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ORIGINAL ARTICLE



Dispersal by gray ratsnakes: Effects of sex, age and time

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Abstract

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Dispersal is one of the most fundamental components of ecology. Dispersal is also particularly relevant in an era of unprecedented habitat loss and climate change. We used a unique dataset to examine dispersal in gray ratsnakes (Pantherophis spiloides). Over a decade, we marked and released >1,500 hatchlings while monitoring the population of ratsnakes over a large area (\approx 1,900 ha). We tested the hypotheses that dispersal should be (a) largely restricted to within the local population given previous genetic evidence of limited gene flow at greater distances and (b) male biased because male gray ratsnakes are under strong sexual selection. We recaptured 69 gray ratsnakes that had been marked as hatchlings after periods ranging from 1 day to 11 years. We found that dispersal distance increased with time, but was not significantly sexbiased, and that gray ratsnakes are extremely faithful to their communal hibernacula (only 2.8% of 497 juvenile and adult ratsnakes captured at least twice at communal hibernacula changed sites between years). Thus, dispersal is largely limited to the period from hatching until an individual joins a communal hibernaculum. Based on the spatial patterns of dispersal we observed, the most plausible explanation for dispersal is that hatchling ratsnakes disperse from their natal site to join a neighboring communal hibernaculum. Our study yielded the most reliable data on dispersal distances from birth by a snake to date.

KEYWORDS

hatchling, hibernacula, mark-recapture, nest, Pantherophis spiloides

1. | INTRODUCTION

Dispersal, one of the most fundamental components of ecology, is the movement of individuals from their natal habitat to their breeding habitat, or movement between breeding habitat patches (Clobert, Le Galliard, Cote, Meylan, & Massot, 2009). Dispersal has implications for individual fitness, population dynamics, metapopulation dynamics, population genetics and species distributions (Cote, Clobert, Brodin, Fogarty, & Sih, 2010; Hansson, 1991; Morales et al., 2010; Ronce, 2007; Stevens et al., 2014). Dispersal is central to, and plays an independent role in the life histories of species (Bonte & Dahirel, 2017; Stevens et al., 2014). Dispersal is also particularly relevant in an era of unprecedented habitat loss and climate change because it affects how well species can move to more hospitable areas when their habitat is destroyed, dispersal can allow the maintenance of functional metapopulations in the face of habitat fragmentation, and dispersal can allow populations to follow their climatic niches as these niches move toward the poles as the climate warms (Baguette, Blanchet, Legrand, Stevens, & Turlure, 2013; Haddad et al., 2015; Stevens et al., 2014; Travis et al., 2013). 146 WILEY- Population Ecology

Dispersal from natal to breeding sites can have multiple causes. The most frequently invoked hypotheses to explain the evolution of dispersal are (a) the avoidance of kin competition where individuals disperse to avoid competing with closely related individuals, thus improving their indirect fitness and (b) inbreeding avoidance where individuals disperse to avoid mating with closely related individuals, thus avoiding inbreeding depression (Clobert et al., 2009; Cote et al., 2010). It should be noted that to avoid inbreeding, dispersal should be sex-biased (Gandon, 1999). Sexbiased dispersal may also be affected by a species' mating system. Greenwood (1980) documented female-biased natal dispersal in birds and male-biased natal dispersal in mammals. Birds are typically socially monogamous and exhibit a resource defense mating system. Thus, familiarity with local resources should be more important for males, who generally defend nests and territories, than for females, and this should favor female-biased dispersal (Clarke, Sæther, Røskaft, Saether, & Roskaft, 1997). Most mammals are socially polygynous and display mate defense mating systems in which females rely on home ranges that contain the resources required to successfully rear offspring. Males, on the other hand, mate with multiple females and often do not participate in the care of young. Familiarity with local resources should thus be more important for females than for males, which should favor malebiased dispersal. The association between sex-biased dispersal and mating system becomes less clear; however, once phylogeny is considered (Mabry, Shelley, Davis, Blumstein, & van Vuren, 2013).

Studying dispersal empirically is challenging for most taxa (Koenig, van Vuren, & Hooge, 1996; Nathan, 2001), so reliable data on dispersal are still required for a broad array of species. This is particularly true of snakes. Scarcity of data on snake natal dispersal is probably a consequence of snakes tending to be very secretive and often occurring at low densities. Thus, recapture rates tend to be low, and most neonatal or hatchling snakes are too small to be followed with radio-telemetry. In fact, we could find no published study in which a large number of neonate or hatchling snakes were marked, released in the wild, and recaptured several years later in a large study area. Webb and Shine (1997) marked 44 juvenile snakes (Hoplocephalus bungaroides) over 3 years and 12 were recaptured from 6 to 34 months later. Dubey, Brown, Madsen, and Shine (2008) marked an unspecified number of hatchling snakes (Stegonotus cucultatus) over 10 years, but the number of marked hatchlings must have been large because 91 individuals were recaptured from a few days up to 4 years after their release. Dubey et al. (2008) documented male-biased natal dispersal, but their estimates of dispersal distances are likely biased because their study area was a 1,300-m earthen embankment topped with a sealed road and they

documented dispersal distances of up to 1,000 m. It is probable that they failed to detect instances of longer dispersal beyond their very narrow and relatively short study area, a problem that plagues most field studies of dispersal (Koenig et al., 1996).

In this study, we use a unique dataset to examine dispersal in gray ratsnakes (Pantherophis spiloides). Over nearly a decade, we marked and released >1,500 hatchlings while monitoring the population of ratsnakes over a large area (\approx 1,900 ha). Previous genetic analyses of this population have indicated that gene flow is substantial among local hibernacula (distances of tens of kilometers), but low across a larger landscape (Howes et al., 2009; Lougheed, Gibbs, Prior, & Weatherhead, 1999). Movement and parentage analyses indicate that mating between individuals from different hibernacula contributes to local gene flow (Blouin-Demers, Gibbs, & Weatherhead, 2005; Blouin-Demers & Weatherhead, 2002), but the contribution by dispersal remains unknown. The first hypothesis we test is that dispersal should be largely restricted to within the local population given the evidence of limited gene flow at greater distances (Howes et al., 2009; Lougheed et al., 1999).

The second hypothesis we test is that sex-specific dispersal of gray ratsnakes is dictated by their mating system, similar to the situation in birds and mammals (Greenwood, 1980; Perrin & Mazalov, 2000) and in animals more generally (Keogh, Webb, & Shine, 2007; Trochet et al., 2016). There appears to be strong sexual selection on male gray ratsnakes. Males are larger than females (Blouin-Demers, Prior, & Weatherhead, 2002; DeGregorio et al., 2018), males engage in combat with one another for access to females (Gillingham, 1980), larger males sire more offspring (Blouin-Demers et al., 2005), and adult males move more than females during the mating season (Blouin-Demers & Weatherhead, 2002). For these reasons, we test the prediction that dispersal should be male biased in gray ratsnakes.

Our final objective is to quantify the extent of dispersal by juvenile and adult snakes in our study population. Previously we reported that site fidelity to communal hibernacula is 98% (Prior, Blouin-Demers, & Weatherhead, 2001), suggesting that once young snakes find a communal hibernaculum, dispersal ends. That initial estimate, however, was based on only two pairs of neighboring hibernacula involving 375 individuals captured a total of 663 times. Here, we use data from a network of 16 hibernacula with 1,121 individuals captured a total of 2,144 times to provide a more robust measure of juvenile and adult dispersal.

The data we report on hatchling and adult dispersal will have implications for the conservation of gray ratsnakes, which are classified as threatened by the Committee on the Status of Endangered Wildlife in Canada. Because inbred populations are at higher risk of extinction (Hoffman et al., 2014; Madsen, Stille, & Shine, 1995), knowing the extent of gene flow and the relative contribution of hatchling, juvenile and adult snakes to that gene flow is the first step in determining how to maintain connectivity within and between populations. Estimating fidelity to communal hibernacula will also help assess how resilient gray ratsnakes may be in case their hibernaculum is destroyed.

2. | METHODS

We studied gray ratsnakes (P. spiloides; note that the taxonomic status of our study population is uncertain because there is a large hybrid zone: Gibbs, Corey, Blouin-Demers, Prior, & Weatherhead, 2006) from 1996 until 2009. Gray ratsnakes are one of the largest snakes in North America, commonly reaching over 2 m in total length and, in our study population, maturing at about 10 years of age and living up to 30 years (Blouin-Demers et al., 2002). Gray ratsnakes are semiarboreal, spending approximately 40% of their time in trees (Blouin-Demers, Bjorgan, & Weatherhead, 2007), and they feed mostly on small mammals and birds (Weatherhead, Blouin-Demers, & Cavey, 2003). We studied gray ratsnakes at the Queen's University Biological Station, approximately 100 km south of Ottawa, Ontario, Canada. The study area was located on the western shore of Lake Opinicon and was approximately 9.5 \times 2.5 km (\approx 1,900 ha, of which \approx 1,500 ha is not open water; Figure 1). Habitat in the study area is primarily deciduous forest, with marshes, beaver ponds, rocky outcrops and old hay fields providing openings in the forest canopy (Blouin-Demers & Weatherhead, 2001; Figure 1). One major challenge in studying dispersal empirically is that it becomes increasingly improbable to detect individuals with increasing dispersal distance, leading to biased estimates of dispersal (Koenig et al., 1996). This potential problem was minimized in our study because our study area was twice as long as the longest detected dispersal distance.

We captured 1,121 gray ratsnakes a total of 2,144 times during their spring egress by erecting fences around 16 traditional and communal hibernacula (Blouin-Demers, Prior, & Weatherhead, 2000; Figure 1). We also captured ratsnakes opportunistically when encountered while we were conducting fieldwork (Prior et al., 2001). We estimated the adult population of gray ratsnakes in our study area to be approximately 400 snakes (Blouin-Demers & Weatherhead, 2002). Communal hibernacula were located by implanting radio-transmitters in previously unmarked snakes captured opportunistically during



FIGURE 1 Map of the study area at the Queen's University Biological Station, Ontario, Canada where dispersal by gray ratsnakes (*Pantherophis spiloides*) was studied between 1996 and 2009. Small filled squares represent the release points of the 69 marked hatchlings that were subsequently recaptured, small filled circles represent the recapture points of those marked hatchlings, and large open circles represent communal hibernacula. Small filled squares and small filled circles often overlap

the active season and following these snakes until they entered their hibernacula in the fall (Blouin-Demers & Weatherhead, 2002; Weatherhead & Blouin-Demers, 2004). All captured snakes were brought back to the laboratory where we determined the sex of each snake by gently probing the cloaca for the presence of hemipenes using a clean probe and we measured them with a flexible tape (Blouin-Demers, 2003). All snakes were permanently identified by subcutaneous injection of a passive integrated transponder tag (2×12 mm) inserted subcutaneously with a specially designed implantation needle. We sealed the skin with surgical glue.

Several of the females became gravid while being followed with radio-telemetry, allowing us to locate their nesting sites. Several of these nesting sites were communal (used by multiple females) and traditional (used year after year). Between 1996 and 2004, we collected all the eggs we found at all nesting sites and incubated them in the laboratory in a bedding of water-saturated vermiculite (Blouin-Demers & Weatherhead, 2007; Patterson & Blouin-Demers, 2008). We also collected all visibly gravid females we encountered at nest sites and during fieldwork, and held them in captivity until they laid their eggs in the artificial nests we provided (Blouin-Demers, Weatherhead, & Row, 2004). After hatching, 1,576 hatchlings (812 females and 764 males; mean snout-vent 148

length = 278 mm, range 168-340 mm; mean mass = 9.5 g, range 3.9-13.9 g) were marked with passive integrated transponder tags (as above) and then released where the eggs they came from had been collected (or where the gravid female was caught if the eggs were laid in captivity).

All locations were mapped with a GPS unit giving <1 m accuracy in the field, using the Universal Transverse Mercator system (North American Datum of 1983). The coordinates obtained with this system were used to calculate all the distances reported herein. By necessity, all distances are straight-line distances. Because gray ratsnakes swim very well (we had hibernacula and nesting sites located on small islands in Lake Opinicon; Figure 1) and climb very well (gray ratsnakes were in trees >40% of the time when located with radio-telemetry; Blouin-Demers et al., 2007), they can navigate in straight lines if they choose to do so.

We built a general linear model (using a normal error structure) with straight-line distance dispersed as the response variable. We entered the number of active days and the sex of the individual as predictor variables. We included individual ID as a random effect to control for multiple recaptures per individual. It would have been of great interest to know whether larger individuals, individuals in better condition or individuals from certain clutches disperse further than others. Unfortunately, however, our modest number of recaptures spread over a decade (see Section 3) precluded the fitting of such a complex model. All analyses were conducted with JMP 13 (SAS Institute). All means are presented ± 1 SE.

3. | RESULTS

Between 1997 and 2009, we recaptured 69 (38 females and 31 males, 186 captures in total) of the 1,576 gray ratsnakes that had been marked as hatchlings (4.4% recapture rate); 25% of individuals were recaptured only once, but some individuals were recaptured up to 10 times. Based on the mean emergence date of 6 May (Blouin-Demers et al., 2000) and the mean submergence date of October (Sperry, Blouin-Demers, Carfagno, 4 Weatherhead, 2010; Weatherhead, Sperry, Carfagno, & Blouin-Demers, 2012), we calculated the active season to be approximately 150 days per year for our study population. Hatchlings were recaptured after periods ranging from 1 active day to 1,686 active days (11.2 years), with a mean of 371 ± 30 active days (2.5 years). Recaptured hatchlings had moved from 1 m (after 1 active day) to a maximum of 4.3 km (after 438 active days, or 3 years), with a mean of 528 ± 52 m. Hatchlings dispersed significantly further with time ($F_{1,170} = 115.90, p < .001$), but males did not disperse significantly further than females $(F_{1,88} = 1.91, p = .17; \text{ mean} = 1.62 \pm 0.25 \text{ m/active day}$ for females and mean = 2.20 ± 0.27 m/active day for males; Figure 2). The mean distance dispersed per active day was 2.06 ± 0.21 m (maximum = 14.50 m). The plateaus in dispersal distances with subsequent recaptures observed for several individuals (Figure 2) occurred because these individuals were captured at communal hibernacula they had joined. Only 19 of the 69 recaptured hatchlings (27%) were never captured at a communal hibernaculum.

During spring egress between 1996 and 2009, we captured 1,121 ratsnakes a total of 2,144 times at the 16 communal hibernacula, and 497 of these ratsnakes were captured at least twice. Fourteen individuals (1.2% of all individuals or 2.8% of individuals captured at least twice; 6 females and 8 males; 3 juveniles and 11 adults based on a size at maturity of 1.050 mm snout-vent length: Blouin-Demers et al., 2002) changed hibernaculum over these 14 years of monitoring. Except in one instance, the hibernaculum to which the snakes moved was one of the closest ones (mean distance = $1,481 \pm 586$ m, range 305-8,369 m). The mean distance to the nearest neighboring hibernaculum in our study area is 811 m, and no hibernaculum is farther than 1,255 m from its nearest neighbor (Blouin-Demers & Weatherhead, 2002). In all but one case, snakes that changed hibernaculum remained at their new hibernaculum in subsequent recaptures (one individual returned to its previous hibernaculum after 1 year).



FIGURE 2 Dispersal distance as a function of the number of days of activity (150 active days per year) for gray ratsnakes (*Pantherophis spiloides*) studied between 1996 and 2009 at the Queen's University Biological Station, Ontario, Canada. Females are drawn in black and males are drawn in gray. Each dot represents a capture and all successive captures for a given individual are joined with straight lines

4. | DISCUSSION

We used an extensive mark-recapture dataset on gray ratsnakes to study dispersal. We found that dispersal distance increased with time and that, although the mean dispersal distance per active day was 15% higher in males than in females, this difference was not statistically significant. We found that gray ratsnakes are extremely faithful to their communal hibernacula; fewer than 3% of individuals changed hibernacula over 14 years of monitoring. Thus, dispersal is largely limited to the period from hatching until an individual joins a communal hibernaculum. Rare instances of long distance dispersal by adult snakes (one individual moved over 8 km when switching hibernacula) appear not to have an important effect on gene flow given the genetic evidence of isolation by distance in ratsnakes (Howes et al., 2009; Lougheed et al., 1999).

The dispersal distances we documented in gray ratsnakes were relatively modest (on average ≈ 500 m). These dispersal distances are on the same spatial scale as the area of home ranges of adult gray ratsnakes (mean of 18.5 ± 2.5 ha; Blouin-Demers & Weatherhead, 2002) and similar to their commuting distance between their hibernacula and home ranges (445 \pm 86 m; Blouin-Demers & Weatherhead, 2002). Dispersal distances also tended to plateau with time because snakes eventually started attending communal hibernacula, to which they then remained extremely faithful. These results support our first hypothesis that dispersal should be largely local, consistent with gene flow being extensive between local hibernacula, but much less at larger spatial scales (i.e., tens of kilometers; Howes et al., 2009; Lougheed et al., 1999).

Sex biases in dispersal distance can be predicted from the species' mating system (Greenwood, 1980). Despite apparent strong sexual selection in male gray ratsnakes (Blouin-Demers et al., 2005) and contrary to our second hypothesis, however, we found no strong male bias in dispersal distances. There is a paucity of studies on squamates in the wild where numerous individuals were marked at birth or hatching and their dispersal followed through time. Therefore, it is impossible to establish general trends in sex biases in dispersal for the group. In addition, individual studies, including our own, often have limited power to detect sex biases in dispersal because of the challenges associated with recapturing large numbers of individuals marked at birth or hatching, especially for cryptic species such as most snakes. As more field studies of squamate dispersal accumulate, however, it will become possible to conduct meta-analyses that allow stronger tests of the hypothesis that the mating system dictates sex biases in

dispersal distance in squamates, as appears to be the case in birds and mammals (Greenwood, 1980; Mabry et al., 2013).

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The balance of costs and benefits of dispersal depends on the environment. For instance, dispersal should be more advantageous when the quality of habitat patches varies drastically and stochastically through time. In this case, individuals should leave habitat patches where quality is deteriorating in search of a patch where quality is improving. Thus, decisions to leave a habitat patch should be both condition-dependent and phenotypedependent (Clobert et al., 2009; Ronce, 2007). In the case of gray ratsnakes in our study area, however, the habitat is generally stable and of high quality. There are very few anthropogenic features and radio-telemetry of numerous individuals has indicated that the various natural habitats (forest, old hav fields, rocky outcrops, wetlands) are all used extensively by gray ratsnakes (Blouin-Demers & Weatherhead, 2001). Thus, it appears unlikely that hatchling gray ratsnakes in our study population disperse to find a better habitat patch. Based on the spatial patterns of dispersal we observed, the most plausible explanation seems to be that hatchling ratsnakes disperse from their hatch site to join a neighboring communal hibernaculum. Once gray ratsnakes join a communal hibernaculum, dispersal ends because they are extremely faithful to their hibernaculum thereafter. For snakes that do not use communal hibernacula, or even hibernate, dispersal may be more continuous, ending when either better or worse habitat is encountered. A study of dispersal in a southern population of ratsnakes would be informative in this regard because those snakes do not hibernate (Sperry & Weatherhead, 2012).

We failed to recapture over 95% of the hatchlings we marked, suggesting either that mortality is extremely high for young ratsnakes, or that we failed to detect substantial dispersal beyond our study area. We favor the first explanation for several reasons. If some snakes dispersed beyond the boundaries of our study area, we would have expected to find longer dispersal distances within the study area. If some individual snakes move more throughout their lives (i.e., long distance dispersal, greater movement as juveniles and adults), we should have detected such movement among our hibernacula populations because some individuals would have dispersed into the study area from elsewhere. Conversely, several ecological aspects of the study population are consistent with high hatchling mortality. The population is at the species' northern range limit, despite apparently suitable habitat continuing well north of our study location, which suggests that climate limits the species' range. Eggs are laid in July and do not hatch until September, by which time temperatures are already becoming -WILEY- Population Ecology

inhospitable for snakes. With only a few weeks at most to find a place to hibernate for 6 months, it seems likely that most hatchlings are unsuccessful and freeze to death. Finally, at about 10 g, hatchlings must be prey for a long list of predators.

An enduring mystery about the ecology of gray ratsnakes is where they spend their first few winters. Few hatchlings are captured at communal hibernacula (Prior et al., 2001; this study) and it took several years for most of our marked hatchlings to start attending communal hibernacula. If ratsnakes can survive their first few winters on their own, why do they join communal hibernacula later on? Answering this question will need to await improvements in tracking technology that would allow following animals that are approximately 10 g at hatching (Blouin-Demers & Weatherhead, 2007) for extended periods of time.

The conservation implication of our work is that suitable habitat has to be maintained between networks of hibernacula to allow the dispersal of hatchling gray ratsnakes from the nests where they hatched to the communal hibernacula that they will eventually attend every winter for the rest of their life. The suitable habitat between hibernacula is also necessary to allow adults of neighboring hibernacula to come into contact during the active season for mating (Blouin-Demers & Weatherhead, 2002). Maintaining the potential for dispersal is essential to maintaining gene flow between hibernacula populations, and thus to reduce the risks associated with inbreeding in this species at risk in Canada. Finally, our work also highlights the paramount importance of conserving the communal hibernacula of gray ratsnakes.

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