Spatial Ecology of the Oregon Gartersnake, *Thamnophis atratus hydrophilus*, in a Free-Flowing Stream Environment

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Spatial patterns of animals have important implications for population dynamics and can reveal other key aspects of a species' ecology. Movements and the resulting spatial arrangements have fitness and genetic consequences for both individuals and populations. We studied the spatial and dispersal patterns of the Oregon Gartersnake, *Thamnophis atratus hydrophilus*, using capture–recapture techniques. Snakes showed aggregated dispersion. Frequency distributions of movement distances were leptokurtic; the degree of kurtosis was highest for juvenile males and lowest for adult females. Males were more frequently recaptured at locations different from their initial capture sites, regardless of age class. Dispersal of neonates was not biased, whereas juvenile and adult dispersal were male-biased, indicating that the mechanisms that motivate individual movements differed by both age class and sex. Males were recaptured within shorter time intervals than females, and juveniles were recaptured within shorter time intervals than adults. We attribute differences in capture intervals to higher detectability of males and juveniles, a likely consequence of their greater mobility. The aggregated dispersion appears to be the result of multi-scale habitat selection, and is consistent with the prey choices and related foraging strategies exhibited by the different age classes. Inbreeding avoidance in juveniles and mate-searching behavior in adults may explain the observed male-biased dispersal patterns.

MULTIPLE interacting factors may affect the movements and resulting spatial patterns of individual animals within a population (e.g., population density, resource distribution and social behavior); consequently, general principles of animal dispersion (the spatial arrangement of individuals) are lacking (Gautestad and Mysterud, 2005). Dispersal, the behaviors that determine these spatial patterns, can be motivated by different factors, may vary across species and also by sex and age. At present most animal movement studies have been focused on mammals and birds. As a result, general trends and explanations for dispersal patterns have been primarily derived from the study of these two taxonomic groups (Lawson Handley and Perrin, 2007). Movement studies of organisms such as snakes may provide valuable new information to test the predictions of more general evolutionary models for dispersion and dispersal patterns.

Few field studies have examined dispersion and the factors that influence these patterns in snakes, partly due to the secretive nature of most ophidian species and the difficulty in sampling young animals (Gregory et al., 1987). Previous research on snakes indicates that dispersion may be influenced by selective use of habitats and movement of individuals between habitats (Gregory et al., 1987). Identifying how habitat use and movement behavior influence dispersion is important in understanding a species' population ecology. Furthermore, knowledge of the spatial ecology of mobile animals is critical to understanding and evaluating potential threats to their fitness and viability. In general, individual snakes are not distributed randomly with respect to others in a population (Gregory et al., 1987; Greene, 1997). In most snake species, individuals do not demonstrate territoriality (Greene, 1997), a behavior often resulting in a uniform (i.e., regular or overdispersed) spacing of individuals (Brown and Orians, 1970). The spatial arrangement most commonly observed in snakes is an aggregated (i.e., clumped) pattern, which may be a result of selection for habitats containing spatially or temporally limited resources such as food, basking sites, hibernacula or mates (Gregory et al., 1987).

The movement and dispersal patterns of mobile animals are the processes by which spatial relationships are achieved and change over time (Pielou, 1977). The extent to which an individual moves may be dependent on a number of factors such as social system, seasonality, habitat, and other ecological or behavioral attributes (Stamps, 2001; Clobert et al., 2001, 2004). Explanations for juvenile-biased dispersal, the most commonly reported age-related dispersal pattern (Greenwood, 1980; Badyaev et al., 1996; Ujvari et al., 2008), include inbreeding avoidance (Dobson, 1982) and resource competition (Dobson, 1982; Lena et al., 1998; Newton, 2001). An understanding of the causes for sex-biased dispersal is convoluted by differences between mammals and birds and exceptions to general trends. In a seminal review on the dispersal of mammals and birds, Greenwood (1980) predicted that the direction of sex-bias is dependent on which sex gains more from maintaining fidelity to a particular location, and this is often associated with the mating system (e.g., monogamous versus polygynous). Dispersal tends to be female-biased in socially monogamous birds, whereas male-biased dispersal is more common in predominantly polygynous mammals (Greenwood, 1980; Pusey, 1987). Sex-bias and reasons for the direction of the bias may also differ by age class (i.e., natal versus breeding dispersal) within a species (Greenwood, 1980). However, studies often examine either natal or breeding dispersal, but rarely both. General patterns regarding the effect of sex and age on snake dispersal have not yet been recognized because of an overall lack of research and incomparability among studies due to variable data quality and dissimilar methodologies (reviewed in Gregory et al., 1987). Our objectives were to describe the spatial arrangements (i.e., dispersion patterns), movements, and dispersal patterns of the Oregon Gartersnake (*Thamnophis atratus hydrophilus*) as they relate to the meso- and microscale habitats of a free-flowing, cold-water stream environment in Northwestern California.

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Table 1. Stream Mesohabitat Types at Hurdygurdy Creek, Del Norte County, California. For definitions and descriptions of all 22 stream mesohabitat types available in northern California, see McCain et al. (1990).

Stream mesohabitat type	Mesohabitat code
Low gradient riffle	01
High gradient riffle	02
Cascade	03
Secondary channel pool	04
Plunge pool	09
Lateral scour pool, bedrock formed	12
Dammed pool	13
Glide	14
Run	15
Mid-channel pool	17
Edgewater	18
Channel confluence pool	19

MATERIALS AND METHODS

Study area.—Our study site along Hurdygurdy Creek, Del Norte County, northwestern California, USA, has been described previously (Lind and Welsh, 1994; Welsh and Lind, 2000). This location is in mixed hardwood/Douglas-fir (*Pseudotsuga menziesii*) forest with cool wet winters and warm dry summers. Rainfall at the nearest gauging station (Gasquet Ranger Station, Smith River National Recreation Area, 12.9 air km north) averages 280 cm annually (range 152–330 cm); summer high air temperatures range from 25 to 35°C and winter lows range from 8 to 13°C. Water temperatures, in the stream where the snakes forage, ranged from 13 to 21°C during the study, but can drop as low as 5°C in winter when snakes are not active. Stream width ranges from 10 to 15 m, and the 4.7-km long study reach contained the full range of lotic mesohabitats (visually distinct units of habitat within the stream; Pardo and Armitage, 1997) typical of a mountain stream (riffles, runs, pools, cascades, and pools [Table 1]; for definitions and descriptions of mesohabitat types see McCain et al., 1990). In terms of natural disturbance regimes (Montgomery, 1999), lower Hurdygurdy Creek shows evidence of annual debris flows, flooding, and some braided channel formations, but most major stream mesohabitats were consistently maintained from year to year. Stream discharge is variable, ranging from 1 m^3/sec in the summer to over 100 m^3/sec in the winter (McCain, 1994), with ten-year flood events documented to 140 m^3/sec (D. Fuller, pers. comm.). During high water from late fall until early spring the usually clear water becomes more turbid, and the current is often too strong to be safely traversed by humans. Snakes are not active during this time.

Snake surveys.—We made all observations during surveys of lower Hurdygurdy Creek, where we conducted three to five surveys per year from 1986 through 2001. We scheduled the minimum three annual surveys to coincide with key aspects of *T. a. hydrophilus* natural history, with the first following spring emergence, the second during the mid-summer peak of activity, and the third following birthing of young, when neonate snakes can be found along the stream margins. Surveys occurred from late spring to early fall (May to October), between 1000 and 1800 hrs, when the sun illuminates the stream channel and snakes are most active and visible along stream banks and in the water. Surveys typically took three to four days each, and were conducted by one to three workers who waded slowly upstream along the wetted channel, watching for snakes along banks, in overhead vegetation, in the water column, or on channel bottom substrates. We captured, measured (snout–vent [SVL] and total lengths), weighed (± g), sexed by manual hemipenes eversion (Cheek and Richards, 2003), and individually marked snakes by clipping belly scutes to form small permanent scars in unique combinations using fine ophthalmology scissors (Ferner, 1979; Fitch, 1987). We used the time of year of sampling and sex-specific sexual maturity information to assign age classes (i.e., presence of sperm in cloacal smears and size of gravid females; HHW, AJL, unpubl. data), with the assumption that size accurately represented age without regard to variable growth rates. This divided our data into neonate, juvenile, and adult age classes, and by sex, for analysis. The smallest snakes were classified as neonates during and immediately following the presumed birthing season and were considered juveniles upon emergence the following spring (see Lind et al., 2005 for details on age class breaks).

We recorded the mesohabitat, microhabitat (the stream environment within a meter of the individual), and localized water depth (± cm) at each capture location. We used the same stream habitat classification system for mesohabitat and microhabitat types (McCain et al., 1990; Table 1). To document snake locations, we used a detailed map based on measured lengths (± m) of each mesohabitat (hereafter mesohabitat unit). Mesohabitat units were identified using a two-digit mesohabitat code (McCain et al., 1990; Table 1) followed by the sequential number of that mesohabitat type from the starting point at the most downstream end of the study reach. For example, unit number 1404 represented the fourth glide (Table 1) encountered along the reach. Snakes were initially recorded as present alongside or within a particular mesohabitat unit; for subsequent recaptures we calculated distances moved between units by using the upstream end points of each mesohabitat unit.

Analyses.—To examine the dispersion of snakes for each age class, we calculated a linear density (Parker and Plummer, 1987) of snakes for each mesohabitat unit (captures/m). In creating this variable, we assumed that there was a linear association between the number of captures and length of mesohabitat unit, and we recognize several confounding factors that should be considered when interpreting our results. First of all, several areas along the stream had multiple channels (braided) that we collapsed into a single channel for our analysis (approximately 16% of the total 4.7-km study reach). Because braided portions of the stream consisted of more than one channel, the actual area searched and the search efforts were greater, resulting in a likely overestimation of snake density for 16% of the sampling units used in the analysis. Secondly, snakes of different age classes behave differently, such that their use of the stream channel can vary. Based on our observations, neonates and juveniles rarely traverse the stream, whereas adults frequently do so. The width of the mesohabitat units as well as the length can therefore differentially influence the amount of available habitat for the different age classes, and thus the area of use, rather than length, may be more appropriate for deriving more accurate adult snake densities.

However, in this study we used mesohabitat length in all of our analyses.

With initial capture data only (omitting recaptures), we assessed the degree of aggregation of snakes, by age class, along the study reach by comparing snake densities in mesohabitat units to snake densities in neighboring mesohabitat units using the test statistic,

$$T = \sum_{i=2}^{n} (x_i - x_{i-1})^2,$$

the sum of squared differences of neighboring densities, where x_i is snake density for the n sampling units ($i = 1,2,\ldots,n$). We used randomization tests (Manly, 2007) to compare observed values of T against the distribution of T values from randomly arranged densities. If there was aggregation (mesohabitats with lower snake densities tending to be near each other and mesohabitats with higher snake densities tending to be near each other), then we would expect the observed value of T to be much smaller than that of the randomization distribution of T values, which assumes no aggregation.

To investigate coarse-scale use of the environment, we categorized mesohabitats (Table 1) based on water flow and turbulence (Hawkins et al., 1993), as fast-water turbulent (riffles and cascades), fast-water non-turbulent (glides and runs), slow-water scour pools (lateral scour pools), and slow-water dammed pools (secondary channel, plunge, mid-channel, and confluence pools). We applied a generalized linear model to test whether mean snake densities were significantly different in these lumped mesohabitat categories for each age class, while accounting for spatial autocorrelation. We examined pair-wise differences using Tukey-Kramer multiple comparison tests. No snakes were captured in slow-water dammed pools; therefore, this category was omitted from the analysis. Data were normalized with a square-root transformation. Because we saw no evidence of year to year differences in the dispersion patterns of snakes, we combined data across years for the spatial analyses. At a finer scale, we categorized microhabitats as fast-water (riffles, cascades, and runs) or slow-water (pools, glides, and edgewaters) and deep-water (> 10 cm) or shallow-water (< 1–10 cm), and created four combination variables: deep fast, deep slow, shallow fast, and shallow slow (based on Lind and Welsh, 1994). We used chi-square contingency tests to examine relationships between microhabitat and snake age class.

To examine movement patterns by age class of snake, where individuals may or may not have changed class between captures, we separated and analyzed the data as follows: (1) no change in age class between captures with both age and sex as effects; (2) captured as neonate, recaptured as juvenile the following year with sex as the effect (to specifically examine natal dispersal); (3) captured as neonate, recaptured as adult with sex as the effect; and (4) captured as juvenile, recaptured as adult with sex as the effect. Because total distance moved is typically influenced by time elapsed between captures, we created the variable ''m/mo'' based on the eight-month active period (March to October only; hereafter referred to as 'activity months'). The time interval between captures ranged from 0.5 to 62 activity months (equates to 0.5–7.75 years). We calculated distance moved over time for all snakes recaptured during the study.

We examined kurtosis (width of peak and length of tails) of distance frequency distributions (m/mo) to compare the degree of kurtosis, an indicator of variation in movement behavior (Skalski and Gilliam, 2000). We classified data distributions as leptokurtic when kurtosis values were greater than three (Hintze, 2007). We used analysis of variance (ANOVA) to test the null hypothesis that there were no differences in movement by sex or age class and examined pair-wise differences using Tukey-Kramer multiple comparison tests. We examined overall, upstream, and downstream movements. Due to the high variability in distances moved, we used a natural log transformation to normalize the data. We also analyzed a subset of the data (first recaptures only for each individual) to evaluate whether the results were affected by pseudo-replication due to non-independence of samples. We used t-tests to examine differences in capture intervals between age, sex and age/sex groupings (e.g., juvenile to adult, described above). We omitted the following observations from this analysis: those with < 0.5 months between captures ($n = 5$), and one group with insufficient samples (neonates subsequently recaptured as neonates; $n = 6$).

RESULTS

We captured and marked 1730 individual snakes, recapturing 532 (some individuals recaptured several times). Initial captures consisted of 240 neonate, 638 juvenile, and 82 adult female snakes; and 174 neonate, 434 juvenile, and 162 adult male snakes. Recaptures consisted of four neonate, 233 juvenile, and 96 adult females; and two neonate, 87 juvenile, and 110 adult males. The annual recapture rate ranged from 13 to 32%, and the annual population estimate for the study reach was 445.01 ± 24.28 (mean ± SE) individuals (first reported in Lind et al., 2005); this equates to approximately 95 snakes per kilometer.

Spatial arrangement and habitat use.—Snakes of all age classes were captured within nearly all mesohabitat units along the reach (Fig. 1); however, analysis indicated that snake densities between neighboring mesohabitat units were more similar than would be expected by chance, indicating that spatial aggregation occurred in all age classes. Aggregation was most evident for juveniles ($T = 27.04$, $P < 0.001$), followed by neonates ($T = 7.13$, $P = 0.02$) and adults ($T = 2.91$, $P = 0.04$). Neonate densities were higher in fast-water non-turbulent compared to fast-water turbulent mesohabitats ($F_{2,104} = 3.29$, $P = 0.04$; Fig. 2A), juvenile densities were higher in fast-water turbulent compared to slow-water scour pool mesohabitats ($F_{2,95} = 2.58$, $P = 0.08$; Fig. 2B), and adult densities were higher in fast-water (turbulent and non-turbulent) compared to slow-water scour pool mesohabitats ($F_{2,145} = 4.72$, $P = 0.01$; Fig. 2C). Frequency of microhabitat use was associated with age class ($\chi^2 = 161.80$, $P < 0.001$). Neonates used primarily shallow edgewaters, juveniles were found in shallow riffles and edgewaters, and adults mainly used deeper and faster-flowing microhabitats (Fig. 3).

Dispersal patterns and capture intervals.—Frequency distributions of movement distances for this population of snakes were leptokurtic (higher peak and longer tails than a normal distribution) for all groups (Table 2; Fig. 4A). For individuals that did not change age class between subsequent captures, the degree of kurtosis was highest for juvenile males and lowest for adult females (Table 2; Fig. 4B). Male juveniles

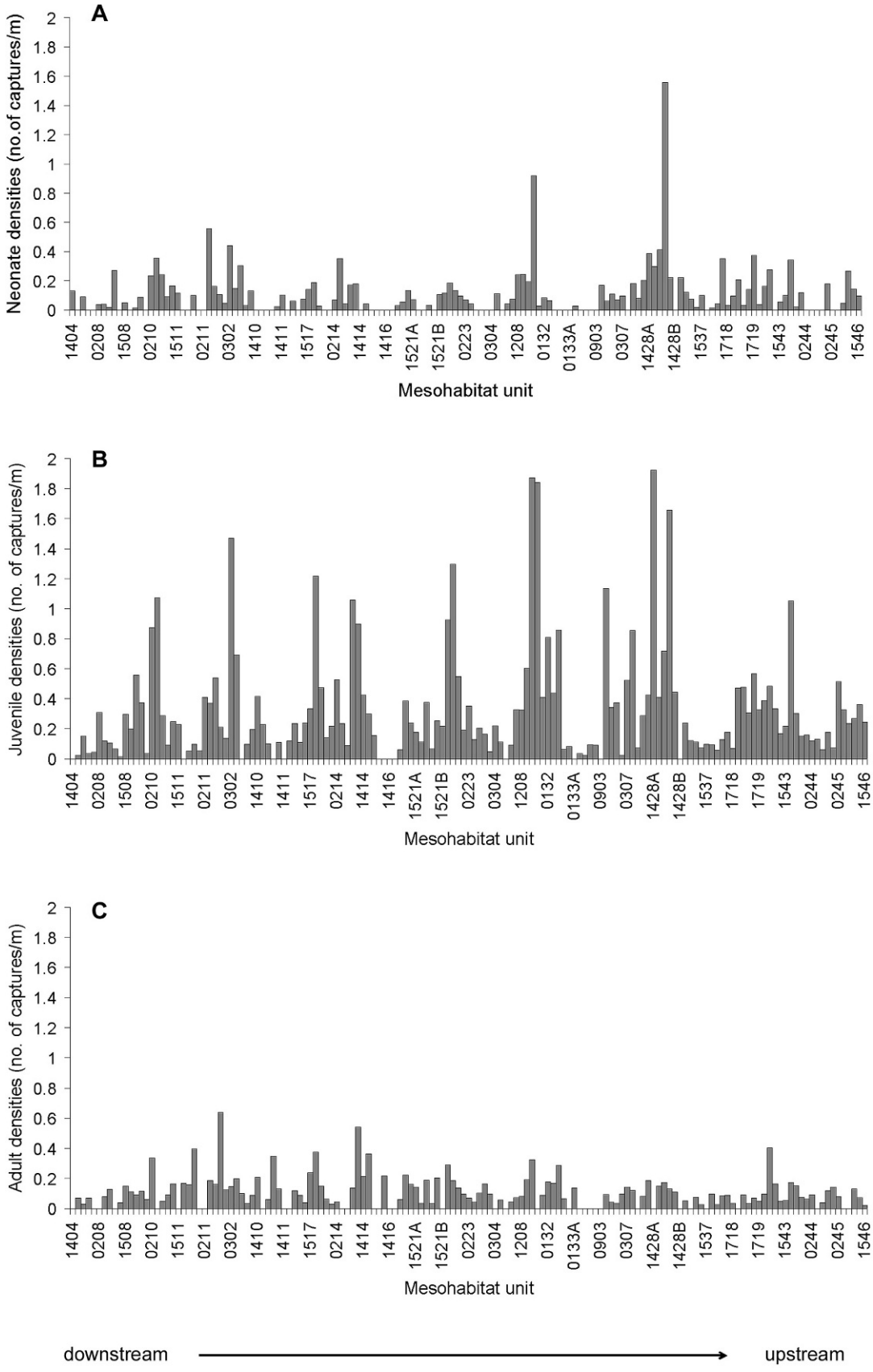

Fig. 1. Linear densities of (A) neonate, (B) juvenile, and (C) adult *Thamnophis atratus hydrophilus* along Hurdygurdy Creek from 1986 to 2001 (initial captures only). The x-axis lists the mesohabitat units of the study reach (downstream end on the left). Labels are provided for some, but not all, mesohabitat units (see text and Table 1). Mesohabitat lengths are not to scale.

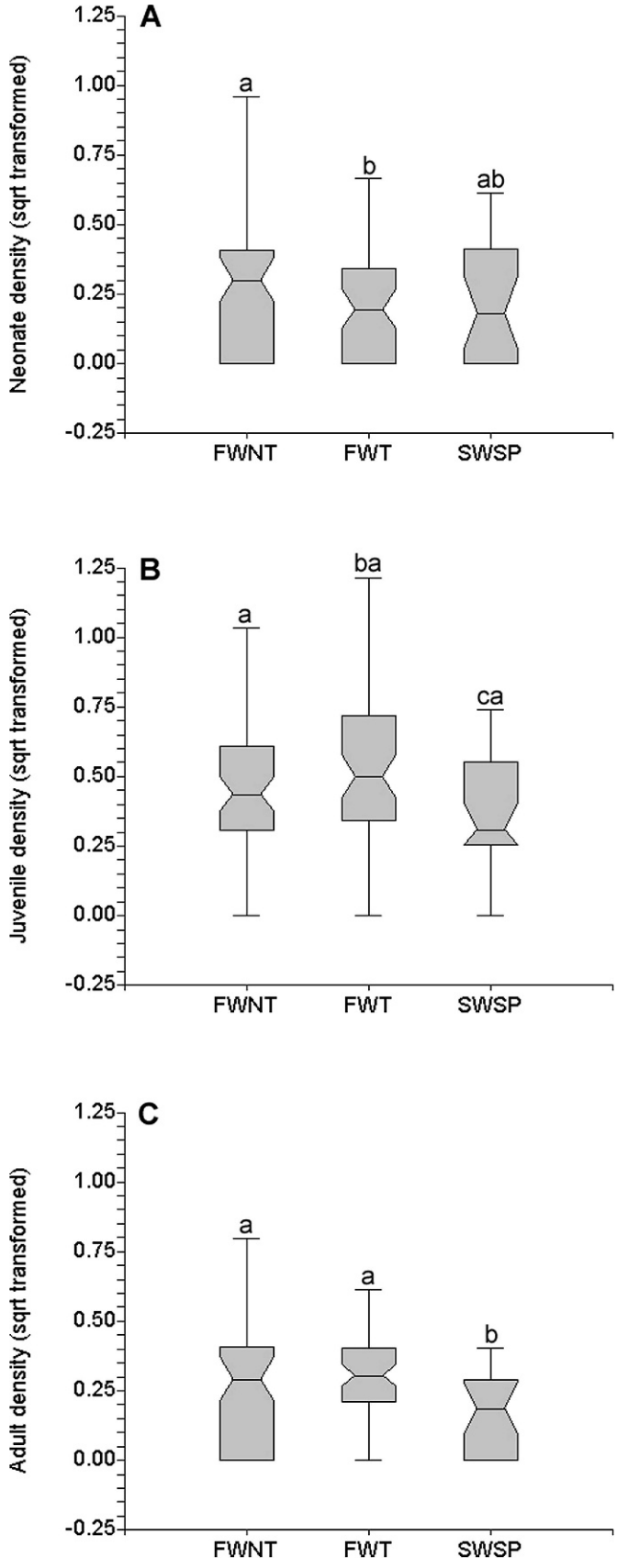

Fig. 2. Boxplots of (A) neonate, (B) juvenile, and (C) adult densities of *Thamnophis atratus hydrophilus* in three mesohabitat types based on water flow and turbulence (Hawkins et al., 1993): fast-water non-turbulent (FWNT), fast-water turbulent (FWT), and slow-water scour pool (SWSP). Letters above boxes represent significance in Tukey-Kramer pair-wise comparisons ($\alpha = 0.10$); groups with the same letter are not significantly different. The center line represents the median value. The top and bottom of the box represent the 25th and 75th percentiles, the notched area represents the 95% confidence interval, and whiskers represent the upper and lower adjacent values, set at 1.5 times the interquartile range. n = number of individuals observed.

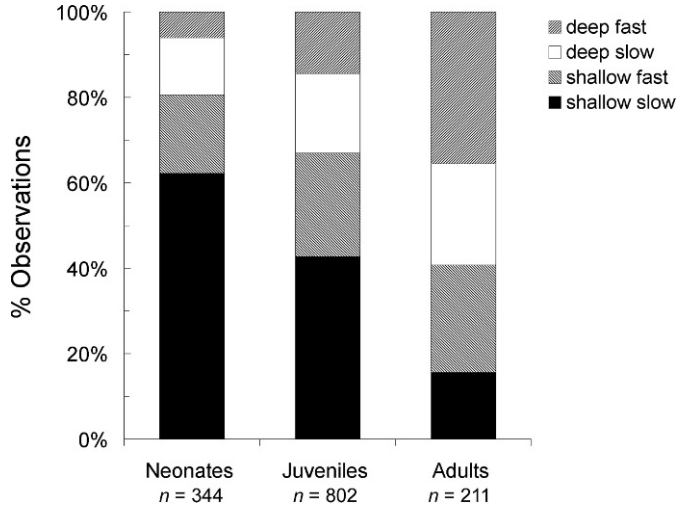

Fig. 3. Frequency of microhabitats used by three age classes of *Thamnophis atratus hydrophilus*. Deep fast microhabitats included fast-water habitats (riffles, cascades, and runs) with > 10 cm water depths; deep slow included slow-water habitats (pools, glides, and edgewaters) with > 10 cm water depths; shallow fast included fast-water habitats with < 1–10 cm water depths; and shallow slow included slow-water habitats with < 1–10 cm water depths (Lind and Welsh, 1994). n = number of individuals observed.

recaptured as adults had a higher degree of kurtosis than corresponding females; however, female neonates that were recaptured as juveniles the following year had higher kurtosis values than male neonate recaptures (Table 2). A high proportion of recaptured snakes exhibited little to no movement relative to particular mesohabitat units, and a few snakes showed long distance movements upstream or downstream (Table 2; Fig. 4). Across all groups, 18–26% of males and 26–33% of females were recaptured in the same mesohabitat unit as their previous capture (Table 2). More female snakes tended to remain at their previous capture location than males, and females, on average, were recaptured closer to their previous capture site than males (Table 2). The greatest distance moved was made by a male, initially captured as a juvenile and recaptured 12 active months later as an adult; this male was recaptured a distance of 3.6 km upstream from the initial capture location. This is in contrast to many snakes that moved little over long time spans, or those that moved up and down stream but with little or no overall displacement during the course of our study.

We found differences in overall movement (m/mo) for those snakes that did not change age class between captures. Juvenile males moved greater distances than juvenile females, which moved greater distances than adult females, and adult males moved greater distances than adult females ($F_{3,249} = 9.41$, $P < 0.01$; Fig. 5A). Male juveniles recaptured as adults moved greater distances than female counterparts ($F_{1,82} = 10.76$, $P < 0.01$; Fig. 5B); however, for neonates recaptured as juveniles the following year, there was no

Table 2. *Thamnophis atratus hydrophilus* Recapture Data. Number of snakes recaptured at the same location (i.e., snakes that did not change mesohabitat unit) and the proportion of snakes within each group that did not move, summary statistics for movement data, and kurtosis values of movement frequency distributions (includes snakes that did not move). n = number of individuals observed.

Effect	No. recaps. at previous capture site (proportion)	Distance moved (m/mo)				Kurtosis	
		Mean	SE	Min	Max	Kurtosis	SE
Age × sex—no change in age class between captures							
Adult female (n = 36)	12 (0.33)	10.8	2.3	0.7	39.8	5.4	1.9
Adult male (n = 53)	14 (0.26)	47.6	10.8	2.9	320.7	10.3	3.2
Juvenile female (n = 182)	48 (0.26)	38.1	4.4	0.6	329.1	14.9	3.1
Juvenile male (n = 68)	16 (0.24)	72.9	16.4	1.8	627.6	17.8	6.1
Sex—captured as juvenile, recaptured as adult							
Female (n = 58)	15 (0.26)	9.5	1.8	0.9	53.9	9.1	2.4
Male (n = 49)	9 (0.18)	38.2	10.3	0.7	304.6	12.7	4.7
Sex—captured as neonate, recaptured as juvenile							
Female (n = 34)	9 (0.26)	31.2	8.8	3.5	208.5	15.0	8.1
Male (n = 14)	3 (0.21)	42.9	12.6	4.8	155.1	6.7	4.2

difference in distances moved between males and females ($F_{1,35}$ = 2.11, P = 0.16; Fig. 5C). For the analysis of movement based on direction, results were generally consistent with overall movement results; juvenile males, adult males, and juvenile females moved greater upstream distances than adult females ($F_{3,117}$ = 6.23, $P < 0.001$), and juvenile males moved greater downstream distances than adult females ($F_{3,127}$ = 4.08, $P < 0.01$). Analysis of the data subset to evaluate the potential influence of pseudoreplication (first recaptures only for each individual) resulted in the same pair-wise differences.

Time intervals between captures were shorter for adult males than adult females (8.35 ± 1.41 and 15.89 ± 2.01, respectively; T = 3.08, df = 67, $P < 0.01$). This pattern was similar for juveniles; juvenile males were recaptured at shorter intervals compared with juvenile females (4.65 ± 0.47 and 7.13 ± 0.43, respectively; T = 3.87, df = 179, $P < 0.001$). For snakes that did not change age class between subsequent captures, we recaptured juveniles, regardless of sex, at shorter time intervals than adults (6.45 ± 0.35 and 11.40 ± 1.23, respectively; T = 3.89, df = 102, $P < 0.001$).

DISCUSSION

The challenges of studying snake spatial patterns and movements have long been recognized (Gregory et al., 1987; Macartney et al., 1988). The lack of research has been attributed in part to the particular difficulties in sampling large numbers of snakes. Snakes are generally cryptic, especially neonates and young, and such studies require a substantial amount of time and effort to yield meaningful results. We believe our long-term study of a population of *T. a. hydrophilus* overcomes these obstacles. These snakes, particularly neonates and juveniles, are relatively abundant at our site (Lind et al., 2005) and forage diurnally in open habitats that permit undisturbed observation (Lind and Welsh, 1994; Welsh and Lind, 2000). The sizeable population and extensive field efforts have resulted in large sample sizes; thus, we captured and recaptured a sufficient number of individually marked snakes of all age classes to investigate spatial and movement patterns. We are aware of only two other comparatively long-term studies, in which capture–recapture data were used to examine snake dispersal (Keogh et al., 2007; Dubey et al., 2008). Other studies of snake spatial ecology used radio-telemetry, a technique that often results in limited sample sizes and durations too short-term to detect and confirm general patterns. However, telemetry studies can detect movements outside of a study area and thereby provide continuous movement data with consistent capture intervals from which accurate pathways of individuals may be determined. These studies can also be very useful in examining finer temporal scale patterns (e.g., seasonal differences, differences between gravid and nongravid females).

Spatial arrangement and habitat use.—Results from our study indicated that the spatial pattern of this population of *T. a. hydrophilus*, like most other snake species studied to date, exhibited aggregated dispersion. Aggregations are expected in snakes because of the heterogeneous distribution of critical resources in most environments and a lack of territorial behavior (Gregory et al., 1987). The abundance and availability of prey is one resource that may influence a species' spatial pattern (Gregory et al., 1987). Schwaner (1991) reported that the distribution of prey influenced dispersion of Tiger Snake (*Notechis ater*); snakes aggregated in areas of high prey densities and/or cover. Based on earlier work (Lind and Welsh, 1994) and current results, we believe that the aggregated patterns we observed can best be explained by differences among snake age classes in habitat selection and the related distributions of their favored prey species.

Lind and Welsh (1994) reported that microhabitat use by *T. a. hydrophilus* differed by age class. Our assessment of microhabitat use, based on a much larger sample, revealed the same general patterns. Neonates were the most specialized, using primarily shallow edgewaters; juveniles were found in shallow riffles and edgewaters; and adults used mainly faster-flowing microhabitats. Lind and Welsh (1994) attributed these habitat relationships to age-specific food choices and foraging strategies. Neonates and juveniles fed on smaller prey, such as tadpoles and young fish that inhabited shallow stream margins (Lind and Welsh, 1994), and used a unique lingual-luring ambush foraging strategy for attracting and capturing fish in shallow water (Welsh and Lind, 2000). Foothill Yellow-legged Frogs (*Rana boylii*) at

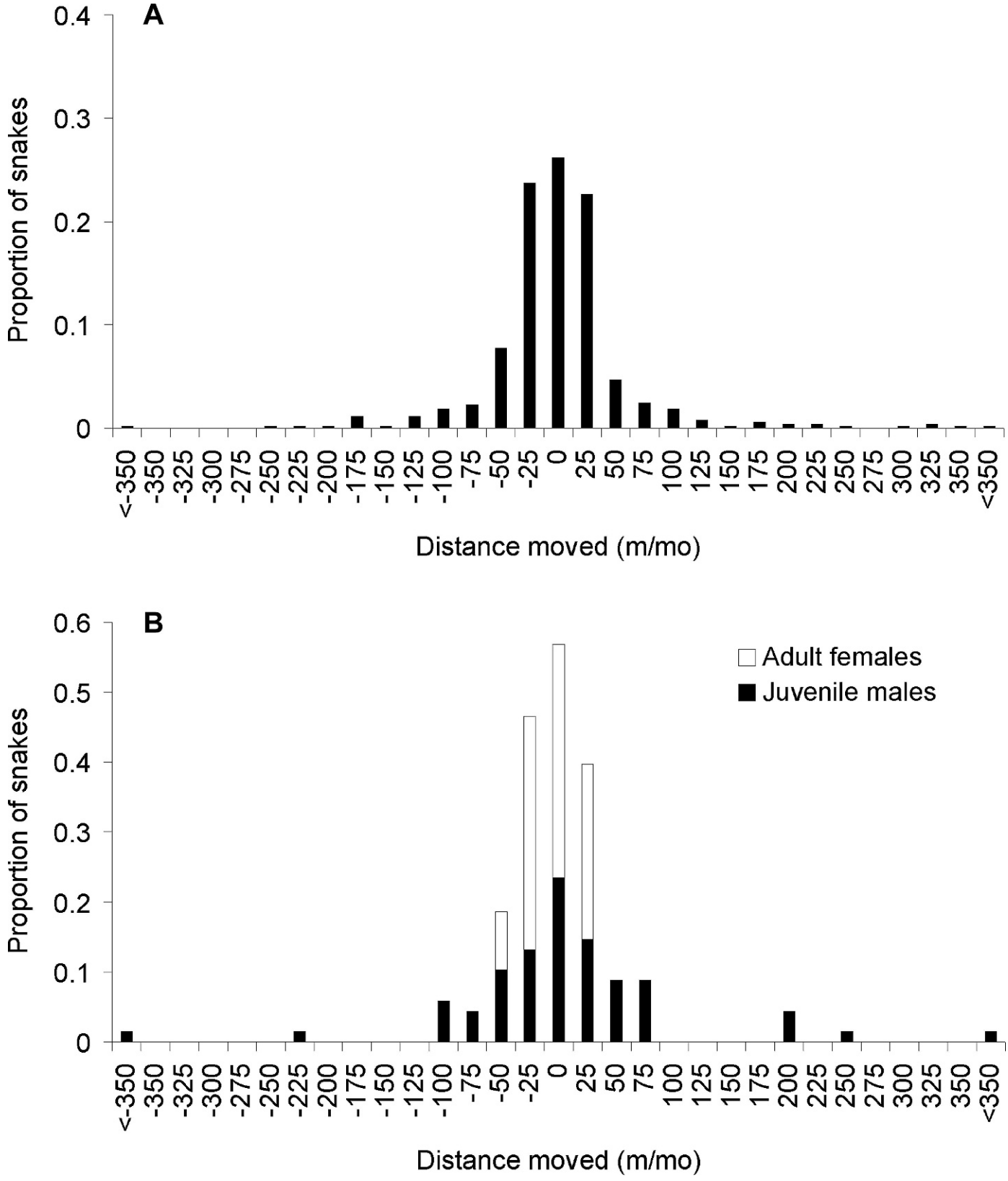

Fig. 4. Frequency histograms of movement distances for *Thamnophis atratus hydrophilus*: (A) all recaptures (n = 532), and (B) juvenile male (n = 68) and adult female (n = 36) recaptures with no change in age class between captures. Zero on the x-axis represents observations of recaptures in the same location as the previous capture; positive values indicate upstream movements and negative values indicate downstream movements.

Hurdygurdy Creek formed breeding aggregations at sites that provided shallow, low velocity microhabitats required for oviposition (Wheeler and Welsh, 2008). Moreover, stream margins provide suitable conditions for Foothill Yellow-legged Frog tadpole rearing (Kupferberg et al., 2008). Young snakes aggregated along these microhabitats that maintained high densities of both tadpoles and young salmonids. In contrast, adults fed on a wider variety of prey

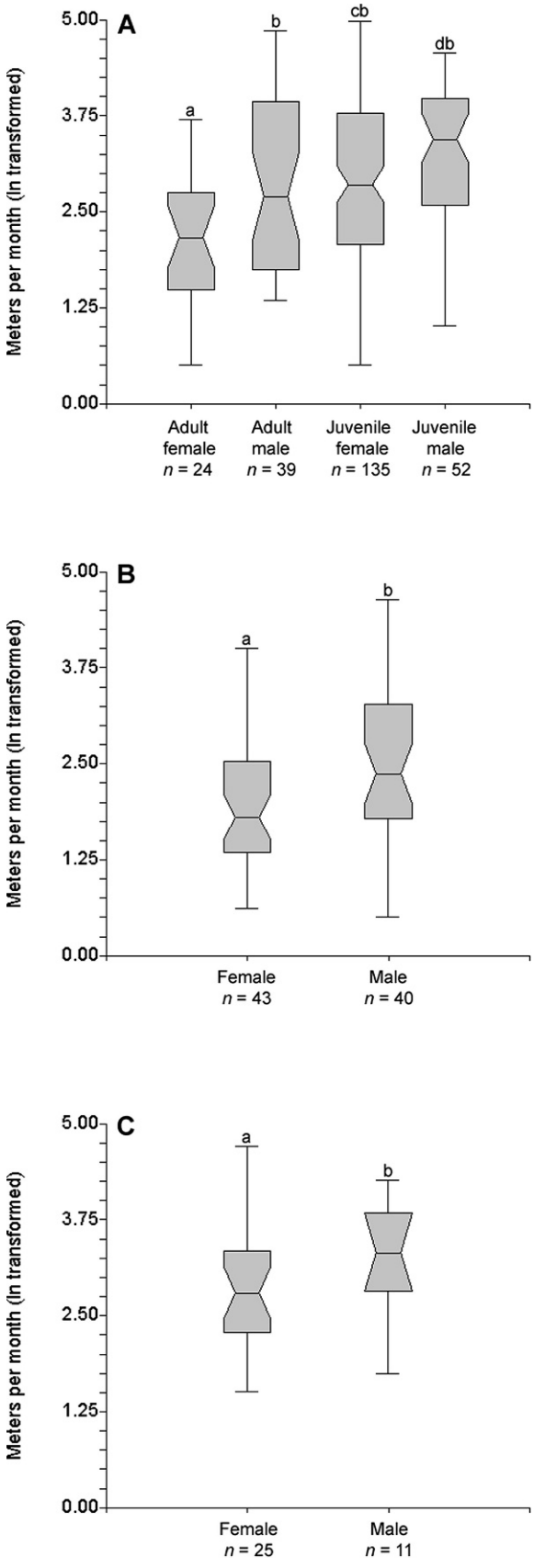

Fig. 5. Boxplots of overall movements in meters per month for *Thamnophis atratus hydrophilus* (A) snakes that did not change age class between subsequent captures; (B) snakes first captured as juveniles and recaptured as adults; and (C) snakes initially captured as neonates and recaptured as juveniles. See caption on Fig. 2 for details on interpreting boxplot letters and symbols.

which included some tadpoles and small salmonids, though their diet consisted primarily of much larger Coastal Giant Salamanders (*Dicamptodon tenebrosus*), both larvae and neotenes. They also foraged in more diverse microhabitats (Lind and Welsh, 1994) and have the physical ability to handle larger prey (Lind and Welsh, 1990). Adult snakes may have been the least aggregated because of these more general food habits and habitat use, depending less on specific types of foraging sites than do neonates and juveniles.

Snakes of all age classes were captured more frequently in fast-water compared to slow-water mesohabitats. We believe that habitat selection at the meso-scale is directly related to snake preferences for microhabitats that are associated with specific mesohabitats. Neonates most frequently used shallow edgewater microhabitats, commonly found along stream margins of fast-water non-turbulent mesohabitats (runs and glides). Shallow riffle microhabitats used by juveniles are associated with fast-water turbulent mesohabitats (primarily low and high gradient riffles). Adults most frequently used fast-flowing microhabitats, near and including the thalweg of fast-water mesohabitats. Therefore, habitat selection at both scales, and the resulting aggregated spatial pattern, are likely influenced by prey availability. However, we do recognize that habitat selection may also reflect the availability of a combination of other resources (e.g., cover and basking sites).

Dispersal patterns and capture intervals.—Our results revealed that the dispersal patterns of *T. a. hydrophilus* differed by life stage, and we suspect factors that influence dispersal also vary. Natal dispersal, the movement of neonates from their initial capture location to the first recapture location the following year, did not differ by sex. These young animals may be diffusing from natal sites to other areas with resources, such as food, that may not be sufficiently abundant to sustain a high density of conspecifics at or near birth sites. However, these movements may also reflect dispersal from birth sites to winter hibernacula (Gregory et al., 1987). In contrast, a male-bias in natal dispersal was observed in hatchlings of Slatey-grey Snake (*Stegonotus cucullatus*), where male neonates moved away, whereas females remained near, their presumed natal sites (mother's capture location; Dubey et al., 2008). As mentioned earlier, there are too few studies on the spatial ecology of snakes, particularly of young snakes, to support general conclusions regarding the effect of age on movement patterns (Gregory et al., 1987).

Juvenile males moved greater distances than both juvenile and adult females. This pattern may be explained by inbreeding avoidance (outcrossing), where dispersal most commonly occurs in pre-reproductive individuals, and predominantly by individuals of one sex (Dobson, 1982). Juvenile males may be voluntarily dispersing to avoid breeding with related females (sisters or mothers; Wolff, 1993, 1994). Juvenile-biased dispersal may also be the result of intraspecific or kin competition for resources (Dobson, 1982; Lena et al., 1998; Newton, 2001). Adults may have higher site fidelity than juveniles because adults have primacy to higher quality habitats, thus displacing younger individuals by forcing them to disperse (Dobson, 1982; Newton, 2001). In this study, however, juvenile females were similar to adult males in the proportion of snakes that moved from the initial capture site and in mean distances

moved. If dispersal was primarily influenced by resource competition between juveniles and adults, we would expect juveniles to move greater distances, regardless of sex.

Adult male *T. a. hydrophilus* moved greater distances than adult females. Extensive movement by males has been associated with mate searching for a number of snakes species (Secor, 1994; Rivera et al., 2006; Todd et al., 2008). Based on an observation we made of a pair of *T. a. hydrophilus* in coitus in September 2003, mating may occur without assemblage (HHW, CAW, unpubl. obs.); however, we do not know if this is characteristic of the species' reproductive behavior. We suspect that *T. a. hydrophilus*, like most snakes, are polygynous (Duvall et al., 1993; but see Rivas and Burghardt, 2005) or promiscuous (Madsen et al., 1993). If these snakes are polygynous or promiscuous and mating occurs without congregation, adult male dispersal may be a mate-seeking strategy, because male reproductive success is limited by the number of mates acquired. Male-biased dispersal is predicted to be favored in these two mating system types (Greenwood, 1980; Perrin and Mazalov, 2000). In several recent studies, capture–recapture data and genetic analysis indicated that dispersal among adult snakes was male-biased in the polygynous Small-eyed Snake (*Rhinoplocephalus nigrescens*; Keogh et al., 2007) and Slatey-grey Snake (Dubey et al., 2008). Genetic methods alone indicated male-biased dispersal in another polygynous snake species, the Argentine Boa Constrictor (*Boa constrictor occidentalis*; Rivera et al., 2006). More research on the mating system, finer-scale tracking of individuals with radiotelemetry, and genetic analysis would allow for further testing of this hypothesis.

Adult females were the most sedentary of all age groups. One potential reason for the apparent low dispersal in adult females may be the type of mating system as well as associated reproductive costs. Females in polygynous mating systems tend to have a greater investment in offspring than males. Gravid females of many viviparous snakes limit foraging and spend most of late gestation time basking, thus reducing movement in order to optimize thermal conditions for the development of their young (Shine, 1993; Brown and Weatherhead, 2000). Because of their parental investment, adult females may benefit from familiarity with their surroundings, having knowledge of local cover, and basking and foraging sites (Winker et al., 1995; Perrin and Goudet, 2001). Moreover, gravid females may be physically incapable of achieving greater mobility because of the additional burden of carrying their young (Shine, 1980; Seigel et al., 1987). Several studies have indicated differences between gravid and non-gravid female movement patterns (Secor, 1992; Johnson, 2000). Unfortunately, our sample was not sufficient to allow us to examine these differences.

Although our results indicated that juvenile and adult dispersal was male-biased, this observation may be confounded by sex-specific capture and survival probabilities (Bonnet and Naulleau, 1996; Koenig et al., 1996). Capture probabilities were low and variable for both female and male snakes; however, we recaptured adult and juvenile males within shorter time intervals than females of the same age classes. We attribute differences among adults to lower detectability of sedentary adult females. Lower detectability may result from them being more secretive, especially in the late spring when gravid females disappear from the stream reach altogether, presumably to incubate and birth their young in hidden retreats. Both behaviors appear to contribute to higher survival probabilities among adult females compared with males and younger age classes (Lind et al., 2005). Lower survival among males may be a result of higher exposure to predators (Greene, 1988; Allan, 1995; Bonnet et al., 1999), which may be a consequence of their greater mobility. Higher female survival may be attributed to their limited movement.

Movement distance distributions for *T. a. hydrophilus* were leptokurtic, regardless of age or sex. Leptokurtic distributions of movement distances have been observed in many species and may be explained by phenotypic or environmental differences such as sex, age, habitat, or presence of predators (Skalski and Gilliam, 2000; Fraser et al., 2001; Zhang et al., 2006). However, leptokurtosis may also be attributed to variation in mobility as a result of differences in behavioral strategies of individuals (Fraser et al., 2001; Hutchings and Gerber, 2002). Determining the reasons for this movement distribution pattern of *T. a. hydrophilus* requires further study.

While we could not establish with certainty the specific factors that affected the spatial and dispersal patterns observed in this population of *T. a. hydrophilus*, we believe the results from our study provide a valuable contribution to the growing information regarding snake spatial ecology. Assessing the distribution and availability of resources (e.g., prey and basking sites) and actual use of these resources is necessary to test the effects on various spatial patterns. Long-term study in combination with the use of genetic tools for multiple species is needed to examine whether there are widespread trends in snake dispersal (Keogh et al., 2007), and if patterns do exist, whether they can be explained by hypotheses set forth for birds and mammals (Greenwood, 1980; Pusey, 1987). More research on snakes will help to test the predictions of evolutionary models based primarily on birds and mammals.

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