TWO SYNTOPIC COLUBRID SNAKES DIFFER IN THEIR ENERGETIC REQUIREMENTS AND IN THEIR USE OF SPACE

Herve Lelièvre^{1,2,4}, Coraline Moreau¹, Gabriel Blouin-Demers³, Xavier Bonnet¹, and Olivier Lourdais¹

¹Centre d'Études Biologiques de Chizé, CNRS, 79360, Villiers en Bois, France
²Université de Poitiers, 40 avenue du Recteur Pineau, 86022 Poitiers, France
³Département de Biologie, Université d'Ottawa, Ottawa, Ontario, K1N 6N5, Canada

ABSTRACT: Spatial ecology is crucial to determining how animals exploit resources in their environment. Snakes display highly varied energetic and space use strategies; we hypothesized that snakes with higher energy demands are more mobile to fulfill their energy needs. We studied the spatial ecology of two syntopic colubrid snakes (*Hierophis viridiflavus* and *Zamenis longissimus*) that show a marked divergence in energetics. Specifically, we predicted that *H. viridiflavus* should be more active than *Z. longissimus* because of its higher energy requirements. Because reproductive status also influences movement patterns, we investigated its effect within each species. We indeed found that *H. viridiflavus* moved more frequently and covered longer distances during the postreproductive period, probably because of foraging activity. Both species displayed similar activity during the reproductive period, however. The extended movements during the reproductive period may be related to mate-searching in males and egg-laying in females.

Key words: Activity; Energetics; Home range; Reproduction; Snakes; Spatial ecology

SPATIAL ECOLOGY is crucial to assessing the exploitation of resources by animals (Schick et al., 2008). Movement patterns may be dictated by complex relations between various factors defining how individuals optimize the access to resources despite environmental variability in space and time (Morales and Ellner, 2002; Armsworth and Roughgarden, 2005; Bowler and Benton, 2005; Christ et al., 2008). These individual strategies depend on resource availability as well as physiological requirements of species or individuals (e.g., diet, energetics, thermal needs; Mace and Harvey, 1983). The lower energy needs of ectothermic reptiles are apparent in their spatial ecology as they generally exploit smaller areas and show limited movement compared to similar-sized endotherms (Pough, 1980; Shine et al., 2003). Despite limited requirements, however, energetics may drive activity and space use in reptiles (Turner et al., 1969; Christian and Waldschmidt, 1984; Perry and Garland, 2002; Smith and Griffiths, 2009).

In snakes, interspecific divergence in energy requirements can result in significant variation in movement patterns and home range size (Carfagno and Weatherhead, 2008). Metabolism is a major biological rate that summarizes the way that organisms process energy (Hochachka and Somero, 2002) and is strongly temperature dependent in ectotherms. Therefore, energy requirements for maintenance will be directly dependent on field body temperatures (Secor and Nagy, 1994). Hence, major differences in thermal strategies are likely to translate in contrasted spatial ecology in ectotherms. Spatial ecology can also be influenced by individual characteristics such as sex (e.g., Webb and Shine, 1997; Bonnet et al., 1999; Blouin-Demers and Weatherhead, 2002; Fitzgerald et al., 2002; Whitaker and Shine, 2003; Brown et al., 2005) and body size (Shine, 1987; Whitaker and Shine, 2003; Roth, 2005; Blouin-Demers et al., 2007). Movements may differ between genders during the reproductive period because of sex-specific activities: mate-searching in males (Secor, 1994; Aldridge and Brown, 1995; Bonnet et al., 1999) and nesting site selection in females (e.g., Madsen, 1984; Blouin-Demers and Weatherhead, 2002; Brown et al., 2005).

In this paper, we tested the hypothesis that interspecific variation in movement patterns can be, at least in part, explained by variation in energetic requirements. To do this, we

⁴ PRESENT ADDRESS: CERA Environnement, 79360, Villiers en Bois, France

⁵ Correspondence: e-mail, hervelelievre@hotmail. com

compared the spatial ecology of two syntopic colubrid snakes, the European Whipsnake (*Hierophis viridiflavus*) and the Aesculapian Snake (Zamenis longissimus). Both species share major ecological traits as they are both medium-sized, oviparous snakes that are generalist predators feeding mostly on mammals (Capizzi et al., 1995; Rugiero and Luiselli, 1995; Rugiero et al., 2002; Capizzi et al., 2008). However, they exhibit contrasted thermal strategies and consequently diverge in energy requirements (Lelièvre et al., 2010). Specifically, we predicted that *H. viridiflavus* should have larger home ranges, more frequent movements, and longer mean distances moved per day than Z. longissimus to satisfy higher maintenance requirements resulting from their selection of higher body temperatures (Lelièvre et al., 2010). Because reproduction can be a major source of variation in movement patterns in snakes (Blouin-Demers and Weatherhead, 2002), we compared the two species both during and after the reproductive period. We are fully cognizant of the limitations associated with comparative studies of two species (Garland and Adolph, 1994), but given the rarity of rich radiotelemetry data sets on more than one species in a given area, we think our study is still a useful first step in testing the energetics hypothesis.

MATERIAL AND METHODS

Study Site and Species

We conducted our study at the Centre d'Etudes Biologiques de Chizé in western France $(46^{\circ}07'N, 00^{\circ}25'W; datum = WGS84)$, a 2600-ha biological reserve. Hierophis viridiflavus and Z. longissimus are medio-European sympatric colubrid snakes that frequently occur in syntopy (Rugiero et al., 2002). Both species have approximately equal body size $(\approx 100-120 \text{ cm in snout-vent length [SVL]})$ and exhibit important overlap in diet (Lelièvre et al., 2012). However, these two species differ strongly in their range of preferred body temperature (T_{set}) : *H. viridiflavus* is a thermophilic snake (T_{set} , 27.5–31°C) whereas Z. longissimus prefers cooler temperatures (T_{set} , 21.5–25.5°C) and these differences are also expressed in the field (Lelièvre et al., 2010). Maintenance requirements are significantly different and reflect the contrasted thermal preference (Lelièvre et al., 2010).

Radiotelemetry

Snakes (SVL = 89.5 \pm 1.3 cm SE and body mass = 234.1 \pm 11.9 g SE in 32 *H*. *viridiflavus*; 95.4 \pm 1.6 cm SE and 249.3 \pm 12.0 g SE in 32 *Z. longissimus*) were captured under undulated concrete boards dispersed throughout the study area. A radio-transmitter (R1650, Advanced Telemetry Systems, Isanti, USA) sterilized in diluted benzalkonium chloride was surgically implanted in the abdominal cavity of each snake under isoflurane anesthesia (Reinert and Cundall, 1982). Transmitter mass was less than 2% of snake body mass. We kept snakes under observation for 6 d and then released them at their exact point of capture.

Snakes were located every 48 h during the day from May until September in 2007 and in 2008 using a radio receiver (Yaesu FT-817, Vertex Standard, Cypress, CA, USA) and a portative Yagi antenna (Wildlife Track Inc., Livermore, CA, USA). We systematically changed the relocation order of the snakes to avoid sampling the same individual at the same time of day every day. Upon locating a snake, we recorded its position using a global positioning system (GPS; eTrex, Garmin, Olathe, KS, USA) at an estimated accuracy of 5–10 m.

Data Analyses

We calculated mean daily distance moved as the straight-line distance between the GPS coordinates of successive telemetry locations divided by the number of days elapsed (usually two) using the Hawth extension in ArcGIS 9.2 (ESRI, Redlands, CA, USA). Frequency of movement was calculated as the proportion of snake relocations more than 10 m from the previous location. We also calculated the mean resting duration as the number of successive days without moving more than 10 m. To assess the effects of reproduction on snake activity, we divided the activity season into reproductive (May–June) and postreproductive (July-September) periods (Bonnet et al., 1999).

Home ranges were calculated with 100% minimum convex polygons (MCP) using Rang-

es6 V1.2 (Anatrack, Wareham, Dorset, UK). MCPs are simple to conceptualize, do not require the data to have some underlying statistical distribution (Powell, 2000), and do not require the estimation of parameters (e.g., smoothing factor) that influence home range size (Row and Blouin-Demers, 2006). Home range size increased significantly with the duration of radio-tracking (linear model: $F_{1.62}$ = 7.13; P < 0.01). Hence, we performed an incremental analysis in Ranges6 on the home ranges estimated with the longest durations (>60 d). This analysis revealed that snakes followed for at least 58 d (i.e., 26 locations) reached the asymptote in home range area (Fig. 1). We then used the relationship between the number of relocations and the proportion of total home range size as a weighting factor to estimate home range size when the number of relocations was below 26 locations. We ensured that weighted home range values were not related to survey duration (linear model: $F_{1,62}$ = 0.34; *P*=0.56). Of the 32 *H. viridiflavus* and 32 Z. longissimus we tracked in 2007–2008, 12 H. viridiflavus (8 males, 4 females) and 14 Z. longissimus (9 males, 5 females) were tracked for more than 60 d.

Habitat type may influence spatial ecology; for instance, snakes could need to move more in certain habitats if some habitats are less productive than others. To control for this effect, we calculated the mean proportions of habitat available (grassland, scrubland, and forest) in each home range using ArcGIS 9.2. We then used the dominant habitat type to categorize each home range and used this as a control variable in our analyses.

Statistical analyses were performed with R (The R Foundation for Statistical Computing, Vienna, Austria). We used linear models or linear mixed models with individual as random effect when the number of contributions varied among individuals (pseudoreplication) to test whether differences were significant (with $\alpha =$ 0.05). Results are presented as means \pm SE.

RESULTS

Movement Patterns

In both species, most of the distances traveled between two successive relocations were shorter than 100 m (Fig. 2). Particularly



radio-tracked for more than 60 d (using Ranges6 software) in Chizé, western France. Mean proportion of total home range size is represented $\pm 95\%$ confidence interval for Zamenis longissimus (A.) and Hierophis viridiflavus (B.). Long dashed line represents the 95% estimate of total size which occurs at ≈ 55 d in both species.

long movements were observed in *H. viridiflavus* (eight observations >600 m, maximum of 1628 m), but not in Z. longissimus (only two observations >600 m, maximum of 768 m). When snakes did not move between relocations, it was usually for less than 2 d (Fig. 3). Resting duration was on average shorter in *H*. viridiflavus than in Z. longissimus during the postreproductive period (linear mixed model with individual as random effect: P = 0.05; Table 1), but not during the reproductive period (P = 0.85). No sex differences in resting duration were detected within species neither during the reproductive period (P = 0.09 in H). *viridiflavus*; P = 0.54 in Z. *longissimus*) nor during the postreproductive period (P = 0.41)in *H. viridiflavus*; P = 0.48 in *Z. longissimus*).

Proportion of home-range

1.2

1.0

0.8

0.6

0.4

0.2

0.0

1.2

1.0

0.8

6 14 22 30 38 46 54 62 70 78

Β.

Α.



FIG. 2.—Frequency distribution of distances traveled between two successive telemetry locations in syntopic *Zamenis longissimus* (ZL) and *Hierophis viridiflavus* (HV) in Chizé, western France.

During the reproductive period, *H. viridi-flavus* moved with similar frequency as *Z. longissimus* (72% vs. 75% of relocations respectively) and traveled similar daily distances ($F_{1,51} = 0.39$, P = 0.54; Table 1; Fig. 4). Males moved more frequently (80% vs. 65% of relocations respectively) and traveled longer distances (43.5 ± 8.0 m vs. 24.0 ± 6.4 m respectively; $F_{1,25} = 5.92$, P = 0.02) than females in *Z. longissimus*, but the sex difference was not significant in *H. viridiflavus* (70% vs. 74% of relocations; 48.3 ± 13.8 m vs. 29.9 ± 10.9 m; $F_{1,24} = 1.77$, P = 0.20).

During the postreproductive period, *H.* viridiflavus moved more frequently (75% vs. 64% of relocations) and traveled longer distances than Z. longissimus ($F_{1,45} = 4.38$, P = 0.04; Table 1). In both species, males and females moved similarly following reproduction (for males and females, respectively: 64% vs. 58% of relocations; 31.3 ± 8.2 m vs. 24.9 ± 7.1 m in Z. longissimus; $F_{1,23} = 0.79$, P =0.44; and 75% vs. 76% of relocations; 47.2 ± 16.5 m vs. 32.0 ± 14.9 m in *H. viridiflavus*; $F_{1,20} = 0.85$, P = 0.37).

Home Ranges

We found no difference in estimated home range size between *H. viridiflavus* and *Z. longissimus*. Both methods gave similar results: using the whole data set with weighted estimates ($F_{1,62} = 1.85$, P = 0.18; Table 1) or using only animals tracked for more than 60 d



FIG. 3.—Frequency distribution of resting durations in syntopic Zamenis longissimus (ZL) and Hierophis viridiflavus (HV) in Chizé, western France.

 $(F_{1,23} = 1.14, P = 0.30;$ Table 1). No sex differences in home range area were observed with the weighted data (for females and males respectively: 5.23 ± 4.87 ha vs. 14.99 ± 5.88 ha in *H. viridiflavus*; $F_{1,30} = 2.76, P = 0.11;$ 6.88 ± 3.98 ha vs. 7.53 ± 4.51 ha in *Z. longissimus*; $F_{1,30} = 0.02, P = 0.89$) or for animals tracked for more than 60 d (10.50 \pm 5.00 ha vs. 11.42 ± 6.26 ha for *H. viridiflavus*; $F_{1,9} = 0.02, P = 0.89; 8.55 \pm 2.86$ ha vs. 7.28 ± 3.57 ha for *Z. longissimus*; $F_{1,12} = 0.13, P = 0.73$).

DISCUSSION

Our study confirmed that contrasted thermal strategies in H. viridiflavus and Z. longissimus translate in different movement patterns. Following our predictions, spatial ecology was correlated with both reproductive and energetic demands in those species. During the reproductive period, individuals from both species, particularly males, moved frequently and traveled longer distances. Reproductive behavior may explain this seasonal pattern (Bonnet et al., 1999; Row et al., 2007; Sperry and Weatherhead, 2009). Matesearching can increase movement distances in spring in males (Ciofi and Chelazzi, 1994; Bonnet et al., 1999), but also in females (Blouin-Demers and Weatherhead, 2002). Females punctually travel long distances in early summer to reach appropriate egg-laying

	Zamenis longissimus		Hierophis viridiflavus	
	Reproductive	Postreproductive	Reproductive	Postreproductive
Resting duration (d)	5.11 ± 0.67	4.88 ± 0.39	4.92 ± 1.00	3.72 ± 0.58
Daily distance moved (m)	41.3 ± 8.0	29.8 ± 4.8	36.3 ± 5.6	44.4 ± 7.0
Home range area (ha), all snakes	7.39 ± 2.37		11.94 ± 3.35	
Home range area (ha), snakes with >60 locations	7.74 ± 2.08		11.09 ± 3.14	

TABLE 1.—Summary of movement statistics for Zamenis longissimus and Hierophis viridiflavus, two colubrid snakes followed by radio-telemetry in Chizé, western France.

sites (Blouin-Demers and Weatherhead, 2002; Lowenborg et al., 2010). We did not assess reproductive state in all tracked females, but the two species are usually annual breeders in our area. Frequent movements of females in spring may also correspond to active foraging to sustain the massive energy requirements of vitellogenesis or to active mate-searching (Blouin-Demers and Weatherhead, 2002). Several females moved suddenly and extensively in late spring, and these movements were probably related to egg-laying as described in other colubrids (Blouin-Demers and Weatherhead, 2002).

Although both species exhibited similar movement patterns during the reproductive period, they diverged markedly during summer. *Zamenis longissimus* became less active whereas *H. viridiflavus* still moved frequently.



FIG. 4.—Daily distances moved by syntopic Zamenis longissimus (ZL) and Hierophis viridiflavus (HV) in Chizé, western France during reproductive (May–June) and postreproductive (July–September) periods. The median is represented by the middle horizontal line in the box plot. Interval between 25% and 75% quartiles is represented by boxes and range is represented by whiskers. Open circles are outliers.

Higher maintenance requirements reported for H. viridiflavus compared to Z. longissimus probably necessitate more active foraging. In addition, we observed that resting duration was longer in Z. longissimus. Contrasted thermal preferences in those species may explain this observation. In a previous study (Lelièvre et al., 2010), we found that Z. longissimus digested and molted at lower temperatures than *H. viridiflavus*, but consequently spent more time doing so. Thus, this ability to operate physiological processes at cooler temperature could be associated with longer resting durations. On the other hand, H. viridiflavus should be thermally more constrained because activity in this species requires elevated environmental temperatures.

Estimation of home range size posed some methodological difficulties because several snakes were not tracked for the duration of the active season. Consequently, we used a new method to estimate home range size for these individuals. Estimated sizes were similar to those of snakes followed for most of the active season, at least when the sexes were pooled. Both species and both sexes within each species exhibited home ranges of similar size due to large distances covered during the reproductive period. Variability among individuals was very high in both species, and some snakes used very large home ranges (up to \approx 50 ha).

The inferential power of comparative studies with only two species is limited (Garland and Adolph, 1994). Fortunately, however, in our case we can compare our results to those of a very similar study on the space use of two North American colubrids that differ in energy requirements. Carfagno and Weatherhead (2008) compared the space use of *Elaphe obsoleta*, a species with low preferred

body temperature, and thus low energy requirements, to that of *Coluber constrictor*, a species with high preferred body temperature, and thus high energy requirements. Mirroring our own results, Carfagno and Weatherhead (2008) found that Coluber moved more often and further per move than *Elaphe*; in their case, however, this difference in movements resulted in Coluber having home ranges approximately four times the area of those of *Elaphe*. Although *H. viridi*flavus moved significantly more frequently than Z. longissimus in our study, there was no statistically significant difference in home range area even though H. viridiflavus had home ranges that were, on average, 40% larger than those of Z. longissimus. The different relationships between frequency of movement and home range area in the two studies may be surprising at first, but we must keep in mind that more frequent movements do not necessarily result in larger home ranges; home range area depends on how those movements are made on the landscape (Whitaker and Shine, 2003). Therefore, a detailed understanding of the causal links between energy requirements, frequency of movements, and home range area requires information on the spatial distribution and heterogeneity of productivity from the snakes' perspective, a measure that will be difficult to obtain.

In conclusion, our results and those of Carfagno and Weatherhead (2008) offer support for the hypothesis that interspecific variation in the spatial ecology of snakes could be explained, at least in part, by variation in energetic requirements. All else being equal, snakes with higher energy needs should move more often and use more space for prey acquisition. The major challenge of most interspecific studies, however, is to satisfy the "all else being equal" condition. We believe we were able to satisfy this critical assumption in the present study. To determine how broadly applicable the energetics hypothesis is, however, will require obtaining detailed information on space use of a larger number of species that differ in energy requirements.

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