Weather effects on intrahabitat movements of the western green lizard, *Lacerta bilineata* (Daudin, 1802), at its northern distribution range border: a radio-tracking study

P. Sound and M. Veith

Abstract: Daily activity patterns of male western green lizards, *Lacerta bilineata* (Daudin, 1802), at the edge of their northern distribution range in western Germany after the breeding season from June to October were recorded using implanted radio transmitters. Different activity indices discriminating between stimulation, duration, and length of movement were correlated with actual weather conditions (d_0) and with weather conditions on the 2 previous days (d_{-1} and d_{-2}). The lizards' dependence on weather showed two different phases throughout the study period. During the first period and in the period preceding a drastic change of weather in midsummer, weather had no significant influence on movement parameters. After that event, temperatures dropped and a strong dependence on weather of all movement parameters except those indicating displacements became apparent. Thresholds for 50% activity during this second phase were a maximum temperature of 17°C and a minimum humidity of 35%. Two days after periods of bad weather, the influence of weather conditions increased again. This can be explained by physiological deficits that require compensation during the period of marginal weather conditions prior to hibernation. Displacement movements were significantly longer than home-range movements and were neither triggered nor modulated by the weather. They must therefore represent activities such as patrolling territory boundaries.

Résumé : Les patterns quotidiens d'activité ont été enregistrés au moyen d'émetteurs radio greffés chez des lézards *Lacerta bilineata* (Daudin, 1802) mâles après la saison de reproduction de juin à octobre, à la limite nord de la répartition de l'espèce en Allemagne de l'ouest. Différents coefficients d'activité permettant de faire la distinction entre la stimulation, la durée et la longueur des mouvements ont été examinés en fonction des conditions climatiques du jour (d_0) et de celles des deux jours précédents (d_{-1} et d_{-2}). La dépendance à l'égard des conditions climatiques a mis en lumière l'existence de deux phases différentes. Durant la première période et durant la période précédant un changement radical de température au milieu de l'été, le climat n'avait pas d'influence significative sur les paramètres du mouvement. Après cela, les températures ont baissé et une dépendance très forte à l'égard des conditions climatiques est devenue manifeste dans tous les paramètres de l'activité sauf ceux reliés aux déplacements. Les seuils mesurés pour que se produise 50 % d'activité au cours de la seconde phase étaient de 17°C (maximum) et de 35 % d'humidité (minimum). Deux jours après des périodes de mauvais temps, l'influence des conditions climatiques augmentait de nouveau. Cette augmentation peut s'expliquer par les déficits physiologiques qui nécessitent d'être compensés durant la période de conditions climatiques marginales avant l'hibernation. Les mouvements de déplacement se sont avérés significativement plus longs que les mouvements à l'intérieur du domaine et ils n'étaient ni déclenchés, ni modulés par les conditions climatiques. Ils représentent donc sans doute des activités telles que les mouvements de reconnaissance le long des frontières du territoire.

[Traduit par la Rédaction]

Introduction

Intrapatch movements or station keeping (Dingle 1996) can be interpreted as foraging (repeatedly performing resource-finding and -utilisation activities), commuting (performing regular short-term movements for resource utilisation), or territorial behaviour. It is essential to discriminate between these alternatives when precise habitat models for conservation purpose are to be inferred. However, analysing such movements and distinguishing between them pose methodological problems. Many species are difficult to follow and most techniques such as mark and recapture, trapping, or simple observation only record single points during this behaviour (Drake and Farrow 1988; Kerlinger 1989; Gauthreaux 1991). Even when highly efficient tracking techniques like radiotelemetry or harmonic radar are applied (e.g., Cochran 1987; Jouventin and Weimerkirch 1990; Riley 1999), only the net results of movement are recorded, and most individual behaviour that occurs between two records may remain undetected. Therefore, indirect criteria, such as overall move-

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ment patterns or analysis of triggering events, may be useful for interpreting different kinds of movement within the framework of station-keeping.

Environmental stimuli combined with endogenous factors may trigger movement. Two principal kinds of external stimuli can be distinguished. Short but regularly occurring events such as rainfall may initiate spontaneous movement. In contrast, continuously changing environmental parameters, such as a longer photoperiod or increasing dryness, may stimulate movement when critical values are reached (Tauber et al. 1986).

Reptiles are suitable organisms for studying the costs and benefits of movement. In temperate zones, most are terrestrial, with a reduced likelihood of migratory movement. Since they are ectothermic vertebrates, their activity patterns depend mainly on environmental temperature and opportunities for thermoregulation. Thermoregulatory movements are especially crucial for reptiles of the temperate zone, since thermally optimal microhabitats are rare and become temporally more unstable. Therefore, costs of thermoregulation are thought to be a major limiting factor for northward range expansion of reptiles (Böhme 1978).

In Germany, the western green lizard, *Lacerta bilineata* (Daudin, 1802), lives at the northern edge of its distribution range (Naulleau 1997). It occupies widespread habitats such as meadows, vineyards, and hedges on the slopes of the River Rhine and some of its tributaries (Niehuis and Sound 1996). Although similar habitats are abundant, no populations are known north of the city of Koblenz. This is due solely to climatic limitations, especially the time needed for egg development (Rykena 1987; Böhme 1989). Nothing is known, however, about temperature constraints on the overall behaviour of lizards in such marginal habitats. Applying Kühnelt's principle of regional stenecy to a Mediterranean species like *L. bilineata*, we would expect that at the northern border of its distribution range, its thermal needs increase and may therefore constrain other behaviour associated with resource utilisation, such as feeding (Böhme 1978, 1989).

Consequently, we would expect lizards' daily movements to be exclusively influenced by actual weather conditions, with little time left for activities other than thermoregulatory behaviour and feeding. Since habitats of the western green lizard in Germany are characterised by a fine-grained mosaic of different microhabitats, thermoregulation and feeding should require frequent moving between appropriate microhabitats. We would therefore expect lizards to permanently commute between shelters, hunting grounds, and basking sites, almost exclusively according to actual weather conditions. To test this expectation under natural conditions, we radio-tracked adult male western green lizards. This remote-sensing technique allows for permanent re-location of individuals without overly disturbing them. To assess the influence of weather conditions on lizard movements we related movement parameters to weather parameters such as temperature, humidity, atmospheric pressure, wind speed, and rainfall.

Material and methods

Study site

We studied a population of western green lizards on the slopes of the River Rhine near the city of Boppard in western Germany. The slope is about 4 km long and covered with vineyards and cherry plantations that were abandoned about 20 years ago. The habitat consists of a mosaic of trees, shrubs, mesophilous vegetation, and open areas interspersed with rocks and stone walls. The lizard population consists of two subpopulations. The larger one occupies a 60-ha patch on the eastern part of the slope. A second, smaller subpopulation occurs in a 20-ha patch at the western edge around a small brook. Occasionally, single individuals are observed between the patches occupied by the two subpopulations along linear habitat elements such as railway embankments at the base of the slope.

The climate of the Middle Rhine valley can be characterised as sub-Atlantic. The average annual rainfall is about 570 mm, with an average maximum of 120 mm in summer, from June to September. The average maximum temperature in summer is 19°C and the average minimum temperature in winter, from December to March, is 1°C. The local xeric climate of the study site is primarily due to its geomorphology (southward exposure, black slate, and high inclination), which can change drastically within a short distance (Eriksen 1967).

Weather recording

Minimum and maximum temperature, relative humidity, and minimum and maximum atmospheric pressure were recorded at the centre and the top of the slope throughout the entire radio-tracking period from 18 June to 2 November 1996. Rainfall was recorded from 31 July to 2 November. Wind speed was determined indirectly by recording its effect on vegetation, following Sönning and Keidel's (1993) method. For correlation analysis with movement data, only weather data recorded during the daily activity period of the lizards between sunrise and sunset were used.

Radio tracking

We radio-tracked 11 male lizards, 10 of which originated from the larger subpopulation, after the breeding season between June and October 1996. After capture, the lizards were taken to the laboratory and transmitters and passive transponders were immediately implanted into the body cavity.

We used radio transmitters from Custom Electronics (Urbana, Ill.) that weighed between 2.6 and 4.9 g and were coated with paraffin. Relative transmitter masses in relation to lizard body masses ranged from 5.5 to 13%, with an average of 9%. They were implanted ventrally into the body cavity (between the 5th and 6th rows of scales). The incision was closed with a surgical suture. The second cut for extracting the first transmitter and implanting the second, where applicable, was made ventrally between the 6th and 7th rows of scales. After 1–3 days' recovery, all individuals were released at the point of capture.

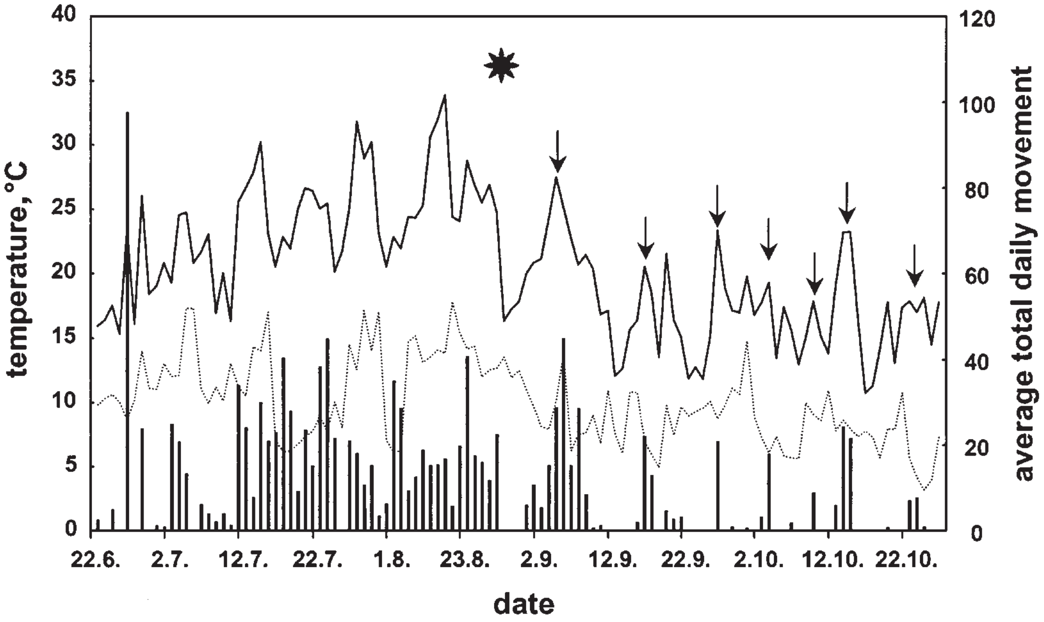
The position of the lizards was recorded 3–12 times per day (= number of scans) from dawn to dusk. Short distances between two successive locations were directly measured to the nearest 1 m. Long distances (>20 m) were estimated to the nearest 5 m from topographic maps (scale 1:5000).

The daily number of radio-tracked lizards ranged from one to eight, with an average of five. Each male was radio-tracked for 62 days, on average, with a minimum of 20 days and a maximum of 104 days. Three lizards (2, 5, and 6) were radio-tracked twice during the study period.

Analysis of movement data

We analysed two kinds of movement data: whether an individual moved (qualitative data) and how far it moved (quantitative data). Qualitative movement data were analysed to quantify the triggering effect of weather parameters and the duration of movements, whereas

Fig. 1. Minimum (dotted line) and maximum (continuous line) temperatures and average total distances covered per day (TDM; bars) throughout the study period (dates are shown as “day.month.”); the asterisk indicates a drastic change of weather on 26 August; in the second half of the study period, movements coincided with high maximum temperatures (arrows).



it was assumed that quantitative movement data would elucidate how weather parameters modulate movement capability.

To analyse the daily net result of a movement, we distinguished between home-range movements and displacement movements (DMs). Home-range movements were defined as daily movements around a shelter to which an animal returns at the end of the day (net movement = 0 m). DMs are daily movements between two shelters (net movement > 0 m) and can be characterised as the gross daily distance (overall distance) covered by an individual or as the net distance between the two shelters (nDM); thus, they represent the displacement distance covered from dawn to dusk. Consequently, total daily movement (TDM) is the average daily movement of all individuals, whether home-range movements or gross daily distance. To minimise the bias due to individual behaviour, all movements were averaged over the number of lizards simultaneously in the experiment. In addition, we only included days when at least three lizards were in the experiment.

We correlated five activity parameters with climate data: (1) the proportion of individuals that were active per day (ASD; i.e., the number of active individuals divided by the number of individuals in the experiment) to describe how climate triggers movements; (2) the daily proportion of individual scans with displacement since the last scan (SDD; i.e., the number of movement events between two successive scans divided by the amount of such movements that was possible) to quantify the consistency of movements throughout the day; (3) total daily movement (TDM; see above) to quantify movement capability; (4) net displacement per day (nDM; see above); and (5) mean nDM divided by TDM. The last index shows how straight the lizards’ DM is, since TDM includes both home-range and DMs. All measurements represent minimum activity levels, since they only recognise net movement between two scans.

The influence of eight weather parameters on movement parameters was analysed in partial regression analyses: minimum and maximum temperature, minimum and maximum atmospheric pressure, minimum and maximum humidity, rainfall, and wind speed. These were correlated with weather data for the day when activity occurred (d_0) and with weather data for the preceding 2 days (d_{-1} and d_{-2}). All test statistics for a day were tablewide, corrected using the sequential Bonferroni procedure as outlined by Rice (1989).

Results

Daily weather conditions

All weather parameters were highly correlated. Between 18 June and 19 August the daily maximum temperature increased to a maximum of 33°C. Thereafter, the average daily temperature steadily decreased. After the 8 September the maximum temperature rose above 20°C only occasionally. The minimum temperature showed a similar pattern; however, the daily temperature amplitude increased with maximum temperature and decreased with temperature. Minimum humidity usually decreased with increasing maximum temperature, while maximum humidity always ranged between about 65 and 70% from 18 June until 23 July. Later it decreased to about 5% and more or less remained at that level for the rest of the study period. Maximum and minimum atmospheric pressure only occasionally fell outside the range 990–1015 mbar (1 bar = 100 kPa). This could change within 2 or 3 days at a rate of about 20 mbar. Low atmospheric pressure was always followed by rainfall, with a maximum of 29 mm/day on 1 October. A drastic change of weather occurred on the 27 August, when strong thunderstorms with 13.6 mm of rainfall caused a drop of about 10°C in the average daily temperature (Fig. 1). Afterwards, the maximum temperature did not rise above 25°C except on 2 days in early September.

Influence of weather conditions on movement patterns

The results of the partial regression analyses for d_0, d_{-1}, and d_{-2} are shown in Table 1. On average, for the whole duration of the experiment, lizard movements were significantly triggered (ASD) by high temperatures, low rainfall, and a high minimum humidity during d_0. The duration of movement (SDD) was also positively correlated with the maximum temperature and negatively correlated with the minimum humidity

Table 1. Influence of weather conditions on days d_0, $d_{-1,}$ and d_{-2} on individual movements of western green lizards, *Lacerta bilineata*.

	Movement parameter									
	SDD		TDM		ASD		nDM		nDM/TDM	
Day	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*
Total study period (22 June to 26 October 1996)										
d_0										
T_{max}	0.24	<0.001	0.20	<0.001	0.16	<0.001				
Rainfall					–0.14	<0.01				
H_{min}	–0.36	<0.01			–0.28	<0.001				
d_{-1}										
T_{min}	0.16	<0.001			0.18	<0.001	0.13	<0.01		
H_{max}			0.16	<0.05						
d_{-2}										
Wind					0.18	<0.001				
Rainfall	0.21	<0.001								
H_{max}					–0.20	<0.001				
Period 1 (22 June to 26 August 1996)										
d_0			No significant partial correlation							
d_{-1}			No significant partial correlation							
d_{-2}			No significant partial correlation							
Period 2 (27 August to 26 October 1996)										
d_0										
T_{max}	0.35	<0.001	0.29	<0.001	0.23	<0.001				
H_{min}	–0.18	<0.05			–0.27	<0.001				
d_{-1}			No significant partial correlation							
d_{-2}										
Wind					0.20	<0.01				
Rainfall	0.24	<0.001								
H_{max}	–0.21	<0.01			–0.26	<0.001				

Note: *r*, partial correlation coefficient; *p*, significance level after tablewide Bonferroni correction; only significant partial correlations are indicated; ASD, triggering index, SDD, index of consistency of movements throughout the day; TDM, index of magnitude of movements; nDM and nDM/TDM, displacement indices.

for d_0, whereas the intensity of movement, either total movement or displacement movement, was only slightly affected by actual weather conditions (Table 1). Weather conditions for d_{-1} only marginally stimulated activities of lizards. However, there seemed to be an increasing positive influence of minimum temperature on several movement parameters. Weather conditions for d_{-2} did not affect movement capability; however, wind and rainfall had a positive effect on the stimulation and consistency of movement 2 days later.

The drastic change in weather on the 27 August was obviously accompanied by a change in the lizards' movement behaviour. Before 27 August, TDM averaged over all individuals in the analysis (for $n \geq 3$) showed no fluctuation coinciding with fluctuations in maximum temperature and minimum humidity. In contrast, after 27 August, considerable activity was only recorded on days when the maximum temperature rose above ca. 17°C (Fig. 1). At the same time, the minimum humidity dropped below 30% (Fig. 2). To test the assumption that summer activity can be divided into two phases separated by a single but extraordinary weather event, we separately analysed the movement patterns before and after 27 August (Table 1). During the first period all movements were performed independently of the weather, including those during the preceding 2 days. During the second period, however, a high maximum temperature and a low minimum humidity, both indicating fine weather, positively influenced several movement parameters on the same day. Strong wind and a large amount of rainfall stimulated movements 2 days later (ASD) and positively influenced their consistency (SDD).

To determine triggering thresholds for maximum temperature and minimum humidity we performed logistic regression analyses for ASD (Figs. 3 and 4). The logistic regression for maximum temperature and minimum humidity explains 53.1 and 54.2% of ASD variance, respectively. There was no activity below a maximum temperature of 14°C and above a minimum humidity of 52%, and the 50% activity threshold was reached at a maximum temperature of ca. 17°C and a minimum humidity of about 35%.

Description of the daily activity pattern

The daily activity patterns of *L. bilineata* remained almost continuous throughout the radio-tracking period. Shortly before sunrise, lizards were visible at the entrances of their shelters. At sunrise, most lizards moved onto fast-heating structures such as moss or compact layers of grass. Owing to

Fig. 2. Minimum (dotted line) and maximum (continuous line) humidity and average distances covered per day (TDM; bars) throughout the study period (dates are shown as "day.month."); the asterisk indicates a drastic change of weather on 26 August; in the second half of the study period, movements coincided with low minimum humidity (arrows).

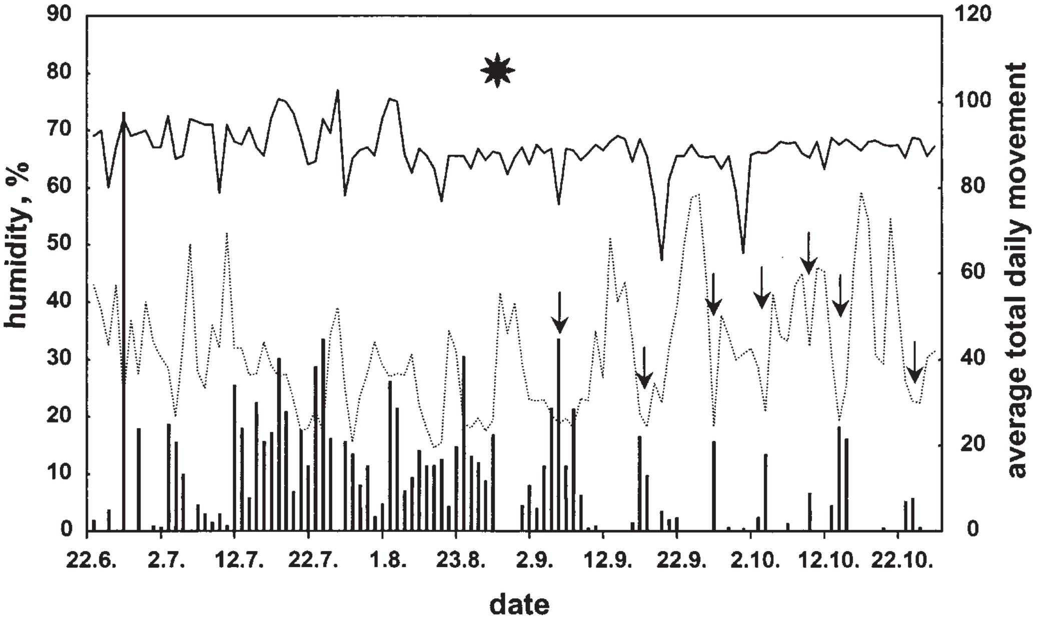
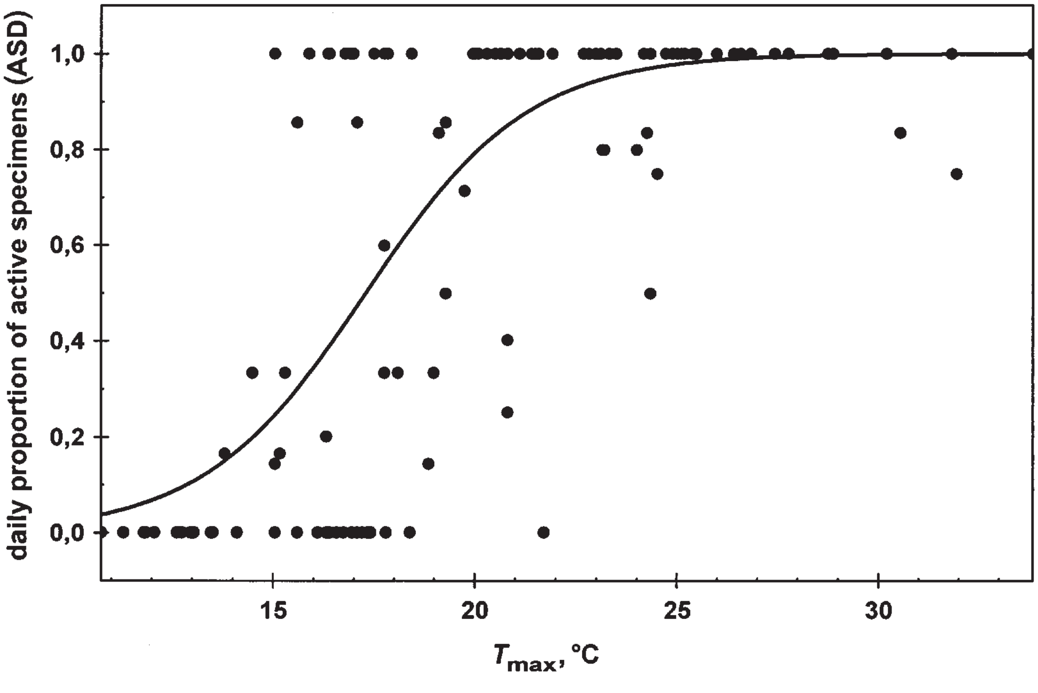


Fig. 3. Logistic regression of the daily proportion of active individuals (ASD) and maximum temperature, T_{max} (r^2 = 0.531, p < 0.001).



the varying geomorphology along the study site, the start of daytime movements could vary by 1 h among individuals. Having heated up, most lizards became active in low vegetation. Only on hot summer days between July and August was their activity interrupted by a resting phase during the hottest time of the day. Only a few individuals moved into their shelters during such days. Lizards mainly hid in the shade of trees or large bushes. At midday they usually reached their most distant point from the shelter. In the afternoon their activity increased again. Before dusk they often rested on fast-heating structures close to their shelters into which they moved at sunset.

Activity ranges

Movement patterns of males were mainly discontinuous. Long inactive periods were briefly interrupted by fast move-

Fig. 4. Logistic regression of ASD and minimum humidity, H_{min} ($r^2 = 0.542$, $p < 0.001$).

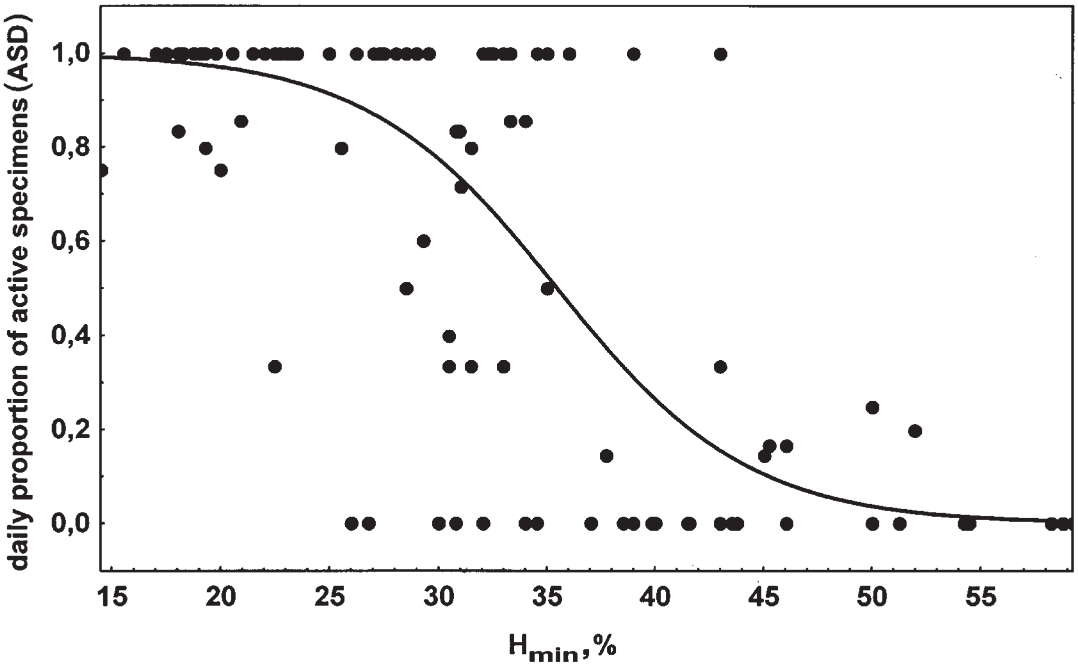
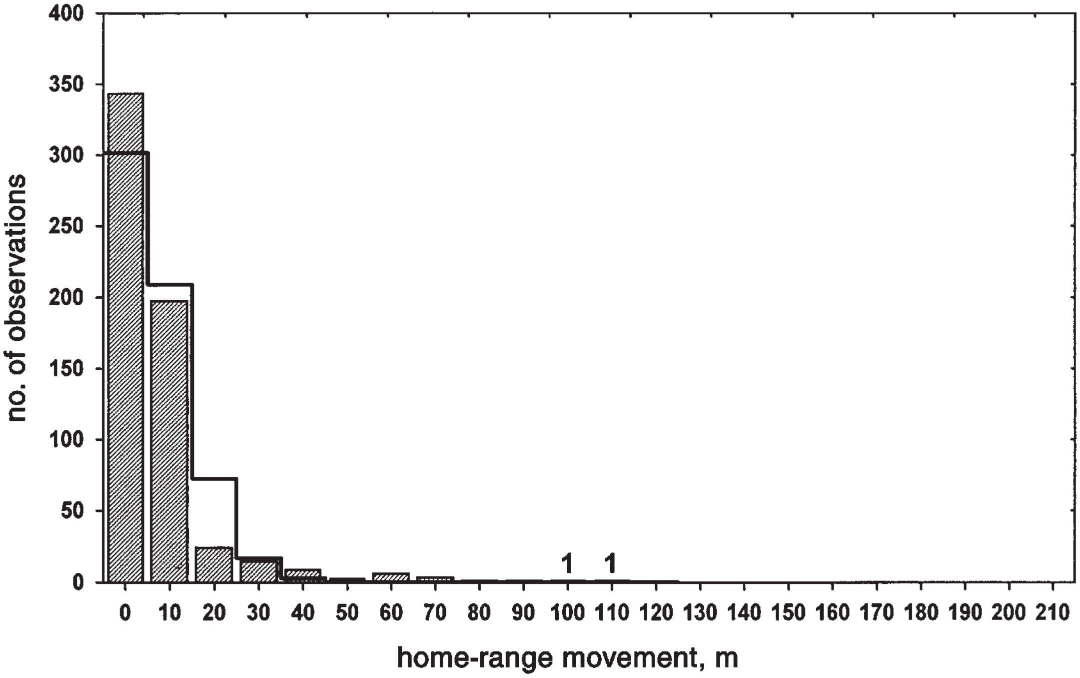


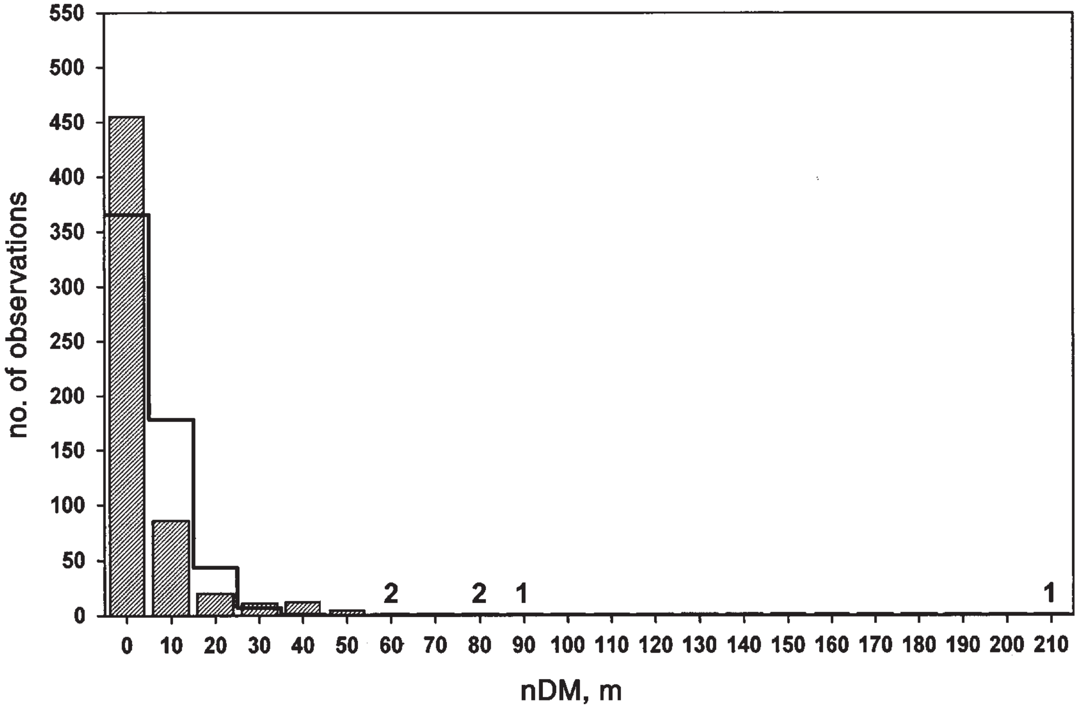
Fig. 5. Distribution of lizards' total daily movements that were not displacement (home-range) movements; the line indicates the expected distribution under a Poisson model; numerals within the graph denote single observations.



ments during which long distances were sometimes covered. Usually, the longest single movements between two successive scans did not exceed 50 m; however, the maximum distance covered was 205 m within 1 h. Long periods of activity were followed by long periods of inactivity. Average activity (SDD) was 34.5%. It varied among individuals from 20.8 to 47.6%. The average for days of inactivity was 35%. Again, during midsummer this proportion was lowest (down to 22%). The average daily movement (TDM) was 10.4 m; however, most individuals moved only a few tenths of a metre per day (Fig. 5). There was a tendency for lizards tracked in midsummer to be more active and move longer distances than lizards tracked in late summer or early autumn.

DMs are part of total activity. Like normal activity they are fast and spontaneous without being triggered by the weather (see above). Most DMs were less than 10 m, and only a few lizards moved more than 50 m in one displacement (Fig. 6).

Fig. 6. Distribution of displacement distances of lizards; the line indicates the expected distribution under a Poisson model; numerals within the graph denote single observations.



Such long DMs were fast and straight. During such activities the individuals could not see the end-point of their movement and had to cross various habitat types. Some individuals moved directly to shelters that they had previously used. No other behaviour, such as feeding and mating, were observed during these displacements, indicating that the lizards knew the area they crossed and exactly where to go. DMs were observed throughout the midsummer period, but only rarely in autumn. Shortly before hibernation, males displaced from their late-summer shelters directly into hibernation shelters, which were only 3–15 m away from their last shelter and which they had never used during summer.

Assuming a random distribution of home-range movements (TDM without nDM) and nDMs and including "zero movements," a goodness-of-fit test showed that neither can be explained by a Poisson distribution, owing to a deficit of short-distance (up to 20 m) movements. In addition, the two distributions are significantly different ($\chi^2 = 152.97$, df = 18, $p < 0.001$), the median of DMs being larger than that of home-range movements.

Discussion

Our analysis of the weather dependence of lizard movements showed that time has a twofold impact on movement patterns: (1) during the course of summer, a phase when there is no apparent weather influence on movement parameters is followed by a phase when movements are strongly dependent on actual weather conditions; and (2) it is typically the actual weather conditions that influence lizard movements, with a decrease in influence and a change in parameters over time. Although our analyses for the whole summer elucidated a significant partial correlation for any day (d_0 – d_{-2}), this influence was strongest on the day when the movements were performed (d_0). It also became obvious that this pattern was caused mainly by the second period (27 August to 26 October), while during the first period, weather conditions did not constrain the lizards' movement behaviour.

Maximum temperature and minimum humidity, both indicating fine weather, played a major role in triggering lizard activities. This is not surprising in the case of temperature, but it is for humidity. Böker (1990, 1992) and Bruno (1986) have already discussed at least a tolerance of the western green lizard for humid habitats. Although they obviously meant soil humidity, this was interpreted as meaning that *L. bilineata*, although undoubtedly thermophilous, is not really xerophilous (Böker 1990). In fact, the largest populations of the western green lizard in the Rhine valley are known from habitats where soil humidity is high or that are close to a spring (Gruschwitz 1992; Niehuis and Sound 1996). However, these are also habitats that are hardly suitable for viniculture, therefore this apparent preference may simply be a side effect of habitat reduction. Rainfall, on the other hand, had a weak negative influence on activity.

The correlation of lizard activity with the weather conditions on the previous day showed an influence of minimum temperature and maximum humidity on three and one activity parameters, respectively. During midsummer in the European sub-Atlantic region, the probability of high temperatures on succeeding days is high. It was therefore not surprising that the temperature on the previous day positively triggered activity. Interestingly, nDM, our displacement parameter, was also significantly correlated with minimum temperature. However, this weak correlation could not be proved for the second period. Such DMs probably represent a kind of "higher level activity" that is not prone to short-term influence by the weather but is controlled by more complex stimuli.

The comparison of activity data with the weather conditions on the preceding 2 days clearly showed that poor weather (rainfall, high humidity, and strong winds) seems to enhance activity 2 days later. Since periods of bad weather did not occur at regular 2-day intervals, this could indicate that after 2 days of forced inactivity, the need to compensate for physiological deficits becomes strong enough to trigger activity, even if the weather is not optimal.

In summary, we may therefore infer the following model of weather dependence of foraging movements for the western green lizard at the northern border of its distribution range: during midsummer the weather does not constrain the lizards' movements within their habitats. A maximum temperature above 16°C and a minimum humidity below 35% (these are thresholds for 50% activity later) are typical for this period. Immediately after the summer has passed its climax (during our study period this was indicated by a sudden change of weather), lizards' activity strongly depends on the weather, and physiological deficits are already apparent after 2 days of inactivity. During midsummer, either such deficits may be less pronounced or the periods of bad weather are too short for detecting these defecits.

Male western green lizards start to accumulate fat for hibernation immediately after the breeding season (Weber 1957). Short active periods of hunting followed by long inactive periods, which we observed, therefore allow for both feeding and thermoregulation. This helps to conserve energy that is needed for fat deposition, minimises the risk of predation, and allows individuals to stay at a thermal optimum. Since western green lizards can afford this, their habitats in the middle Rhine valley are not marginal with regard to these basic requirements, and the absence of the species farther north may actually indicate thermal constraints on egg development.

Movements of *L. bilineata* were usually short (10–20 m). When lizards moved over long distances, especially during displacements, these movements were very fast. The major reason could be avoidance of predation. However, long-distance movements bear further risks. Individuals have to pass through areas in which resources such as suitable shelters, food, and sunny resting places may be rare. The fact that in our study area, individuals moving for long distances passed microhabitats that seemed to provide sufficient food raises the question of why males regularly cover long distances. One reason may be territorial behaviour. Although the breeding season had finished prior to our study, maintaining territories can benefit males. Western green lizards are known to be cannibalistic (Holec and Kminiak 1970). A male that prevents other males from intruding into its territory reduces the risk that offspring born in its territory, and likely to be its own, will be killed by cannibalistic conspecifics. However, this implies that (*i*) males can recognise their own offspring, and (*ii*) in the absence of direct male–male interactions, territory boundaries can be permanently marked. Kin recognition is known from several reptile species, including lizards (Werner et al. 1987), and an indicator of the ability of male western green lizards to mark their territory boundaries may be the presence of femoral pores that are enlarged during summer (Weber 1957; Fergusson et al. 1985). Although the function of these pores is not fully understood (Mason 1992), it seems obvious that they play an important role during the breeding season. Abel (1951) and Alberts (1989) were able to show that femoral pores play no role in sex recognition in lizards. Indirect evidence of the use of femoral pores for territory marking, however, comes from the fact that they are reduced in species of the lizard genera *Aporosaurus* and *Tacydromus* that live on dunes (in Namibia) or on blades of grass (in Southeast Asia), respectively. In both habitats chemical marks would not persist for a long time. In contrast, such femoral pores exist in closely related species of both genera that live on solid ground. If these pores played a role in female attraction or stimulation, their presence would not depend on habitat type. The ability to mark territory boundaries would explain why males occasionally perform long-distance movements (patrolling territory boundaries and chemical marking), especially during displacements. Further evidence comes from the fact that displacement performance is not correlated with actual weather conditions, showing that displacements must be triggered by endogenous factors.

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