

Energetics and space use: intraspecific and interspecific comparisons of movements and home ranges of two Colubrid snakes

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Summary

1. Energy requirements explain substantial variation in movement and home range size among birds and mammals. This study assesses whether the same is true of snakes by comparing ratsnakes (*Elaphe obsoleta*) and racers (*Coluber constrictor*), ecologically similar species whose energy requirements appear to differ substantially (racers > ratsnakes).
2. Over 4 years 22 *Elaphe* and 16 *Coluber* were radio-tracked at the same site in Illinois to examine how movement and home ranges varied by sex and season.
3. *Coluber* moved more often and further per move than *Elaphe*, resulting in their estimated mean day range being almost four times larger than that of *Elaphe* (88.0 m day⁻¹ vs. 23.1 m day⁻¹).
4. Both male and female *Elaphe* moved more frequently early in the season consistent with mate-searching, but mean distances moved did not differ seasonally or by sex. Both sexes of *Coluber* moved more later in the season and overall males moved further than females.
5. Interspecifically, patterns were consistent with the energetics hypothesis – *Coluber* had mean home ranges approximately four times larger than those of *Elaphe*.
6. Intraspecifically, increased movement did not always produce larger home ranges. Male *Elaphe* had larger home ranges than females despite not moving further, whereas male *Coluber* had comparable home ranges to females despite moving further. Also, *Elaphe* home ranges in Illinois were substantially smaller than has been documented in Ontario, despite Ontario *Elaphe* moving less.
7. Our results generally support the energetics hypothesis, but indicate that knowledge of ecology and energetics increases our understanding of area requirements beyond simple allometric predictions.

Key-words: *Coluber constrictor*, *Elaphe obsoleta*, energetics, radio telemetry, spatial ecology

Introduction

How often and far an animal moves and how much space it uses are fundamental aspects of its ecology and important indicators of its resource requirements (Plummer & Congdon 1994; Charland & Gregory 1995; Johnson 2000). Understanding of movement and spatial patterns is also required for developing reserves of appropriate size (Dodd 1987; Webb & Shine 1997; Fitzgerald, Shine & Lemckert 2002). Energy requirements appear to play a key role in animal spatial ecology. For example, home ranges of birds and mammals increase with body mass and decreased habitat productivity (e.g. McNab 1963; Schoener 1968; Harestad & Bunnell 1979; Mace & Harvey 1983; Lindstedt, Miller & Buskirk 1986; Kelt & Van Vuren 1999). Also, differences in home ranges between

animals of different trophic position are expected, with carnivores requiring larger home ranges because less energy per unit area is available to them relative to herbivores (e.g. McNab 1963; Schoener 1968; Harestad & Bunnell 1979; Swihart, Slade & Bergstrom 1988; Gompfer & Gittleman 1991).

Rules governing spatial ecology of terrestrial vertebrates are based largely on birds and mammals. These rules are unlikely to apply to reptiles because, relative to birds and mammals, lower metabolic rates, and thus energy demands of ectotherms, should affect their spatial ecology (Shine *et al.* 2003; Pough 1980). Specifically, ectotherms should require less space than an endotherm of similar size. Also, because reptile behaviour and ultimately fitness is influenced directly by environmental conditions (Huey 1982; Huey & Kingsolver 1989) relative to endothermic vertebrates, reptile movement patterns may be influenced more by environmental conditions.

Reptiles move more in response to increasing energetic requirements, reflected by a positive association between body size and home range size in lizards (e.g.; Turner, Jennrich

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& Weintraub 1969; Christian & Waldschmidt 1984; Perry & Garland 2002). However, a detailed understanding of the movement patterns of most reptiles is lacking (Webb & Shine 1997). Snake spatial ecology is particularly poorly understood. The effects of body size on home range size have been examined within species in snakes (e.g. Shine 1987; Whitaker & Shine 2003; Roth 2005; Blouin-Demers, Bjorgan & Weatherhead 2007), but hypotheses on the causes of these patterns have not been tested (Whitaker & Shine 2003). Lack of standardized techniques and differences among study locations in habitat and resource availability have made comparisons between species and studies problematic, although some effort has been made to make generalized comparisons across populations (Gregory *et al.* 1987; Macartney *et al.* 1988; Pearson, Shine & Williams 2005). Our general goal in this study is to examine how space use by two snake species at the same study site varies with assumed differences in energetic requirements.

All else being equal, larger snakes should require more energy than smaller snakes, and more active snakes should require more energy than less active snakes of similar size. Satisfying the 'all else being equal' condition is, of course, the major challenge in testing the hypothesis that energy demands underlie space use and movement. We identified a pair of species that largely satisfy that condition while appearing to differ substantially in their energy budgets. Ratsnakes (*Elaphe obsoleta*, Say in James, 1823) and racers (*Coluber constrictor*, Linnaeus, 1758) are two common terrestrial Colubrid species that occur together in areas characterized by a mixture of forests and fields (Conant & Collins 1998; Keller & Heske 2000). Both species are well-documented avian nest predators that also prey extensively on small mammals (Fitch 1963a,b; Weatherhead, Blouin-Demers & Cavey 2003; Carfagno, Heske & Weatherhead 2006). The species are also similar in size and colour as adults, making their physical properties associated with thermoregulation similar. By comparing similar-sized snake species that use similar habitat and have similar diets at the same study site, we can control for some of the variability inherent in past attempts at interspecific comparisons (Gregory *et al.* 1987).

Despite the similarities, the energy requirements of *Coluber* should differ from those of *Elaphe*. Determining energy budgets of ectotherms can be complex (Peterson, Walton & Bennett 1999), but it appears that more active heliothermic reptiles tend to have higher body temperatures, greater daily field metabolic rates measured with doubly labelled water and both greater foraging costs and energy intake (Secor & Nagy 1994). As their name (racers) suggests, *Coluber* are fast-moving snakes relative to *Elaphe* (ratsnakes). Compared to *Elaphe*, at our study site *Coluber* maintains higher experimentally determined preferred (32.6 ± 0.8 °C vs. 28.7 ± 0.7 °C) and field daytime temperatures (27.4 ± 1.1 °C vs. 24.7 ± 0.5 °C) (Carfagno 2007), probably related to *Coluber*'s higher behavioural and metabolic activity (Lillywhite 1987; Fitch 1999). The energetic costs of movement for widely foraging snakes such as *Coluber* are likely to be greater than for most snakes (Walton, Jayne & Bennett 1990; Plummer & Congdon 1996). When active, *Coluber* greatly exceeds energy consump-

tion of more sedentary snakes both in the laboratory (Ruben 1976) and in the field (Secor 1994; Plummer & Congdon 1996), and displays among the highest active metabolic rates reported for any reptile (Lillywhite 1987). Finally, *Coluber* appears to grow and mature more quickly than *Elaphe* at the same location (Turner 1977; Fitch 1999), which would require more frequent foraging and feeding (Murphy & Campbell 1987; Plummer & Congdon 1996).

Given these species differences, we predicted that *Coluber* should move more often and further than *Elaphe*. Furthermore, if home range size increases with an animal's energy requirements or the extent of its movements, then *Coluber* home ranges should be larger than those of *Elaphe*. In addition to testing these predictions overall, we also controlled for possible effects of habitat by comparing movements within the same habitat. At our study site both species use forest edges extensively, despite *Coluber* otherwise using successional fields more and forest interior less relative to *Elaphe* (Carfagno & Weatherhead 2006).

Within species, sex and reproductive condition affect space use by snakes (e.g.; Webb & Shine 1997; Blouin-Demers & Weatherhead 2002; Fitzgerald *et al.* 2002; Whitaker & Shine 2003; Brown, Shine & Madsen 2005). By considering movements during the reproductive season separately, one can assume that movements during the rest of the active season are probably driven by foraging requirements. However, during the mating season, males are thought to make more extensive movements while mate-searching (Gibbons & Semlitsch 1987; Gregory *et al.* 1987; Secor 1994; Aldridge & Brown 1995; Bonnet, Naulleau & Shine 1999). Females may also move more during the mating season (Blouin-Demers & Weatherhead 2002), whereas females tend to move less while burdened with developing ova (Seigel, Huggins & Ford 1987; Charland & Gregory 1995; Brown & Shine 2004), although they may make occasional long-distance movements to oviposition sites (e.g.; Madsen 1984; Blouin-Demers & Weatherhead 2002; Brown *et al.* 2005). Therefore, our second general goal was to test the prediction that within *Elaphe* and *Coluber*, males would have larger home ranges than females because many females would be reproductive for at least part of the year, but that for just the period after egg laying, home range size should be similar for males and females.

Materials and methods

STUDY SITE AND SPECIES

This study was conducted from 2002 to 2005 at the Cache River State Natural Area in southern Illinois. Habitat at the study site was classified into five categories: upland forest, bottomland forest, old fields, successional fields and edges (Carfagno & Weatherhead 2006). Edge was defined as 15 m from the interface between closed and open canopy habitats (including forest-field and forest-river interfaces).

Most snakes were captured as they emerged from shared hibernacula each spring, but also opportunistically throughout the season. Reproductive condition of females was assessed by palpation of the abdomen periodically throughout the field season, and by observation

of mating behaviour. A female was classified as non-reproductive that season when there was no evidence of mating or the presence of eggs. However, the reproductive condition of many female *Elaphe* was uncertain because they were unobservable most of the time (e.g. under cover, in trees).

RADIO-TELEMETRY

Snakes had transmitters (Model SI-2T; Holohil Systems Inc., Ontario, Canada) implanted surgically under the supervision of a wildlife veterinarian, and in compliance with the University of Illinois' Animal Care and Use Committee. Transmitters were implanted only when the transmitter mass was < 3% of snake body mass. At the time of implantation, *Elaphe* males and females averaged 758.6 ± 72.8 and 527.0 ± 18.1 g, respectively, with snout-vent lengths of 134.6 ± 5.1 and 118.9 ± 3.1 cm. *Coluber* males and females averaged 558.7 ± 28.7 and 553.6 ± 33.6 g, respectively, with snout-vent lengths of 119.6 ± 2.5 and 120.6 ± 2.9 cm. Snakes were treated with antibiotics and analgesics, and released 3 days following surgery.

Snakes were usually relocated every other day from spring emergence (February–March) through to hibernation (October–November), using a receiver (Model R-1000; Communication Specialists Inc., Orange, CA, USA). Every location was mapped using a hand-held global positioning system unit (Model GPS V; Garmin International Inc., Olathe, KS, USA), and habitat was recorded. Although snakes were tracked only during the day (07.00–18.00 h), it is unlikely that in this part of their range either species moved greatly at night (Stake *et al.* 2005).

SHORT-TERM CONTINUOUS OBSERVATIONS

Estimating movement from positions determined every 2 days risks missing short-term movements. Such movements could involve a snake changing locations between visits. Also, a snake at the same location on successive visits could have made additional moves but returned to its starting location. To estimate the extent of movement that occurred between relocations, in 2005 we observed six *Elaphe* (three males and three females) and four *Coluber* (three males and one female) continuously over randomly selected 3-hour periods throughout the day. Each snake was monitored four to six times between May and August. We remained distant and hidden from the snakes and used binoculars for observation, allowing 30 min before beginning to record observations if snakes were disturbed upon initial location. It is unlikely that the snakes' behaviour was affected seriously. In fact, during these observations we observed three predation events by the snakes.

Our short-term continuous observations also allowed us to estimate daily movement distance or day range (Carbone *et al.* 2005), a short-term measure of space use that reflects, at least partly, differences in resource needs among similar-sized animals (Garland 1983). We calculated our estimates by assuming that snakes were active only during the day (12 h), and that during that time they moved in proportion to how frequently we found them active during the 3 h monitored. We used our telemetry data to correct for the fact that snakes did not move every day by multiplying the distance potentially moved over a 2-day span, by the probability that each species moved within those 2 days.

DATA ANALYSIS

Analyses were performed using SYSTAT version 10.0 (Systat Software, Inc., San Jose, CA, USA), using individual animals as the unit of

replication. Frequency of movement was calculated as the probability that a snake had moved each time it was relocated. The straight-line distances between the mapped coordinates of each snake's successive telemetry locations were used to estimate mean distances travelled per move. The total distance covered by each snake was divided by the number of days tracked, to derive a minimum estimate of how far snakes travelled per day. This variable is a more comprehensive estimate of activity because it incorporates both distance and frequency of movement. The season was divided into reproductive (April–June) and post-reproductive periods (July–September) based on observations during each year of both species mating in April and May and laying eggs throughout June. Interspecific comparisons were repeated for snake locations restricted to edges. All means are reported ± 1 standard error.

An animal's home range is the area in which an individual performs its normal activities (Burt 1943). For each snake, active season home ranges were calculated with 100% minimum convex polygons using HomeRange (version 1.1; Huber & Bradbury 1995, University of California San Diego, CA, USA). The minimum convex polygon is simple to conceptualize, does not require that data have some underlying statistical distribution (Powell 2000), and is the most reliable method for representing the maximum home range area for most herpetofauna (Row & Blouin-Demers 2006). Because there was no evidence that home ranges shifted between years, with snakes frequently using the same general areas and even specific trees or logs across years, data were pooled for snakes that were tracked in multiple years. Seasonal home ranges were also calculated to test the prediction that any difference between males and females in overall home range size was attributable to females being less active when gravid.

Results

We tracked 22 individual *Elaphe* and 16 individual *Coluber* over the 4-year study. We had sufficient (> 2 months) global positioning system (GPS) locations during the active season for movement analyses for 18 of the *Elaphe* (nine males and nine females) and 15 of the *Coluber* (seven males and eight females). For these snakes, *Elaphe* were relocated 1686 times and *Coluber* 1419 times between April and September. Observations per individual averaged 93.7 for *Elaphe* and 94.6 for *Coluber*, yielding 930 *Elaphe* and 1150 *Coluber* locations. Occasionally snakes were not relocated sequentially (e.g. when snakes were removed briefly from the field for thermal preference trials), which reduced the number of locations for movement analyses to 887 for *Elaphe* and 1120 for *Coluber*. These totals excluded locations where snakes were commuting to or from hibernacula outside their active season home ranges, although most snakes hibernated within their home ranges. All female *Coluber* were reproductive, but because we were uncertain about the status of most female *Elaphe* data were analysed by sex, but not reproductive condition.

RATSNAKES

Two-way analyses of variance (ANOVAS) with sex and season as factors were used to test for differences between the sexes and across the season for each movement variable. *Elaphe* moved more frequently during the reproductive season ($80.7 \pm 1.9\%$ of relocations) than later in the season ($73.7 \pm$

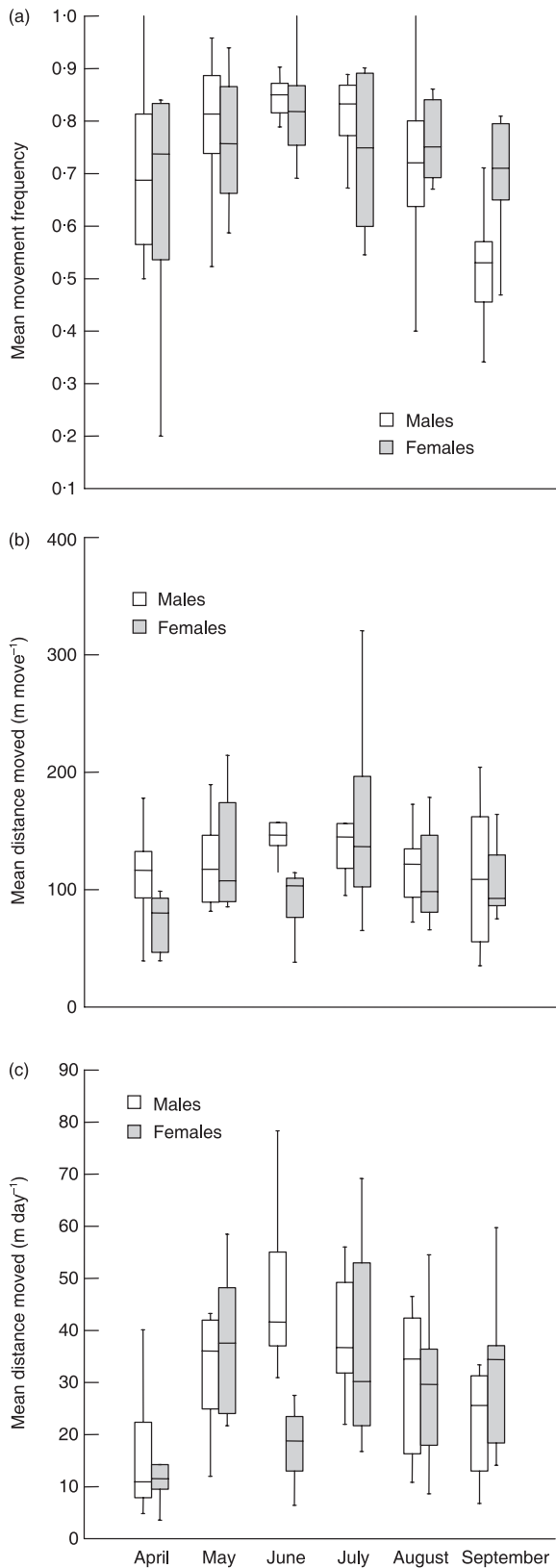


Fig. 1. Box plots of the mean monthly movement frequencies (a), distances moved per relocation (b) and distances moved per day (c) of male and female *Elaphe* over the course of the active season. In these and all subsequent box plots, we report group medians, the upper and lower quartiles and the lower and upper inner fences. In all cases, the reproductive season was assumed to be April–June.

1.9% of relocations; $F_{1,31} = 6.26$, $P = 0.02$). Overall, males did not move more frequently than females ($78.0 \pm 2.3\%$ vs. $76.2 \pm 1.9\%$ of relocations; $F_{1,31} = 0.34$, $P = 0.56$), with no significant interaction between factors ($F_{1,31} = 0.83$, $P = 0.37$). By month, movement frequencies were consistent across the season, except when males became less active relative to females at the end of the season (Fig. 1a).

The mean distance travelled per move by *Elaphe* did not differ significantly between the reproductive season (122.3 ± 9.0 m) and post-reproductive season (126.5 ± 7.5 m; $F_{1,31} = 0.18$, $P = 0.68$), or between males and females (131.6 ± 5.8 m vs. 117.0 ± 10.1 m; $F_{1,31} = 1.67$, $P = 0.21$), with no significant interaction between factors ($F_{1,31} = 0.76$, $P = 0.39$). By month, females moved shorter distances than males in April and June (during the reproductive season), and moved furthest in July (Fig. 1b).

The mean distance travelled per day by *Elaphe* did not differ significantly between the reproductive season (32.8 ± 3.4 m) and post-reproductive season (33.2 ± 2.8 m; $F_{1,31} = 0.02$, $P = 0.88$) or between males and females (35.7 ± 2.7 m vs. 30.1 ± 3.3 m; $F_{1,31} = 1.80$, $P = 0.19$), with no significant interaction between factors ($F_{1,31} = 1.43$, $P = 0.24$). By month, females were less active than males in June, whereas males became less active than females in September (Fig. 1c).

HOME RANGES

Linear regression revealed that ratsnake home range sizes did not vary with the number of observations (range of 39–159) used to estimate them ($r = 0.19$, $P = 0.44$), indicating that differences in number of observations among individuals did not bias home range estimates. Two-way ANOVA with sex and season as factors produced results for home ranges that were qualitatively consistent with those from analyses of movement frequency and movement distance. Mean home range size did not differ significantly between the reproductive season (5.2 ± 0.8 ha) and post-reproductive season (4.6 ± 0.9 ha; $F_{1,31} = 0.19$, $P = 0.67$). Overall, males had larger home ranges than females (6.2 ± 0.9 ha vs. 3.5 ± 0.5 ha; $F_{1,31} = 5.74$, $P = 0.02$), with no significant interaction between factors ($F_{1,31} = 0.72$, $P = 0.40$). The difference between the sexes was greatest during the reproductive season, due to larger male ranges (Fig. 2). Combining data for all ratsnakes, home range size increased as a function of distance travelled per day (linear regression: $r = 0.51$, $P = 0.002$).

RACERS

Two-way ANOVAs with sex and season as factors were used to test for differences between the sexes and across the season for each movement variable. *Coluber* movement probabilities did not differ significantly between the reproductive season ($90.6 \pm 1.1\%$ of relocations) and post-reproductive season ($87.7 \pm 1.4\%$ of relocations; $F_{1,23} = 2.73$, $P = 0.11$) or between males and females ($89.8 \pm 1.3\%$ vs. $88.9 \pm 1.4\%$ of relocations; $F_{1,23} = 0.43$, $P = 0.52$), with no significant interaction between factors ($F_{1,23} = 0.03$, $P = 0.88$). By month, movement

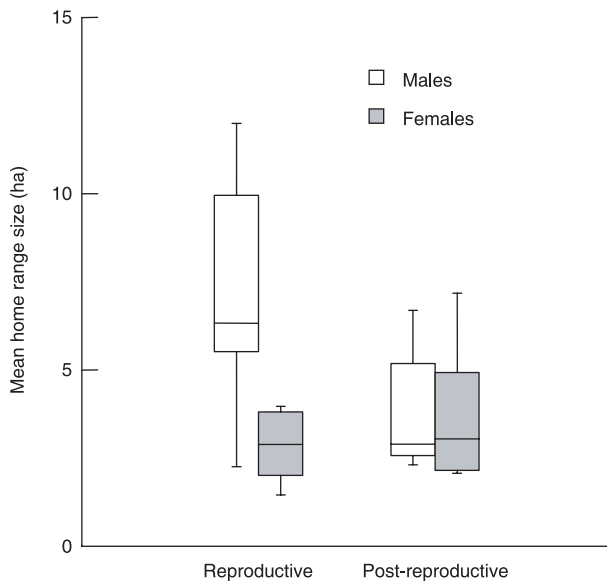


Fig. 2. Box plots of mean home range sizes of *Elaphe* males and females during and after the reproductive season.

frequencies were fairly consistent across the season, with some decline in September (Fig. 3a).

Relative to the reproductive season, the mean distance travelled by *Coluber* per move was greater after the reproductive season (140.2 ± 13.7 m vs. 190.1 ± 13.8 m; $F_{1,23} = 6.11$, $P = 0.02$). Overall, males did not move further than females (181.0 ± 14.2 m vs. 142.3 ± 14.9 m; $F_{1,23} = 2.65$, $P = 0.12$), with no significant interaction between factors ($F_{1,23} = 0.99$, $P = 0.33$). By month, females moved shorter distances than males in April and May, with peak movement distances for females in July (Fig. 3b).

Relative to the reproductive season, the mean distance travelled per day by *Coluber* tended to be further after the reproductive season (56.4 ± 6.3 m vs. 72.0 ± 5.3 m; $F_{1,23} = 3.38$, $P = 0.08$). Overall, males tended to move further than females (71.9 ± 5.7 m vs. 54.1 ± 6.0 m; $F_{1,23} = 3.52$, $P = 0.07$), with no significant interaction between factors ($F_{1,23} = 2.31$, $P = 0.14$). By month, females were less active than males through the early reproductive season, with peak activity in the middle of the season (Fig. 3c).

HOME RANGES

Linear regression revealed that racer home range sizes did not vary with the number of observations (range of 26–158) used to estimate them ($r = 0.08$, $P = 0.79$), again indicating that frequency of observation did not affect these estimates. Two-way ANOVA with sex and season as factors indicated that home range results were qualitatively consistent with those for the frequency of movement but not for movement distances. Mean home range size was larger but did not differ significantly between the reproductive season (25.3 ± 5.3 ha) and the post-reproductive season (15.1 ± 3.4 ha; $F_{1,23} = 2.28$, $P = 0.15$), and home ranges of males were not significantly different

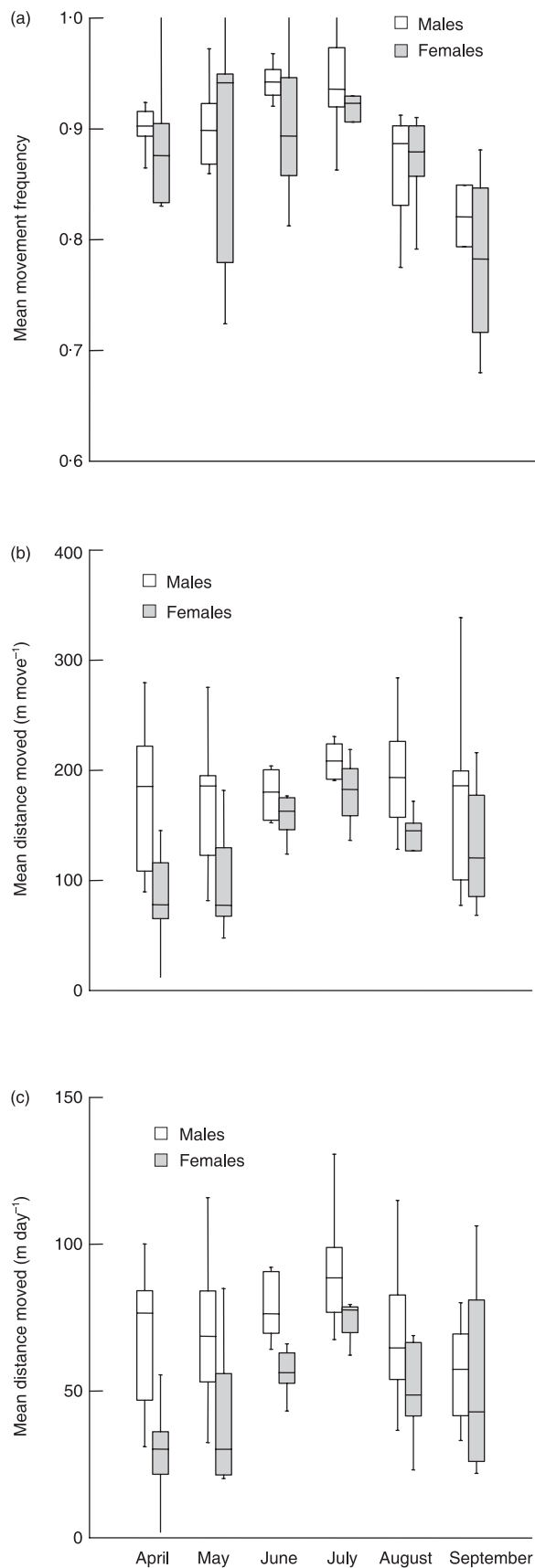


Fig. 3. Box plots of mean monthly movement frequencies (a), distances moved per relocation (b) and distances moved per day (c) of male and female *Coluber* over the course of the active season.

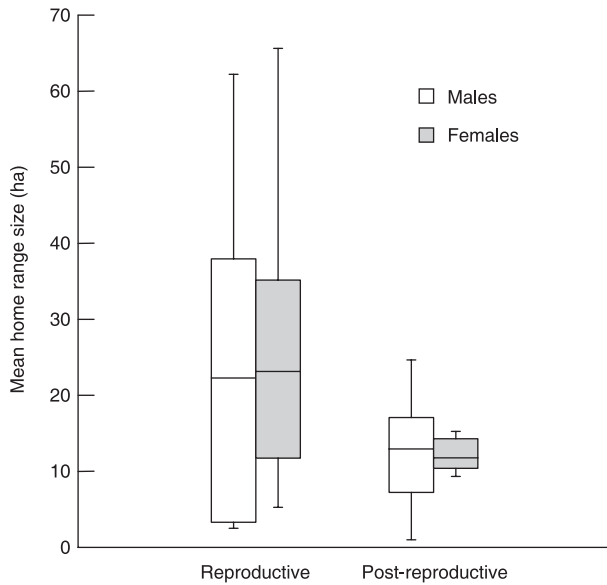


Fig. 4. Box plots of mean home range sizes of *Coluber* males and females during and after the reproductive season.

from those of females (21.9 ± 4.8 ha vs. 19.6 ± 5.1 ha; $F_{1,23} = 0.26$, $P = 0.61$), with no significant interaction between factors ($F_{1,23} = 0.01$, $P = 0.92$; Fig. 4). Unlike ratsnakes, racer home range size did not vary significantly with distance travelled per day (linear regression: $r = 0.14$, $P = 0.50$).

INTERSPECIFIC COMPARISONS

One-way ANOVAS, with species as the factor, were used to test for differences between species for each of the movement variables. Overall, *Coluber* moved more frequently than *Elaphe* ($89.2 \pm 1.0\%$ vs. $77.6 \pm 1.6\%$ of relocations; $F_{1,31} = 34.10$, $P < 0.001$). These results were consistent when observations were limited to those from the most frequently used habitat type; *Coluber* moved more frequently than *Elaphe* ($89.8 \pm 1.1\%$ vs. $78.7 \pm 2.7\%$ of relocations) while in edges ($F_{1,28} = 14.59$, $P < 0.001$). Movement frequencies were consistently greater for *Coluber* across the season, with both species showing peak activity through the middle of the season.

Coluber travelled further per move than *Elaphe*, both overall (152.6 ± 13.0 m vs. 123.9 ± 6.6 m; $F_{1,31} = 4.29$, $P = 0.05$), and while in edges (154.0 ± 15.1 m vs. 116.5 ± 8.6 m; $F_{1,28} = 4.65$, $P = 0.04$). Differences between species were greatest later in the active season (June–September) and both species showed peaks in movement distances in July.

Coluber travelled almost twice as far per day as *Elaphe* overall (59.5 ± 5.6 m vs. 33.3 ± 2.8 m; $F_{1,31} = 19.32$, $P < 0.001$) and while in edges (59.5 ± 7.5 m vs. 29.0 ± 3.5 m; $F_{1,28} = 13.40$, $P < 0.001$). Movements were consistently greater for *Coluber* across the season. Differences between species were greatest later in the active season (June–September), with both species showing peak activity through the middle of the season (Fig. 5).

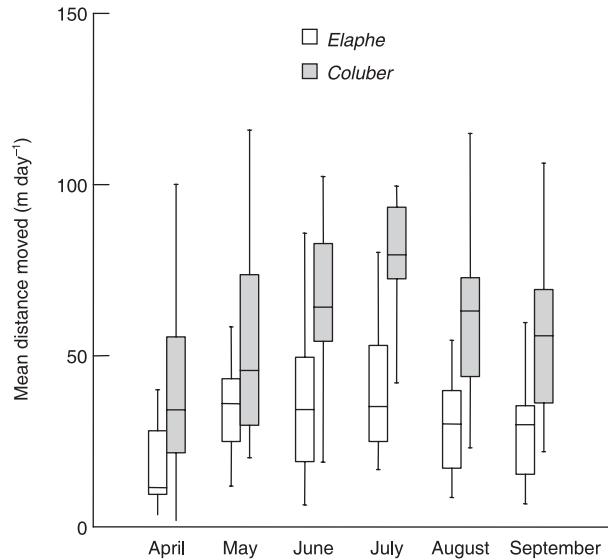


Fig. 5. Box plots of mean distances moved per day of *Elaphe* and *Coluber* over the course of the active season.

SHORT-TERM CONTINUOUS OBSERVATIONS

Differences in movement documented using telemetry become even greater when we consider movements that occurred between regular relocations. *Coluber* was almost three times more likely to move during the short-term, continuous observations: *Elaphe* moved in only 24.2% of the sessions, whereas *Coluber* moved in 71.4% of sessions. We never observed an instance for either species where a snake returned to its original location after having moved during these sessions, so it is likely that snakes found in the same location on consecutive tracking days would rarely have moved between relocations. The estimated mean distance moved by those individuals that were active during a session was 30.8 ± 3.7 m for *Elaphe* and 34.5 ± 4.1 m for *Coluber*. Therefore, when they moved during these short-term observations, individuals of these species did not differ in how far they travelled ($t_{20} = 0.69$, $P = 0.50$).

Combining our estimates of distances travelled by active snakes using our short-term observations, with our estimates of movement probabilities over a 2-day span, we derived mean day ranges for each species. *Coluber* travelled almost four times as far per day as *Elaphe* (88.0 ± 10.4 m/day vs. 23.1 ± 2.8 m/day; $t_{16} = 6.05$, $P < 0.001$). Although individuals of both species travelled similar distances within short periods, racers travelled much further throughout the day because they moved more frequently.

HOME RANGES

A one-way ANOVA, with species as the factor, was used to test for home range size differences between species. Over the entire active season, *Coluber* home ranges were four times larger than *Elaphe* home ranges (24.2 ± 5.8 ha vs. 5.6 ± 0.8 ha; $F_{1,31} = 12.12$, $P = 0.002$; Fig. 6). We also observed substantial intraspecific and interspecific overlap of home ranges. Because

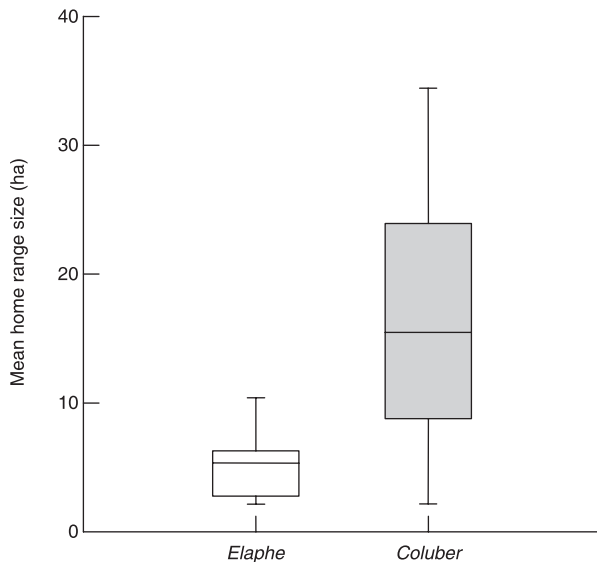


Fig. 6. Box plots of mean overall home range sizes of *Elaphe* and *Coluber*.

we tracked only a subset of the local populations, overlap in space use by individuals of each species is probably quite extensive, and consistent with previous studies of both ratsnakes (Weatherhead & Hoysak 1989; Blouin-Demers & Weatherhead 2002) and racers (Plummer & Congdon 1994).

Discussion

Our goal in this study was to examine the spatial ecology of two snake species that were assumed to differ in their energy requirements. As predicted, the two species differed markedly in their activity levels throughout the season. *Coluber* moved more often and further than *Elaphe*, both overall and only when in the habitat that the species shared most commonly. Because day range differences between species were large, it is likely that the differences in space use that we observed are due at least partly to differences in resource needs. Further, although inactive snakes were unlikely to have moved between regular relocations, active snakes could have made additional moves in the time between relocations. Therefore, our estimates of differences in activity between species were conservative. Also, because all our telemetry distance measures are minimum estimates that almost certainly under-estimate the actual paths taken by snakes, differences in movement distances between species are also probably greater than we were able to document.

We found expected differences between male and female *Elaphe*, and these differences were generally consistent with other studies of this species (Weatherhead & Hoysak 1989; Durner & Gates 1993; Blouin-Demers & Weatherhead 2002). At the end of the reproductive season female *Elaphe* were less active, presumably because at least some were burdened by developing eggs and were foraging less (Seigel *et al.* 1987; Reinert & Zappalorti 1988; Charland & Gregory 1995; Gregory, Crampton & Skebo 1999; Brown & Shine 2004). However,

there was no difference in activity between males and females early in the reproductive season, which could be evidence for mate-searching by both sexes (Gregory *et al.* 1987; Blouin-Demers & Weatherhead 2002).

The *Coluber* sexes also differed in activity during the reproductive season but unlike *Elaphe*, female *Coluber* were less active throughout the reproductive season. This was as expected if gravid females forgo feeding during these months (Reinert & Zappalorti 1988; Gregory *et al.* 1999), and are less capable of extensive locomotion while gravid (Seigel *et al.* 1987; Charland & Gregory 1995; Brown & Shine 2004). Also, given that the cost of being gravid should be greater for females of a species that depends on speed for escape or foraging (Cooper *et al.* 1990), we might expect normal activity of gravid *Coluber* to be more constrained than that of female *Elaphe* while carrying eggs. Because the *Coluber* sexes differed most early in the reproductive season, however, that difference in movement could reflect the effects of mating behaviour. Unlike *Elaphe*, perhaps the high activity level of male *Coluber* makes it unnecessary for female *Coluber* to search actively for mates.

Our home range results generally support the hypothesis that space use by snakes is influenced by energetic requirements. *Coluber* had substantially larger home ranges than the more energetically conservative *Elaphe* (24.2 ha vs. 5.6 ha). Because *Elaphe* are more arboreal than *Coluber* (Carfagno & Weatherhead 2006), we may have under-estimated the home ranges of *Elaphe* by not considering the three-dimensionality of their space use (Lillywhite & Henderson 1993; Perry & Garland 2002). We found little evidence that *Elaphe* moved through the tree canopy, however, so their functional space use was not substantially greater than we have estimated. Seasonal patterns of movement by both snake species were also consistent with the energy hypothesis. Following the reproductive season, when movement should have been influenced primarily by foraging, the difference in movement between *Coluber* and *Elaphe* was most pronounced.

Intraspecifically, differences in home range size were not consistent with differences in movements. Male *Elaphe* had larger home ranges than females despite not moving further, whereas the *Coluber* sexes had comparable home ranges despite males moving further. As well, *Coluber* home ranges tended to be larger during the reproductive season, despite the snakes' increasing movement after the reproductive season. These results could reflect a difference in how movements associated with foraging and those associated with mate-searching affect home ranges, because larger home ranges do not result necessarily from larger or more frequent movements (e.g.; Reinert & Kodrich 1982; Reinert & Zappalorti 1988; Secor 1994; Wunderle *et al.* 2004), but also depend upon how those movements are made on the landscape (Whitaker & Shine 2003; Pearson *et al.* 2005).

Decreased productivity at higher latitudes is associated with larger home ranges in mammals and birds (Harestad & Bunnell 1979; Lindstedt *et al.* 1986; Buskirk & McDonald 1989; Gompper & Gittleman 1991), consistent with energy driving space use. For ectotherms, however, more challenging

thermal conditions at higher latitudes could constrain activity, countering effects of productivity on home range size, although Arvisais *et al.* (2002) did find that home range size increased with latitude in a turtle. At the northern limit of *Elaphe* distribution, home ranges were three to four times larger than in Illinois, despite the snakes moving less frequently and shorter distances per move (Weatherhead & Hoysak 1989; Blouin-Demers & Weatherhead 2002). Thus, even though reduced movement, a shorter active season and slower growth (Blouin-Demers, Prior & Weatherhead 2002) all indicate that *Elaphe* in Ontario require less energy than *Elaphe* further south, in Ontario the snakes use much larger home ranges. Clearly, one requires information on both energy needs and energy availability to predict a snake's space needs (Gregory *et al.* 1987; Plummer & Congdon 1994; Johnson 2000).

Our results are consistent with the assumption that the increase in home range size with body size in animals (both ectothermic and endothermic) is a consequence of larger animals requiring more energy, which requires in turn that they use more space (e.g.; McNab 1963; Schoener 1968; Turner *et al.* 1969; Christian & Waldschmidt 1984; Perry & Garland 2002). The difference in day ranges is also consistent with the notion that species with greater energy requirements move more. Our estimates of daily movements were far lower than those reported for mammals (including carnivores) of similar mass (Garland 1983; Carbone *et al.* 2005), consistent with ectotherms requiring relatively less energy and thus using less space.

Despite the general relationship between body size, energy requirements and home range size, predicting a particular snake species' space needs is not straightforward (Webb & Shine 1997; Whitaker & Shine 2003). We demonstrated that two species of similar size and with similar ecologies can differ substantially in their space use. In turn, activity alone can be a poor predictor of space use, both within and particularly among populations, where habitat productivity differences are likely to play an important role. Additional comparative studies and analyses should make it possible to begin incorporating some of these complexities into predictive models, although precise measures of a snake species' or population's space needs may ultimately always require an empirical approach.

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