeia* **1969**(1): 189–191.

LANDRETH, H. F. (1973) Orientation and behavior of the rattlesnake, Crotalus atrox. *Copeia* **1973**(1): 26–31.

LILLYWHITE, H. B. (1980) Behavioral thermoregulation in Australian elapid snakes. *Copeia* **1980**(3): 452–458.

LUTTELSCHMIDT, W. I. & REINERT, H. K. (1990) The effect of ingested transmitters upon the temperature preference of the northern water snake, Nerodia s. sipedon. *Herpetologica* **46**(1): 39–42.

MACARTNEY, J. M., GREGORY, P. T. & LARSEN, K. W. (1988) A tabular survey of data on movements and home ranges of snakes. *J. Herpetology* **22**: 61–73.

MADSEN, T. (1984) Movements, home range size and habitat use of radio-tracked grass snakes (Natrix natrix) in Southern Sweden. *Copeia* **1984**(3): 707–713.

MCDONALD, H. S. (1976) Methods for the physiological study of reptiles. Pp. 19–126. *In* GANS, C. & DAWSON, W. R. (eds): *Biology of the Reptiles, Vol. 5*, Academic Press, London.

MCGINNIS, S. M. & MOORE, R. G. (1969) Thermoregulation in the Boa constrictor. *Herpetologica* **25**(1): 38–45.

MCGINNIS, S. M. (1967) The adaptation of biotelemetry techniques to small reptiles. *Copeia* **1967**(2): 472–473.

MERTENS, D. (1994) Some aspects of thermoregulation and activity in free-ranging grass snakes (Natrix natrix L.). *Amphibia-Reptilia* **15**: 322–326.

MOHR, C. O. & STUMPF, W. A. (1966) Comparison of methods for calculating areas of animal activity. *J. Wildlife Management* **30**(2): 293–304.

MONTGOMERY, G. G. & RAND, A. S. (1978) Movements, body temperature and hunting strategy of a Boa constrictor. *Copeia* **1978**(3): 532–533.

MOORE, R. G. (1978) Seasonal and daily activity patterns and thermoregulation in the southwestern speckled rattlesnake (Crotalus mitchelli pyrrhus) and the Colorado desert sidewinder (Crotalus cerastes laterorepens). *Copeia* **1978**(3): 439–442.

NAGY, Z. T. & KORSÓS, Z. (1999): Data on movements and thermal biology of grass snake (Natrix natrix L.) using radiotelemetry. In MIAUD, C. & R. GUYÉTANT (eds): *Current studies in Herpetology, Le Bourget du Lac (SEH)*, pp.339–343.

NAULLEAU, G. & MARQUES, M. (1973) Étude biotélémetrique préliminaire de la thermorégulation de la digestion chez Vipera aspis. *C. R. Acad. Sci.* **276**: 3433–3436.

NAULLEAU, G. (1979) Étude biotélémetrique de la thermorégulation chez Vipera aspis (L.) elevée on conditions artificielles. *J. Herpetology* **13**(2): 203–208.

NAULLEAU, G. (1987) Étude biotélémetrique des déplacements et de la tempértature chez la couleuvre d'esculape, Elaphe longissima (Squamata, Colubridae) en zone forestiere. *Bull. Soc. Herp. Fr.* **52**: 45–53.

NAULLEAU, G. (1987*a*) Use of biotelemetry in the study of free ranging snakes: example of Elaphe longissima. *In* GELDER, J. J. VAN, STRIJBOSCH, H. & BERGERS (eds): *Proc. Fourth Ord. Gen. Meet. S. E. H., Nijmegen*, pp. 289–292.

NAULLEAU, G. (1987*b*) Les serpents de France. *Revue francaise d'aquariologie (herpetologie) Extrait*, 1984, 2. ed., **11**(3–4): 5.

NAULLEAU, G. (1989) Étude biotélémetrique des déplacements et de la température chez la couleuvre d'Esculape Elaphe longissima (Squamata, Colubridae) en zone forestiere. *Bull. Soc. Herp. Fr.* **52**: 45–53.

NULAND, G. J. VAN & CLAUS, P. F. H. (1981) The development of a radio tracking system for anuran species. *Amphibia-Reptilia* **2**: 107–116.

OLDERS, J. H. J., GELDER, J. J. VAN & KRAMMER, J. (1985) A thermo-sensitive transmitter for radio tracking small animals. *Netherlands J. Zool.* **35**(3): 479–485.

OLDHAM, R. S. & SWAN, M. J. S. (1992) Effects of ingested radio transmitters on Bufo bufo and Rana temporaria. *Herpetological J.* **2**: 82–85.

OSGOOD, D. W. (1970) Thermoregulation in water snakes studied by telemetry. *Copeia* **1970**(3): 568–571.

PARKER, W. S. & BROWN, W. S. (1972) Telemetric study of movements and oviposition of two female Masticophis t. taeniatus. *Copeia* **1972**(4): 892–895.

PETERSON, C. R. (1987) Daily variation in the body temperatures of free-ranging garter snakes. *Ecology* **68**(1): 160–169.

PLUMMER, M. V. & CONGDON, J. D. (1994) Radiotelemetric study of activity and movements of racers (Coluber constrictor) associated with a Carolina Bay in South Carolina. *Copeia* **1994**(1): 20–26.

PRIEDE, I. G. & SWIFT, S. M. (1992) *Wildlife telemetry: Remote monitoring and tracking of animals.* Ellis Horwood. Devon, UK.

REGAL, P. J. (1966): Thermophilic response following feeding in certain reptiles. *Copeia* **1966**(3): 588–590.

REINERT, H. K. & KODRICH, W. R. (1982) Movements and habitat utilization by the massasauga (Sistrurus catenatus catenatus). *J. Herpetology* **16**: 162–171.

REINERT, H. K. & CUNDALL, D. (1982) An improved surgical implantation method for radio-tracking snakes. *Copeia* **1982**(3): 702–705.

REINERT, H. K. & ZAPPALORTI, R. T. (1988) Timber rattlesnake (Crotalus horridus) of the Pine Barrens: their movement patterns and habitat preference. *Copeia* **1988**(4): 964–978.

REINERT, H. K., CUNDALL, D. & BUSHAR, L. M. (1984) Foraging behavior of the timber rattlesnake, Crotalus horridus. *Copeia* **1984**(4): 976–981.

REINERT, K. H. (1992) Radiotelemetric field studies of pitvipers: data acquisition and analysis. Pp. 185–197. *In* CAMPBELL, J. A. & BRODIE, E. D., Jr. (eds): *Biology of the pitvipers.* Tyler, Texas, Selva.

ROLAND, J., MCKINNON, G., BACKHOUSE, C. & TAYLOR, P. D. (1996) Even smaller radar tags on insects. *Nature* **381**: 6324.

ROSE, B. (1982) Lizard home ranges: methodology and functions. *J. Herpetology* **16**(3): 253–269.

SECOR, S. M. (1994) Ecological significance of movements and activity range for the sidewinder, Crotalus cerastes. *Copeia* **1994**(3): 631–645.

SHINE, R. & LAMBECK, R. (1985) A radiotelemetric study of movements, thermoregulation of Arafura filesnakes (Serpentes: Achrochordidae). *Herpetologica* **41**(3): 351–361.

SPELLERBERG, I. F. & PHELPS, T. E. (1975) Voluntary temperatures of the snake, Coronella austriaca. *Copeia* **1975**(1): 183–185.

SZEMETHY, L. (ed.) (1995) A rádiótelemetria alkalmazásának gyakorlati kérdései. [Practical questions in the use of radiotelemetry.] GATE, Gödöllő, 80 pp. [In Hungarian]

TAIT, J. (1928) Surgical removal of the poison glands of rattlesnakes. *Copeia* **1928**(1): 10–13.

TIEBOUT, H. M. & CARY, J. R. (1987) Dynamic spatial ecology of the water snake, Nerodia sipedon. *Copeia* **1987**(1): 1–18.

TOMKO, D. S. (1972) Telemetric study of movements and oviposition of two female Masticophis t. taeniatus. *Copeia* **1972**(4): 892–895.

ÚJVÁRI, B. & KORSÓS, Z. (1997) Thermoregulation and movements of radio-tracked Vipera ursinii rakosiensis in Hungary. Pp. 367–372. *In* BÖHME, W., BISCHOFF, W. & ZIEGLER, T. (eds): *Herpetologia Bonnensis.* Bonn (SEH).

ÚJVÁRI, B. & KORSÓS, Z. (1999): First observation in situ on the hibernation of the Hungarian Meadow Viper (Vipera ursinii rakosiensis). Pp. 435–438. *In* MIAUD C. & R. GUYÉTANT (eds): *Current studies in Herpetology*, Le Bourget du Lac (SEH).

ÚJVÁRI, B., SÁTORHELYI, T. & MEZŐSI, L. (1999) Kígyók altatása. *Magyar Állatorvosok Lapja* **121**(8): 482–486. [In Hungarian, with English summary]

WADA, Y., TANAKA, H., OGUMA, Y., SASA, M., IKEDA, K., MOTOI, E., KAWAI, J. & ONO, T. (1971) Radio-tracking of movement of habu, Trimeresurus flavoviridis. *The Snake* **3**: 20–23. [In Japanese with English summary]

WEATHERHEAD, P. J. & ANDERKA, F. W. (1984) An improved radio transmitter and implantation tecnhique for snakes. *J. Herpetology* **18** (3): 264–269.

WHITE, G. C. & GARROTT, R. A. (1990) *Analysis of wildlife radio-tracking data.* Academic Press, New York, 384 pp.

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