Use of artificial refuges by the northern viper *Vipera berus* - 2. Thermal ecology

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ABSTRACT - The body-surface temperatures (T_b) of northern vipers (*Vipera berus*), under galvanised corrugated-iron refuges ('tins') or basking in the open, were investigated in a chalk downland reserve. Corresponding operative temperatures (T_e) were demonstrated by physical models. Although viper T_b under tins reached 34.4˚C, once T_e had reached 32.9˚C no viper T_b exceeded this temperature; 32.9˚C appears to be a practical estimate of the vipers' upper thermal set point ($T_{set\ upper}$). In March/April, there was little or no difference in T_e between locations in the shade and under tins, resulting in no incentive for vipers to use tins. At this time, males basking openly had body temperatures that averaged 8.6˚C warmer than the T_e under tins. The heating rate of vipers below tins averaged 0.08˚C±0.03˚/min, much lower than the observed rates for basking in the open reported previously. The relatively poor thermal performance of tins suggests that design improvements could deliver better results.

INTRODUCTION

Artificial refuges are a valuable asset in reptile monitoring programmes and may also have conservation value where there is a trade-off between predator avoidance and the needs of thermoregulation (Lelièvre et al., 2010). The provision of artificial refuges has also been shown to be an effective approach to the recolonisation of degraded sites (Croak et al., 2010). Consequently, a better understanding of refuge use by reptiles offers potential advantages for both monitoring and conservation management.

As a component of a long-term monitoring programme for the northern viper (*Vipera berus*) on chalk downland in Kent (UK), we deployed both tin and felt refuges (Hodges & Seabrook, 2016a). When the vipers attempt to attain optimal body temperatures (T_b) they may bask openly in sunshine and/or use refuges; in this chalk downland reserve vipers were much more commonly found under tins than felt refuges (Hodges & Seabrook, 2016b). Gross control of body temperature may be achieved by shuttling between shade and sunshine, or by careful positioning between the two when partially concealed by vegetation ('mosaic basking'). Fine control is achieved by changing both body orientation to the sun and body posture; *V. berus* has been described as a posturing heliotherm (Spellerberg, 1976). The upper thermal set point ($T_{set\ upper}$) of *V. berus*, effectively the body temperature that is optimal for current physiological requirements, has been determined in a thermal gradient and ranges from 31.7˚-33.8˚C (Herczeg et al., 2007); data from other authors is consistent with this (Saint Girons, 1975, 1978; Spellerberg, 1976; Vanner, 1990; Gaywood, 1990; Gaywood & Spellerberg, 1995). Vipers at spring emergence, during digestion of meals, or pre-moult spend longer periods basking and control their T_b within a narrow range, this is referred to as K-thermoregulation. Alternatively, vipers engaging in extensive foraging enter cooler areas resulting in a more variable T_b, referred to as r-thermoregulation. It is suggested that there is a continuous range between r- and K-thermoregulation determined by physiological state (Vanner, 1990). Physiological state is also important as slightly higher temperatures were reported from vipers digesting large meals (Saint Girons, 1978) and on average gravid females selected higher temperatures (Lourdais et al., 2013). Life stage may also affect the selected body temperature although to date almost all studies of *V. berus* thermal ecology have focused on adults. However, when juvenile *V. berus* were presented with a temperature gradient in springtime their selected temperature was on average only 28˚C, which was 5˚C cooler than adults (Herczeg et al., 2007).

The circumstances under which *V. berus* selects, remains under, and leaves tins are poorly known; this limits the interpretation of monitoring data. Furthermore, the potential role of refuges in the conservation management of *V. berus* appears not to have been considered in any detail. Consequently, in 2014 we initiated investigations into the use of tins in relation to the thermal ecology of *V. berus*. These included measurement of viper body temperatures (T_b) and of physical models that estimate the operative temperatures (T_e) of associated microhabitats.

MATERIALS AND METHODS

Study site and refuges

Details of the study site and refuges are presented in Hodges& Seabrook (2016a). In brief, the investigation was part of a long-term monitoring study on a chalk downland nature reserve at about 51˚N, 0˚E, with a total open area of 11.1ha. The study was confined to 2014 and included observation of vipers under 46 pairs of refuges of galvanised corrugated-iron sheets ('tins') and roofing felt, deployed at a density of about 4 pairs/ha. The ground below refuges lacked vegetation.

The site was visited 79 times for many hours from March to October. Observations were made morning and afternoon on days when weather conditions were not excessively wet or windy. A standard route was followed between refuge locations. Photographs were taken of viper head-scale patterns; these were coded then entered into a database to facilitate individual recognition (Benson, 1999). Adult recruitment tables suggested that on average there were about 4-5 adult vipers/ha in 2014. Life stages were defined as before (Hodges& Seabrook, 2016a) and observations disaggregated by gender except for juveniles. The study involved no animal handling in order to minimise disturbance and stress.

Physical models

Operative temperatures (T_e) were estimated using physical models (Peterson et al., 1993; Shine & Kearney, 2001). These consisted of copper pipe (ID 20mm, wall 1mm thick, length 150mm) flattened so that about 40% of surface was in contact with the substrate beneath, sprayed with grey paint (Surface primer, matt, Rust-oleum), and sealed at either end with silicon sealant and fixed into the ground towards each end with an overlapping strand of wire. The models indicated the temperatures of microhabitats available to vipers and served as null models for quantifying the extent of thermoregulation. Twenty one tins had models beneath them. In addition, at five widely spaced refuge positions each tin had two other closely located models, one exposed to direct sunlight and one in the permanent shade of taller vegetation.

Temperature measurement

Infrared thermometer guns (Foxnovo DT8380) were used to collect surface temperatures of vipers, physical models and tin refuges. These thermometers measure in the range -50˚C to +380˚C, have a distance to spot ratio of 8:1, and a resolution of 0.1˚C. Different units, when measuring the same surface temperature, gave reading that varied by <0.3˚C. A clear plastic tube, 1.8 cm long and 1.8 cm wide, was fixed to the front of each thermometer to act as spacer. To make measurements, the spacer was brought to almost touch the upper surface at the middle of a viper, or in the case of small specimens the centre of the coiled body, ensuring that only the animal was included within the measurement. The recorded temperature was of the dorsal body surface and may be different from internal or ventral surface temperatures. In nearly all cases, measurements were made of vipers that were individually distinguishable using their head-scale patterns.

Calibrations were prepared for the various subjects of temperature measurement. A digital thermometer (6802II) with thermocouples was calibrated against a laboratory certified calibration thermometer at temperatures ranging from 0˚C to 50˚C. The thermocouples were placed inside the cadaver of an adult male viper and inside a physical model. These were located on a brewing heat mat. As temperatures rose readings were taken at regular intervals with the IR thermometer from 10˚ to 40˚C and calibration curves prepared for the model and the snake. A calibration was also constructed for corrugated iron refuges by taping thermocouples to the under surface of a refuge, exposing it to sun light, and taking IR thermometer readings as the refuge warmed from 15˚ to 55˚C.

Where possible, temperature measurements were taken from vipers both under and away from tins. Occasionally, multiple temperature measurements of the same viper beneath tins were made on the same day and when these were made on consistently sunny days it was possible to use the measures to estimate the rate at which vipers were warming up under the tins. All times of temperature measurement are quoted as Greenwich Mean Time.

Statistical analysis

Differences between viper life stages in numbers above and below T_e were evaluated for statistical significance using χ^2 tests (Siegal, 1956). The statistical significance of simple linear correlation coefficients (r) was determined from standard tables (Bailey, 1966). Differences were treated as statistically significant when the probability of them occurring by chance was 5% or less ($p \leq 0.05$).

RESULTS

Operative temperatures (T_e)

In March, the models located in direct sunlight were warmer than those in the shade or under tins by an average of about 7˚C (Fig. 1), the models in the shade were about 0.8˚C warmer than those under tins (Fig. 1). As shade temperatures and those under tins were similar, there can have been little or no incentive for vipers to rest under tins. This is confirmed by measurements in March of 11 males basking in sunshine. When compared with the temperatures of models under the closest tins, the viper body temperatures (T_b) were on average 8.6˚± 5.6˚C warmer than the models. Likewise the models in sunlight were warmer than those under tins by an average of 6.7˚ ± 5.2˚C.

From May to August temperature records from models under tins were higher than those in shade by 6.0˚ to 7.5˚C (Fig. 1). In the autumn, the temperatures under tins began to decline and the difference from models in the shade started to narrow in September to about 3.0˚C and then in October to only 2˚C (Fig. 1).

Taking one of these five refuge locations as an example, it can be seen that, as expected, the model exposed to direct sunshine was generally warmer than the model on the ground beneath the tin (Fig. 2) which in turn was generally warmer than the model in the shade.

Viper body temperatures (T_b)

The T_b of roughly similar numbers of known individual vipers of each life stage were recorded (7-10 individuals, Table 1); however adult females, especially those that were gravid, were measured more frequently resulting in about 50% more recordings (63) than average (40). Juveniles were seen less frequently with about 50% fewer records (21) than average.

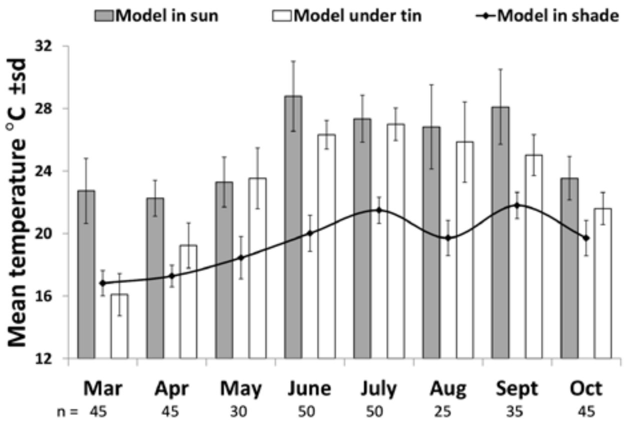

Figure 1. Mean (±SD) monthly temperatures ˚C of variously located physical models at five locations on chalk downland in 2014 in the period 09.00h to 12.00h (n = number of observations per bar)

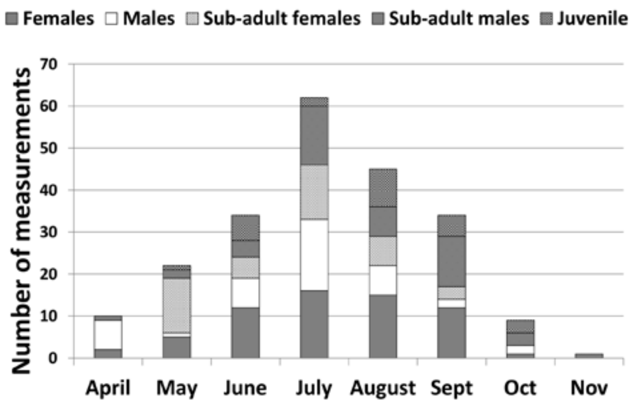

Figure 3. The frequency distribution of body-surface temperature measurements of different life stages according to months of the year in 2014.

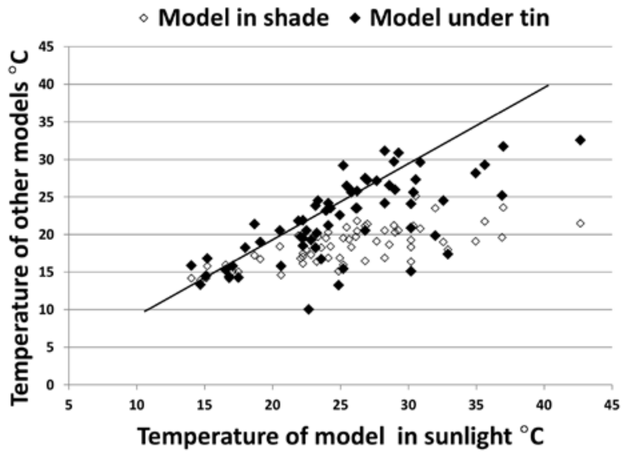

Figure 2. Relationship between the temperatures of the physical model in sunshine and the corresponding temperatures of models under tins or shaded by vegetation. Records are from March to October and made between 08.00h and 17.00h (N = 64). Above the solid line other models are warmer than the model in sunshine.

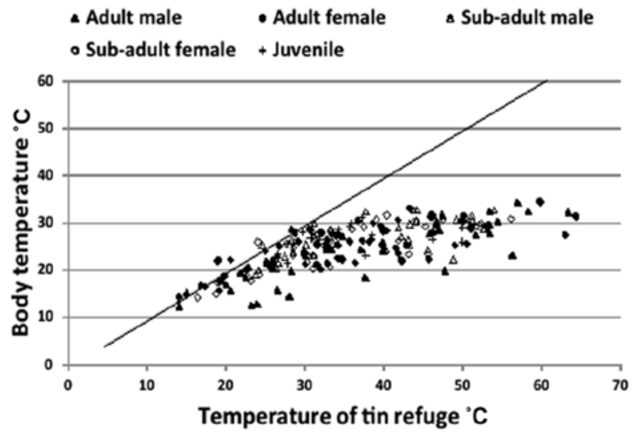

Figure 4. Relationship between the temperature of tin refuges and the body-surface temperatures of *V. berus* (T_b) of all life stage found beneath tin refuges (N = 211). Above the solid line, viper T_b was warmer than the corresponding refuge tin.

Table 1. Number and identity of individual vipers from each life stage for which temperature measurements were made while they were under tins in 2014 and the total numbers of temperature records for each life stage (n).

Male	n	Female	n	Sub-adult male	n	Sub-adult female	n	Juv	n
M39	23	F50	16	SM?	1	SF?	1	J162	2
M52	7	F53	14	SM33	7	SF40	2	J174	3
M53	2	F59	3	SM38	16	SF41	1	J176	2
M69	2	F60	2	SM43	6	SF54	17	J179	2
M85	2	F61	4	SM44	8	SF65	3	J191	1
M87	5	F64	1	SM45	5	SF69	5	J192	1
M88	1	F81	13	SM51	1	SF71	1	J194	4
		F84	1			SF73	2	J197	5
		F92	9			SF75	8	J?	1
						SF79	1		
7	**42**	**9**	**63**	**7**	**44**	**10**	**41**	**9**	**21**

The temperature measurements for each life stage were distributed over the period April to October (Fig. 3); there was just a single observation in November.

When in full sunshine, the tins reached quite high operational temperatures; up to 65˚C. However, no viper life stages below these refuges were observed with body temperatures (T_b) more than 34.4˚C (Fig. 4).

Viper T_b frequently exceeded T_e beneath the tin (Fig. 5) and was recorded as high as 34.4˚C (Fig. 4). However, when models under tins reached a T_e of 32.9˚C or above all corresponding viper temperatures were at or below T_e (Fig. 5). This gives an approximation of $T_{set\ upper}$. The T_e under tins did not exceed 38˚C and only 8% of measures exceeded 32.9˚C.

For both adult and sub-adult males the majority of T_b measures were below T_e (Table 3), adult and sub-adult females were more evenly distributed between hotter and colder, while juveniles were on average mostly hotter than

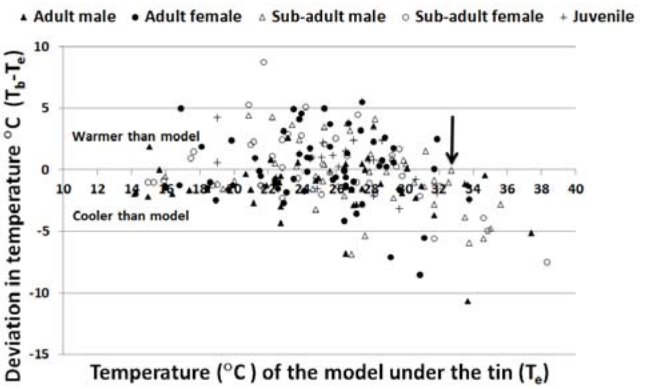

Figure 5. Deviation of *V. berus* body-surface temperature (T_b) from the temperature of the model on bare ground beneath the tin refuge (T_e). The arrow indicates the maximum T_e value for which there was an equally high viper T_b, to the right of the arrow all T_b values are lower than T_e.

Table 3. Numbers of records of body temperature (T_b) of each life stage under tin refuges that were warmer or cooler than the corresponding physical model (T_e), values with no letter in common are significantly different (p<0.05)

	Males		Females		Juveniles
	Adult	Sub-adult	Adult	Sub-adult	
n=	42	44	63	41	21
Warmer than model	10	16	29	26	12
Cooler than model	32	28	34	15	9
% warmer	23.8% a	36.4% abc	46.0% bc	51.0% c	57.9% c

T_e (Table 3). There was significant heterogeneity between life stages in the numbers of individuals that were warmer or cooler than the model under the tin (χ^2 = 15.83, df = 4, p<0.01). Pairwise comparisons suggest statistically significant differences between adult males and females, sub-adult males and females, while only adult males were significantly different from juveniles (Table 3).

On most days, individual vipers had T_b measured only once. Occasionally, a viper would remain under the tin for an extended period and this gave the opportunity for a sequence of measurements that allowed daily fluctuations to be observed. The best case of this was a sub-adult female on the 1st July (Fig. 6). Initially, at 08.00h, the refuge was in partial shade. At this time the tin and model under the tin were just a little warmer than the viper, while the model exposed to direct sunlight was already some 6˚C warmer (Fig. 6). In the following 25 minutes the tin became exposed to full sunshine so that its temperature rose by about 15˚C, making it about 5˚C hotter than the model in sunshine. Below the tin this resulted in an increase of 3˚C of both the viper and model. There followed a sunny period of 65 minutes that heated the tin to about 52˚C, making it about 15˚C hotter than the model in sunshine. Below the tin the viper and model both reached about 30˚C. Later in the day (16.00h) the temperature of both the tin and model in sunshine fell quite sharply. However, below the tin there was a lag in the temperature fall of model and viper. Interestingly, the lag in temperature decline of the viper was greater than the model giving the viper a 1˚C temperature advantage at 16.00h and, 55 minutes later, an advantage of just over 2˚C, presumably due to active thermoregulation by the viper and/or slightly greater thermal inertia. The observed temperature of the model placed in the shade of vegetation was very stable over the whole period of observation, fluctuating close to 20˚C (Fig. 6).

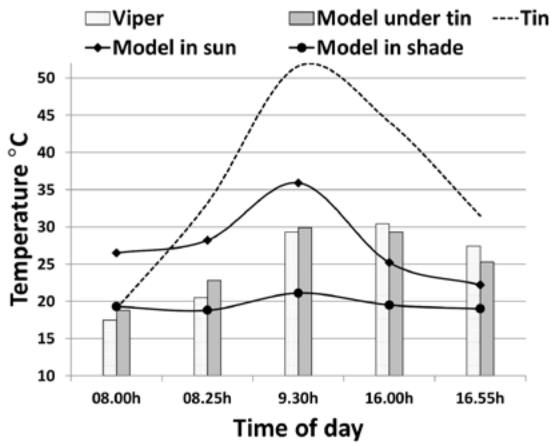

Figure 6. Body surface temperatures of a sub-adult female measured on five occasions on 1st July with corresponding temperatures of the tin under which it rested and physical models in the sun, in the shade or beneath the tin (note x-axis scale is not even)

From April to September, there were 18 occasions when the same vipers had more than one body temperature measurement on the same sunny day (adult males - 5, adult females - 3, sub-adult females - 8, sub-adult males 1, juvenile - 1). The temperature readings were on average 70±34 minutes apart and from this data the estimated heating rates ranged from 0.05˚C to 0.14˚C/min with an average of 0.08˚C±0.03˚/min.

DISCUSSION

The quickest way for vipers to warm themselves would appear to be to bask directly in sunlight rather than resting under tin refuges. This was demonstrated very clearly by temperatures of adult males in the open in March 2014 that were 8.6˚±5.6˚C warmer than the models under tins. Typically, males are very rarely found under refuges in the spring time prior to their first moult. At this time of year the operational temperature (T_e) indicated by physical models under tins was little different from that in the shade of vegetation suggesting that males are unlikely to select positions under tins as they would obtain little or no thermal advantage (Fig. 1). The months in which tin use by vipers are likely to be most favourable are when the models under tins are consistently warmer than in the shade, in this case May through to September (i.e. those months where the error bars of the models in the shade and under the tin show no overlap in Fig. 1). However, it seems likely that even under warm conditions the heating rates of vipers under tins are much lower than those in direct sunlight. In the summer, heating rates of vipers in the open of 0.48˚ - 0.58˚C/min have been recorded (Vanner, 1990) which are about x7 greater than the average of 0.08˚C/min (range 0.05˚ to 0.14˚C/min) observed in the current study. This is understandable as tins would be expected to reflect a significant proportion of solar radiation and radiate the remainder as much to the air above as to the ground below the tin; in effect the tins act as screens against rapid temperature rise.

When in full sunshine, tins were heated to as much as 65˚C and model beneath tins to 38˚C. However, no viper life stages below these refuges were observed with body temperature (T_b) exceeding 34.4˚C (Fig. 4). This implies active thermoregulation by moving to the coolest location below the tin, adopting postures and orientations that limit heat uptake and then, if necessary, leaving the tins for cooler places. The maximum T_b of 34.4˚C is a little higher than the expected upper thermal set point ($T_{set\ upper}$). It seems that vipers sometimes overshoot the preferred maximum and Gaywood (1990) recorded a maximum T_b of 40.4˚C. However, in this study at higher T_e the viper T_b became more constrained until T_e 32.9˚C when all viper T_b measurements were lower than T_e (Fig. 5). It would appear that 32.9˚C is a convenient and practical estimate of $T_{set\ upper}$ that fits within the range already suggested for this parameter, 31.7˚-33.8˚C (Herczeg et al., 2007). It may be more than a coincidence that observations on *V. berus* during mosaic basking, in thermally unlimiting conditions, returned an average T_b of 32.8±3.4˚C (Gaywood, 1990). The use of a refuge, such as a tin, that warms in the sunshine might reasonably be considered to be a variant of the more natural mosaic basking in providing warmth and cover simultaneously.

The majority of males, both adult and sub-adult, under tins were cooler than the T_e indicated by the corresponding model. Adult and sub-adult females were more or less evenly distributed above and below T_e, and juveniles were on average mostly hotter than T_e (Table 3). This suggests that the behaviour of the vipers in relation to refuges may differ, for examples if males are more inclined than other stages to leave refuges once $T_{set\ upper}$ is reached then those males observed would be more likely to be below T_e. Likewise if females are more inclined to remain under refuges when at or approaching $T_{set\ upper}$ then recorded temperature would be inclined to be higher. No evidence was found to support the earlier records of juveniles selecting lower $T_{set\ upper}$ than adults (Herczeg et al., 2007). However the original study referred only to springtime and as the immature stages emerge later from hibernation than adults then the lower temperature preference may well be a reflection of a time of year when the juveniles are still in a physiological transition that the adults have completed.

There is evidence to suggest that the thermal performance of tin refuges is relatively poor in relation to the needs of vipers. The low ground temperature below tins early in the season may account for the rarity of tin use by male vipers that emerge first from hibernation. Also the very slow warming rate of vipers below tins suggests that there are significant advantages in basking in direct sunshine, despite the obvious risks from predation. If the thermal properties of refuge tins were improved then vipers may gain increased benefits from them. This has been investigated by placing insulation mats beneath tins and is reported elsewhere (Hodges & Seabrook, 2016b).

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