HERPETOLOGICAL JOURNAL, Vol. 3, pp. 140-146 (1993)

MOVEMENT RATES OF THE SMOOTH SNAKE *CORONELLA AUSTRIACA* (COLUBRIDAE): A RADIO-TELEMETRIC STUDY

A. H. GENT* AND I. F. SPELLERBERG

Department of Biology, University of Southampton, Highfield, Southampton SO9 5NH, UK

Present address: English Nature, Northminster House, Peterborough PE1 1UA, UK

(Accepted 5.4.93)

ABSTRACT

The movement behaviour of free ranging smooth snakes (*Coronella austriaca*) was studied by radio-telemetry. The species exhibits a low median hourly-movement rate (0.54 m h^{-1}, range = 0.00 to 44.26 m h^{-1}, n= 1074) and a correspondingly low daily-movement rate (median = 13.30 m day^{-1}, range = 0.00 to 166.81 m day^{-1}, n= 138). There were no significant differences in movement rates between the sexes. Smooth snakes do not generally occupy specific features (such as dens) and move through parts of sites at differing rates; some animals will remain within small areas for some while whilst others move through an area quite quickly.The effect of attachment of radio-transmitters on the behaviour of the snakes was investigated via a short laboratory study using time-lapse video recording. Only minor differences were observed between movement rates and behaviours of tagged and untagged animals and no differences were detected for changes in body weight over the period. These observations indicated that the attachment of a radio-transmitter did not significantly affect the behaviour of smooth snakes.

INTRODUCTION

An understanding of movement behaviour is important when studying the ecology of an animal. This allows an assessment of the dispersal potential of the species. Studies of movement ecology also provide information about foraging behaviour and site tenacity. These, in turn, can be related to energy expenditure and all other aspects of the species' ecology. Such knowledge is valuable when considering conservation management; this is particularly so where habitats of reptiles are becoming fragmented.

Many studies of movement behaviour of snakes have been published (e.g. Freedman & Catling, 1979; Tiebout & Cary, 1987). Indeed movement behaviour of the smooth snake *Coronella austriaca* has previously been studied (Breeds, 1973; Spellerberg & Phelps, 1977; Goddard, 1981). These studies suggested that the species is relatively sedentary and therefore has only a limited potential for dispersal and for colonising new areas. In addition, smooth snakes do not appear to occupy separate summer and winter ranges (Phelps, 1978) and hence would not be expected to show seasonal migration.

These earlier workers, however, relied upon recapture studies. Due to the secretive nature of the species and the difficulty in obtaining regular observations, detailed studies of movement rate in this species have not been possible. Furthermore, recapture studies will be subject to observer bias (Tiebout & Cary, 1987). During the present study radio-transmitters were attached to *C. austriaca*. This enabled regular and frequent locations and thus permitted a more detailed investigation of smooth snake movement behaviours than had previously been possible.

With a view to evaluating the effect of the methodology on the behaviour of the snakes, a short behavioural study was undertaken in the laboratory using time-lapse video-recording.

MATERIALS AND METHODS

FIELD STUDY

Smooth snakes were studied at two sites in the south west of the New Forest (southern England). Site 1 was a forestry inclosure planted mostly with coniferous species (including *Pinus* spp. and *Picea sitchensis*) and incorporated the immediately surrounding heathland and adjacent grass 'grazing area'. The site had formerly been heathland and considerable areas within the inclosure had been left unplanted. These unplanted areas were predominantly heathland of ling *Calluna vulgaris*, bell-heather *Erica cinerea* and cross-leaved heath *E. tetralix*, grasses e.g. *Molinia caerulea* and *Agrostis curtisii*, bracken *Pteridium aquilinum* and gorse *Ulex europaeus* and *U. minor*.

Site 2 was located approximately 2 km south-west of Site 1. The site was bisected by the course of a dismantled railway line which provided two steep embankments. The southern embankment and the north facing hill behind was heathland that had been burnt some five years before the start of the study. The vegetation here was quite short and sparse as a consequence. Gorse species were abundant over much of the embankments. The area to the north of the railway cutting was a heathland dominated by heather species which gradually merged into a wet bog system predominantly of purple moor grass *Molinia caerulea* and bog myrtle *Myrica gale* over a distance of approximately 300 m. To the north of the bog was a southerly slope of mature humid and dry heathland.

Snakes were fitted with small radio-transmitters (173.20 to 173.35 MHz range), weighing approximately 2.5 g. These were attached externally to the base of the tail using surgical adhesive tape (Fig. 1). Once released, snakes were located at intervals of approximately two hours during daylight (typically 0800 to 2000 hrs BST). This interval was chosen to give regular observations throughout the day whilst minimising disturbance. The time of each location was recorded and the

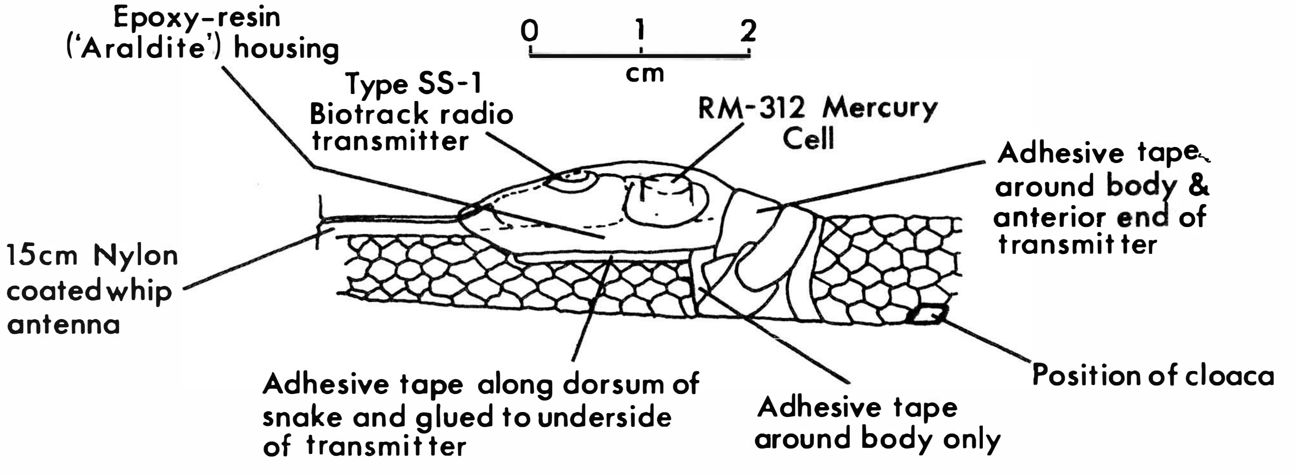

Fig. 1. Design and attachment of radio transmitter.

exact interval calculated. The position of the snake was described relative to pre-positioned markers in the field and this allowed subsequent calculation of the straight line distance between locations. Hourly movement rates were calculated by dividing this distance by the time interval and daily movement rates determined by summing all monitored distances recorded during a day.

The interval between sightings may influence estimates of movement rates. With a view to ensuring consistency, hourly movement rates were only calculated where the sampling interval was between 1 and 3 hr. Estimates of daily movement rate are affected by the number of observations used in the calculation (Fig. 2). Although no clear asymptote was observed in the relationship between daily movement rate and number of monitored distances, a division was made between those estimates where the movement rate was based on five or less distances and those where six or more had been summed. Consequently, only those daily movement rates where six or more distances were used in their calculation were considered for subsequent analysis.

The direction of movement was determined by relating the straight line distance between successive locations to a compass bearing. Each measured distance was assigned to one of eight 45° bearing classes. Directional movement was analyzed in three ways. Firstly, where total distances moved were in excess of 40 m (smaller values were excluded as they were too small to allow statistical analysis), the observed pattern of dispersal was compared against a theoretical equal movement in all eight defined directions. Secondly, as an indication of net dispersion over short time periods, a ratio was calculated by dividing the distance between first and last locations (net dispersion) by the sum of all monitored movement distances (total movement). This Net movement/Total movement ratio allowed an assessment of dispersal that was independent of the variation in periods of time over which animals were studied and the amount of movement shown in those periods. However, to provide a degree of standardisation, periods of observation that yielded total movements less than 20 m were (arbitrarily) excluded from analysis. Thirdly, the rate of net dispersion was also calculated, by dividing the net distance moved by the time period (in days). This value gives a comparable measure of site tenacity during the short term. With a view to removing likely inherent errors within very small data sets, these rates were only calculated for periods of observation in excess of two days (i.e. in excess of 48 hr).

Radio-transmitters were attached to snakes for a total of 236.05 days (5665.1 hr) during 50 separate periods each of which lasted between 0.07 and 9.71 days (mean = 4.72 ± 2.81 days) [i.e. 1.73 to 232.9 hr (mean = 113.3 ± 67.4 hr)] in three consecutive years (April 1984 to July 1986) (Fig. 3). Thirty-nine different animals were studied (24 males and 15 females); most animals were studied only on one occasion, although seven were radio-tracked twice (four males, three females) and two were radio-tracked on three occasions (both males).

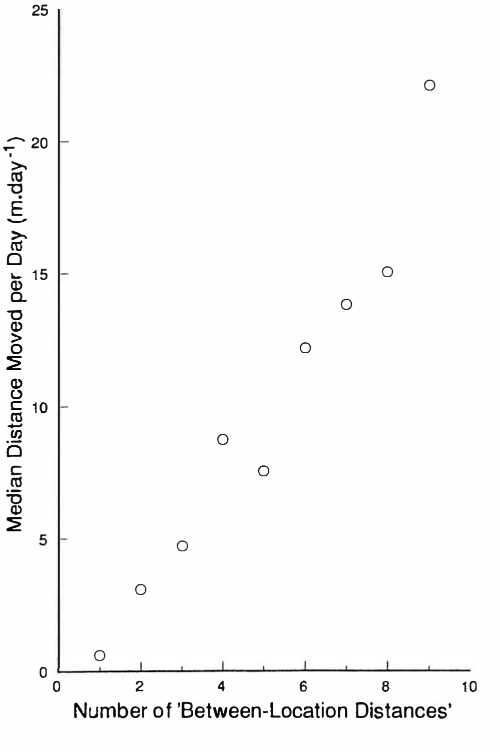

Fig. 2. Median distances moved during a day (m day^{-1}) and the number of between locations distances used in the calculation of daily movement rates (distances moved during a day were calculated from the sum of all straight line distances measured between subsequent sightings during each day [n = 8, 37, 12, 23, 44, 61, 69, 6 and 2 for 1 to 9 measured distances in any day, respectively]).

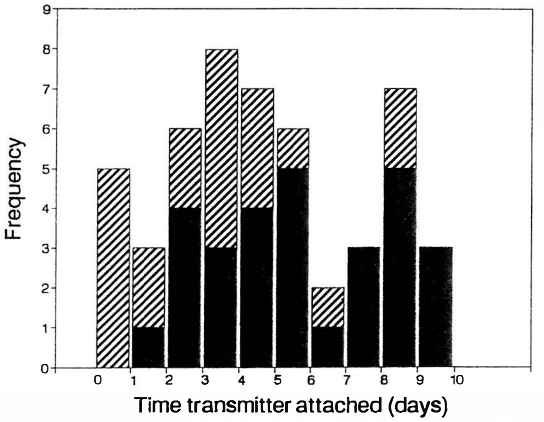

Fig. 3. Duration of attachment of radio-transmitters to *Coronella austriaca* showing those occasions where the transmitter was removed as planned (solid shading) and those cases where the radio-tracking period was terminated early due to experimental difficulties (hatched shading) [see text for details].

Radio-tracking periods were intentionally kept short with transmitters being deliberately removed between 1.34 and 9.71 days after attachment. In the majority of cases transmitters were left on for more than 4 days before removal. The short tracking periods were considered desirable due to the short life expectancy of the radio-transmitter batteries (maximum of 21 days) and with a view to minimising the possibility of harm to the animal. Seventeen experiments were terminated early due to experimental difficulties (and on five of these occasions transmitters were detached less than one day after attachment); on seven occasions the transmitter was removed from the animal when it was found to be snagged on vegetation or below ground, on six occasions the transmitter was shed (twice in connection due to the snake shedding its skin) and in three cases the transmitters malfunctioned. There was a single fatality of a radio-tagged snake; this, however, appeared to be as a result of predation rather than as a direct result of the attachment of the radio-transmitter. On five occasions the transmitter on the snake became snagged early during a radio-tracking period and the animal could be freed and subsequently followed. In all cases where the transmitter was not shed, the animal was recaptured and the radio-transmitter removed.

For the purpose of analysis three seasons were identified (which included all observations). These were defined as: spring = 1 March to 31 May; summer = 1 June to 31 August and autumn = 1 September to 31 October. Eight radio-tracking periods were exclusively or mostly in the spring, 29 in summer and 13 in autumn. These periods ranged between 1.84 and 6.17 days (mean=4.07$\pm$1.44 days), 0.07 and 9.71 days (mean=4.31$\pm$2.96 days) and 0.76 and 9.03 days (mean=6.03$\pm$2.85 days) for spring, summer and autumn respectively.

ASSESSMENT OF METHODOLOGY

The effect of attachment of a radio-transmitter on the movement and activity behaviours of smooth snakes was investigated in the laboratory using time-lapse video recording.

Two smooth snakes (three males, one female) were observed during each of two experiments. A metal and brick indoor vivarium was divided centrally into two identical arenas. Each measured 168 cm by 109 cm with walls 61 cm high and an overhanging lip to prevent escape. The floors were concrete and covered with a generous layer of sand. Each arena had a 275 W heat lamp positioned at the centre of one side (and 30 cm above the ground), a centrally positioned wooden board providing cover and four petri dishes of water. A video camera was positioned such that the floor of both arenas could be filmed at the same time. The heat lamp and overhead fluorescent lighting in the room were controlled via time switches to simulate approximately current day lengths (Heat lamp on 0745 to 1645 hr; overhead lighting on 0500 to 2100 hr). Two red 60 W bulbs were used to allow filming at night.

One snake was introduced to each of the arenas and left to become accustomed to the surroundings for at least 24 hr. Each snake was then removed from the arenas and handled as if being first captured in the field (i.e. weighed and measured). A radio-transmitter was then attached to one of the snakes and then both animals were released back to the their respective sides of the vivarium. The time-lapse recording was then started.

Between two and three days later, both snakes were removed from the arenas, 'processed' as before and the transmitter removed from the first animal and attached to the second. On release the trial continued for two to three days. The two trials were necessarily short; the smooth snake is a protected species and the licensing conditions restricted keeping animals in captivity to a total period of seven days.

Behaviour was assigned to five different categories: "Below cover", "Inactive in open", "Active", "Movement thermoregulation" (the animals moving such that all or part of the body was in a circle where the ground temperature was raised above normal due to the influence of the heat lamp [this area had been determined prior to the experiments]) and "Non-movement thermoregulation" (stationary within the area warmed by the heat lamp). Hourly movement rates were determined by tracing the movement of the animals from the video screen using a map measurer. Analysis of both activity and movement behaviour was performed on data for the whole day and where the data were divided into six 4-hr time periods (0100-0459 hr, 0500-0859 hr, 0900-1259 hr, 1300-1659 hr, 1700-2059 hr and 2100-0059 hr).

Changes in weight were described as rates per day (g day^{-1}) and compared between radio-tagged and untagged animals.

RESULTS

HOURLY MOVEMENT RATES

Hourly movement rates showed a strong positively skewed distribution. No difference was detected in hourly movement rates between sexes (Mann-Whitney U-test; U= 128498.5, n_1= 652, n_2= 422, $P>0.05$) and thus data were pooled for further analysis.

The frequency distribution of hourly movement rates for both sexes (with 0.5 m h^{-1} intervals) is presented in Fig. 4. Movement rates varied between 0.00 m h^{-1} and 44.26 m h^{-1} (n=1074). A median movement rate of 0.54 m h^{-1} was obtained. Notably 672 observations (62.6%) were of movements under 1.00 m h^{-1} and only 41 observations (3.8%) were of movements over 10 m h^{-1}.

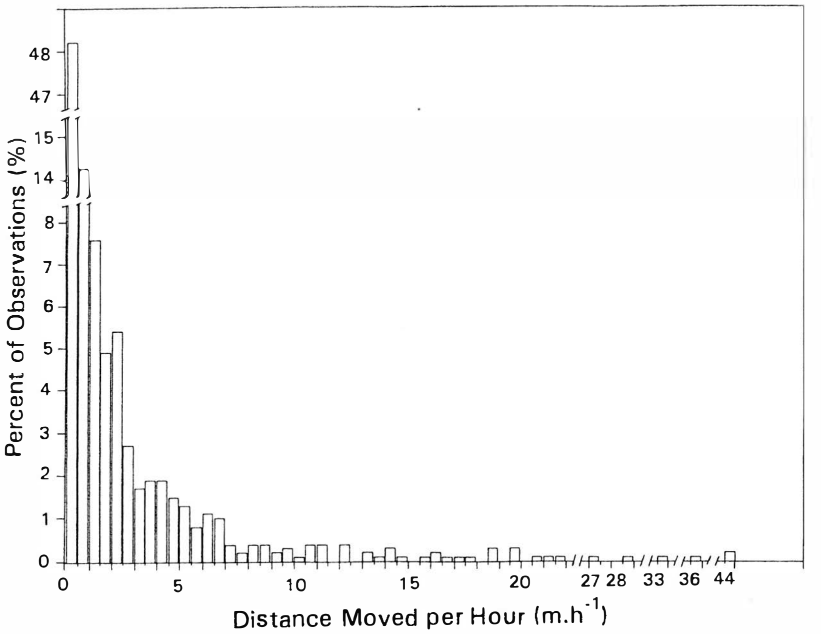

Fig. 4. Hourly movement rates (m h⁻¹) of *Coronella austriaca* as determined by radio-tracking (n=1074); intervals between successive locations were between 1 and 3 hr. Data are presented as classes with increments of 0.5 m h⁻¹.

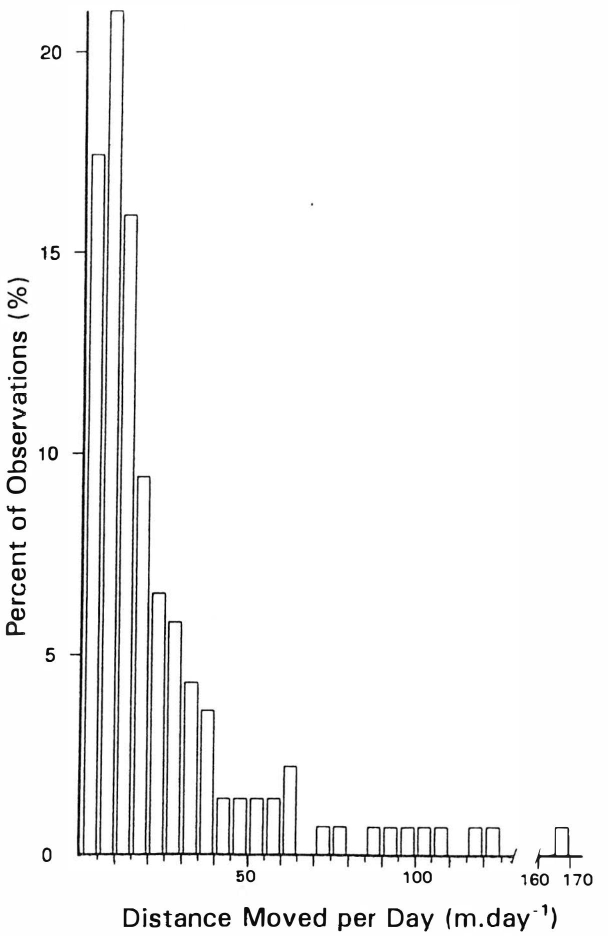

Fig. 5. Daily movement rates (m day⁻¹) of *Coronella austriaca* as determined by radio-tracking (n= 138); daily movement rates were calculated only where six or more 'between locations distances' were record. Data are presented as classes with increments of 5 m day⁻¹.

DAILY MOVEMENT RATES

No difference was detected between daily movement rates of males and females (Mann-Whitney U-test; U= 1890.0, n_1 = 80, n_2= 58, P>0.05); subsequent analysis was therefore restricted to combined data.

A strong positively skewed distribution was obtained for daily movement rate (Fig. 5, where data are presented using 5 m day⁻¹ intervals) with values ranging between 0.00 and 166.81 m h⁻¹. From 138 estimates of daily movement rate, a median value of 13.30 m day⁻¹ was obtained. Twenty-four records (17.4%) were less than 5 m day⁻¹ and 53 (38.4%) were less than 10 m day⁻¹. Only 5 observations (2.9%) were of movement rates greater than 100 m day⁻¹ and 18 (12.3%) were in excess of 50 m day⁻¹.

SEASONAL VARIATION OF MOVEMENT RATE

No differences were detected for either hourly or daily rates of movement between the three seasons (Hourly rate : Kruskal-Wallis test, χ^2= 2.765, n= 1074, P>0.05; Daily rate : Kruskal-Wallis test, χ^2= 0.206, n= 138, P>0.05).

DIRECTION OF MOVEMENT

Total distances recorded during all 50 radio-tracking periods varied between 0.3 m and 317.0 m (this included four cases where only two consecutive observations were made which accounted for the lowest four readings (all below 2 m); the next lowest value was 4.7 m). In all cases where total distances moved exceeded 40 m, thus allowing statistical analysis (n=30), a significant deviation from even dispersion was detected (G-test; P<0.001 in each case).

Excluding the four values obtained from only two consecutive readings, net movements (distances between first and final observations) ranged from 1.6 m to 203.4 m (n= 46). Where values of the ratio of Net movement/Total movement were calculated, i.e. where Total movement exceeded 20 m (n=39), values ranged between 0.03 and 0.90. No difference was detected between the values of the ratio between males and females (Wilcoxon pairs test; $Z=1.603$, $n_1=15$, $n_2=24$, $P>0.05$) nor between any of the seasons when analyzed pair-wise (Wilcoxon pairs test; spring and summer: $Z=1.343$, $n_1=22$, $n_2=5$; spring and autumn: $Z=1.637$, $n_1=12$, $n_2=5$; summer and autumn: $Z=0.252$, $n_1=12$, $n_2=22$; $P>0.05$ in all cases).

These data can be divided into two categories; those in which the value of the ratio is less than 0.50 (such that under half of the total movement contributes to net dispersion) and those with a ratio value of 0.50 or more (such that half of more of the total movement contributes to net dispersion). This division shows that on 20 occasions (51.3%) a ratio of less than 0.50 was obtained and in 19 cases (48.7%) the ratio was 0.50 or more. The majority (74.4%) of these values lie between a value of 0.25 and 0.75 (29 cases) with 5 observations each being below 0.25 and above 0.75 (12.8%).

Where greater than two days data were available, net dispersion rates varied between 0.19 and 52.9 m day^{-1} ($n=40$). No differences were detected in this rate between the sexes (Wilcoxon pairs test; $Z=1.311$, $n_1=16$, $n_2=24$, $P>0.05$) nor between any of the seasons when analyzed pair-wise (Wilcoxon pairs test; spring and summer: $Z=1.371$, $n_1=22$, $n_2=6$; spring and autumn: $Z=0.983$, $n_1=12$, $n_2=6$; summer and autumn: $Z=0.523$, $n_1=12$, $n_2=22$; $P>0.05$ in all cases). The data were highly skewed, with 12 observations (30.0%) being of rates below 5 m day^{-1}, 15 (37.5%) between 5 and 10 m day^{-1} and four (10.0%) being in the range 10 to 15 m day^{-1}. The remaining nine records (22.5%) were fairly evenly spread between values of 15 and the upper value of 52.9 m day^{-1}.

ASSESSMENT OF METHODOLOGY

As with data recorded in the field, the frequency distributions of hourly movement rates were highly positively skewed. No significant differences were observed between the hourly movement rates of those animals with radio-transmitters attached and those without when looking at pooled data for observations over the whole 24 hr period (Wilcoxon pairs test; $Z=0.520$, $n_1=237$, $n_2=239$, $P>0.05$). A significant difference in movement rate was observed during only one of the six 4-hourly periods, 0500-0859 hr, during which snakes without transmitters moved a greater distance than those with transmitters attached (Wilcoxon pairs test; $Z=2.082$, $n_1=40$, $n_2=40$, $P<0.05$). During the other five periods no differences were detected in movement rate (Wilcoxon pairs test; 0100-0459 hr: $Z=0.138$, $n_1=42$, $n_2=40$, $P>0.05$; 0900-1259 hr: $Z=0.306$, $n_1=37$, $n_2=37$, $P>0.05$; 1300-1659 hr: $Z=1.613$, $n_1=40$, $n_2=40$, $P>0.05$; 1700-2059 hr: $Z=0.712$, $n_1=40$, $n_2=40$, $P>0.05$; 2100-0059 hr: $Z=0.363$, $n_1=40$, $n_2=40$, $P>0.05$).

The proportions of time spent in each activity are summarised in Fig. 6. No differences were detected in pair-wise comparisons of behaviours using Mann-Whitney U-tests ($P>0.05$) for the whole day nor for any behaviours in any time period except for 'Active' (05-0859 hr) and 'Below cover' (05-0859 hr). During this period snakes fitted with radio-transmitters were under cover more often (29.7% of time cf. 15%: $U=584$, $n_1=40$, $n_2=40$, $P<0.05$) and were active for a smaller proportion of time than were those that were not radio-tagged (32.8% cf. 49.1%: $U=570$, $n_1=40$, $n_2=40$, $P<0.05$).

Mean rates of change of body weights of captive animals during these experiments were -0.325 g day^{-1} $\pm$ 0.442 ($n=4$) for animals with radio-transmitters attached and -0.578 g day^{1} $\pm$ 0.889 ($n=4$) for snakes without transmitters. These values are not significantly different (Student's t-test; $t=0.513$, df=6, $P>0.05$).

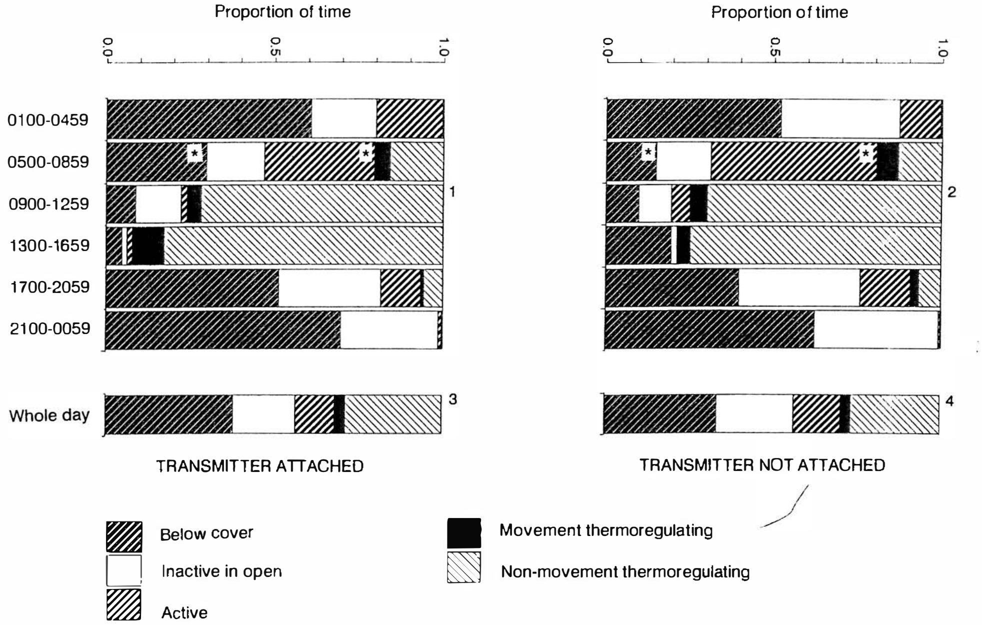

Fig. 6. Proportion of time assigned to each of five defined behaviours by snakes with radio transmitters attached and those without radio transmitters attached during six 4 hr periods and over the whole day ($n=40$ hourly observations in all cases except 1. $n=37$; 2. $n=36$; 3. $n=237$ and 4. $n=236$.) * denotes a significant difference between proportions of time spent on each behaviour by snakes with and without transmitters attached (at 5% level).

DISCUSSION

Radio-telemetry proved to be a very valuable technique for studying the movement behaviour of smooth snakes, since this allowed a reliable and consistent sampling regime to be followed. The laboratory study, although necessarily short in duration, corroborated the subjective observations made in the field that the attachment of radio-transmitters did not affect the behaviour of the snakes. However the physical bulk of the transmitters did occasionally impede movement of animals particularly when they were travelling through vegetation or moving below ground. Notwithstanding this, most snakes were able to free themselves quickly, or where this was not the case data were discarded, and it is the view of the experimenters that the movement data obtained by this method are representative of the species.

The external attachment of transmitters was not considered an ideal solution; however it was one borne of necessity. Force feeding transmitters has been used on this species (de Bont, van Gelder & Olders, 1986) but was not considered during this study for two reasons. Practically there was concern about being able to develop a transmitter package of dimensions that allowed it to be force fed to a small snake like *C. austriaca* (and have an aerial that gave adequate range). In addition, behaviour may be affected by the presence of food (or similar) in the gut which has reportedly induced thermophilic responses (Regal, 1966; Lutterschmidt & Reinert, 1990). Surgical implantation could not be entertained since at the time of the study such methods were not permitted in British law; further such a method would be impractical given the size of the available transmitters (and their short battery life) relative to the size of the animal and would provide an unacceptable risk to an endangered species.

The external attachment of transmitters together with a short study period, during which the animal would be regularly located, meant that welfare of the animal could be closely monitored and the radio-transmitter removed if problems occurred. Accepted consequences of this approach were the need to have only short tracking periods and the fact that transmitters would be shed when the animal sloughed its skin. Regular location allowed detailed study of short term movements which compensated for the short period over which transmitters were fitted. Thus movement behaviours were 'sampled' during intensive study of different animals. Extended study periods where transmitters are left attached for greater lengths of time (which are possible using internally fixed transmitters) would have provided greater information about seasonal movements and range use. Frequently though, during such studies, the detailed observation of animals during each day is neglected.

The absence of detectable differences between the sexes in either hourly or daily movement rate, or in the degree of directional movement, indicated that both sexes have similar dispersal potentials during the short term. Thus, for further discussion, comments will be restricted to dealing with the two sexes together.

Radio-tracking data from the present study showed that movement rates of *C. austriaca* are small, with 62.6% of hourly movement rates being less than 1 m h^{-1} and 18.7% showing no movement at all. These observations were restricted to day time (and hence the active period of this diurnal species), and thus excluded the period of over night inactivity. This therefore corroborated the generally reported thesis that this species is relatively immobile (Breeds, 1973; Spellerberg & Phelps, 1977; Goddard, 1981; Nature Conservancy Council, 1983). A comparison with studies of the movement rates of the two other species of snake found in Britain (*Vipera berus* (family Viperidae) and *Natrix natrix* (family Colubridae)) indicates that *C. austriaca* is the least mobile of the three (Prestt, 1971; Madsen, 1984; Brown, 1991).

A habitually low movement rate will confer several advantages to an animal. In an ectotherm, such as *C. austriaca*, movement will greatly increase metabolic rate, typically up to ten fold (Bennett, 1982). In addition, rapid movements in reptiles generally require anaerobiosis. Thus it is energetically and metabolically beneficial for a reptile to minimise its movements. Lowered energy expenditure, in turn, results in a decreased need to actively forage for food.

It is worth considering the need for movement at all during much of the day. One of the primary concerns of an ectotherm is the maintenance of body temperature. Selection of a thermally heterogenous environment may allow behavioural thermoregulation, and avoidance of extremes of temperature, through only small movements. In addition the smooth snake is cryptically coloured and seemingly relies on this to avoid detection by both predators and prey. Crypsis may be enhanced through long periods of immobility.

A consideration of maximum movement rates will give an indication of the species' dispersal potential. Hourly movement rates were based on approximately two hourly intervals; thus the minimum straight line distance used in the calculation of hourly rate were sometimes quite large. The four highest movement rates (32.99, 35.72, 44.07 and 44.26 m h^{-1}) were obtained from measured distances of 62.7, 81.55, 94.02 and 98.11 m. It is likely that a greater estimate of hourly movement rate would have been obtained if shorter time intervals had been used.

Only five observations (2.9%) of daily movement rates exceeded 100 m day^{-1}, with these data being obtained from both male ($n=3$) and female ($n=2$) snakes. (It is worth noting that there was one additional case where movement during one day was in excess of 100 m, and in fact was the largest observed movement during any day. However this record was excluded from the above analysis since it was based on the summation of only four straight line distances after which the transmitter was removed; this was a female that moved 170.92 m during its final period of radio-tracking).

Similar maximum movement rates were reported by Breeds (1973) who, in his recapture studies, observed movement rates of 20, 36 and 46 m h^{-1} for two individuals (recapture intervals of between 1.75 and 5.0 h); he also reported a further movement of 180 m between two successive afternoons by one animal. The absence of clearly distinguishable differences in movement rates between seasons could indicate that there are not distinct 'migration movements' at either end of the activity period. This is consistent with Phelp's (1978) observations of range use in which he suggested that *C. austriaca* do not use separate summer and winter ranges. Dispersion is a product of net directional movement and not simply a reflection of the total amount of movement that occurred. In over half the cases studied, under 50% of the measured movement contributed to overall dispersion and in over 12% of the cases this figure was under 25%. Thus much movement would have been responses to local factors; perhaps determined by thermoregulatory needs or movement between places offering shelter. However in just under half the cases there was the tendency to disperse, with over half the recorded movement during a period resulting in movement away from the original point of capture. Over 12% (5) of observations were of snakes whose net movement was 75% or more of their total distance moved. The daily rate of 'dispersion' too indicates a slow, but gradual movement away from any particular location.

These data indicate that *C. austriaca* do not, as a rule, occupy fixed dens for prolonged periods (compared with, for example, *Coluber viridiflavus* (Ciofi, Chelazzi & Della Santina, 1992)). However they move through the habitat at differing rates; some staying resident in a general area for some while whilst others will pass through an area quite quickly. Gravid female snakes seemed to be more frequently encountered in restricted areas, often in association with a favourable aspect for basking and some even showed repeated use of certain features for over night refuges. However the data reported here indicate that this is not always the case (and some female snakes were quite mobile).

These observations are further corroborated by looking at the incidence of recaptures of smooth snakes at the two study sites during the course of the three year study period (Gent, 1988). In total 111 different animals were captured by hand at the two sites (52 at Site 1 and 59 at Site 2). Of these 81 (73.0%) were only seen in one year, 25 in two years (22.5%) and only 5 (4.5%) were seen in all three years of the study. Further, excluding radio-tracking data, 53 were only caught on one occasion (47.7%) and 91 (82.0%) were caught five times or less. Only thirteen animals (11.7%) were caught ten or more times.

This generally restricted movement behaviour shown by *C. austriaca* is pertinent to those involved with habitat management. The low movement of the species means that animals are likely to remain within a limited home range during the short term. Sites should therefore be managed to ensure that all features needed by the species are available within relatively discrete patches; thus feeding and thermoregulatory requirements and the provision of shelter and protection should all be available within a limited area. Nonetheless, the actual ranges used by the species during the longer term are likely to be relatively large. Thus a further consideration arising from the nature of movement of the species is that the likely impact of habitat fragmentation on the species will be greater than it would be for a species that is able to travel much greater distances and move much more rapidly.

The behaviour also has notable implications for survey and site assessment. Observations of smooth snakes in a particular part of a site at any one time are likely to considerably under represent the total population that uses that area.

ACKNOWLEDGEMENTS

The authors are grateful to the Forestry Commission for permission to work on their land and to the Nature Conservancy Council for providing the necessary licences to work on *C. austriaca* and for some supplementary funding. In particular the assistance of Peter Eccles (Forestry Commission), Nick Smith and Peter Hillier (Southampton University) is acknowledged. The study was made during a Natural Environment Research Council studentship (to AHG).

REFERENCES

Bennett, A. F. (1982). The energetics of reptilian activity. In *Biology of the Reptilia* Vol. 13, 155-199. Gans, C. and Pough, F. H., (Eds). New York and London: Academic Press.

Breeds, J. M. (1973). *A study of the smooth snake (Coronella austriaca) in the Purbeck area.* Unpublished report, Nature Conservancy Council, 23 pp (plus Appendices).

Brown, P. R. (1991). *Ecology and vagility of the grass snake, Natrix natrix helvetica LACEPEDE.* Unpublished PhD thesis, Southampton University, 197 pp.

Ciofi, C., Chelazzi, G. & Della Santina, P. (1992). A new technique of radio-tracking snakes: external implantation of transmitters. In *Wildlife Telemetry: remote monitoring and tracking of animals*, 491-494. Priede, I. G. & Swift, S. M. (Eds) New York and London: Ellis Horwood Limited.

Freedman, B. & Catling, P. M. (1979). Movement of sympatric species of snake at Amherstburg, Ontario. *Can. Field Nat.* **93**, 399-401, illustr.

de Bont, R. G., van Gelder, J. J. and Olders, J. H. J. (1986). Thermal ecology of the smooth snake, *Coronella austriaca* Laurenti, during spring. *Oecologia* **69**, 72-78.

Gent, A. H. (1988). *Movement and dispersion of the smooth snake Coronella austriaca Laurenti in relation to habitat.* Unpublished PhD thesis, Southampton University, 529 pp.

Goddard, P. (1981). *Ecology of the smooth snake Coronella austriaca LAURENTI in Britain.* Unpublished PhD thesis, Southampton University, 222 pp.

Lutterschmidt, 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**, 39-42.

Madsen, T. (1984). Movements, home range size and habitat use of radio-tagged grass snakes (*Natrix natrix*) in southern Sweden. *Copeia* **1984**, 707-713.

Nature Conservancy Council (1983). The ecology and conservation of amphibian and reptile species endangered in Britain. *Report of ad hoc working committee (Wildlife Advisory Branch)*, 93 pp.

Phelps, T. E. (1978). Seasonal movements of the snakes *Coronella austriaca, Vipera berus* and *Natrix natrix* in southern England. *Br. J. Herpet.* **5**, 775-761.

Prestt, I. (1971). An ecological study of the viper *Vipera berus* in southern Britain. *J. Zool. Lond.* **164**, 373-418.

Regal, P. J. (1966). Thermophilic response following feeding in certain reptiles. *Copeia* **1966**, 588-590.

Spellerberg, I. F. & Phelps, T. E (1977). Biology, general ecology and behaviour of the snake *Coronella austriaca* LAURENTI. *Biol. J. Linn. Soc.* **9**, 133-164.

Tiebout III, H. M. & Cary, J. R. (1987). Dynamic spatial ecology of the water snake, *Nerodia sipedon. Copeia* **1987**, 1-18.