

Common Gartersnakes show density dependence in habitat selection despite no density dependence in growth

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Abstract. Density-dependent habitat selection is widespread and is caused by a decrease in mean fitness in a habitat as density in that habitat increases. Yet density dependence may not be at work in all organisms. Snakes, for example, eat infrequently and have thus been inferred to have weak responses to density, although no empirical evidence has demonstrated this yet. In this study, we used an enclosure experiment with different densities of Common Gartersnakes (*Thamnophis sirtalis* [Linnaeus, 1758]) to examine whether density dependence affects growth and habitat selection. We found no evidence of density dependence in growth. Surprisingly given the absence of density dependence in growth, we did find evidence of density-dependent habitat selection, although gartersnakes did not select habitat based on the location of food supplementation within our enclosures. Our study is the first to demonstrate density-dependent habitat selection by snakes.

Keywords: fitness; growth rate; ideal free distribution; isodar; *Thamnophis sirtalis*

Introduction

The pioneering essay of Malthus (1798) in which he argued that populations grow geometrically whereas food supplies increase arithmetically, thus predicting that populations will eventually outgrow their food supplies, established the principle of density dependence of population growth. The classic experiments by Gause (1934) in which he demonstrated density-dependent population growth and density-dependent competitive exclusion between *Paramecium* Müller, 1773 species empirically demonstrated the importance of density dependence. We now know that processes that vary with population density are prevalent (Turchin, 1990; Ray and Hastings, 1996; Brook and Bradshaw, 2006). Population density affects the growth (e.g., Björnsson, 1994) and reproductive output (e.g., Ferrer and Donazar, 1996; Halliday, Thomas and Blouin-Demers, 2015) of individuals, growth rates of populations (e.g., Lin and

Batzli, 2001), habitat selection patterns (e.g., Morris, 1989; Halliday and Blouin-Demers, 2014), and even community organization through the effects of density on interspecific competition (Morris, 1988; Harms et al., 2000; Morris, Dupuch and Halliday, 2012). Population density affects all types of organisms; for instance, density dependence has been documented in bacteria (e.g., Stevens and Holbert, 1995), in single-celled algae (Moses, Morris and Qin, 2013), in plants (Goldberg et al., 2001), in insects (Halliday, Thomas and Blouin-Demers, 2015), and in most vertebrate classes (mammals: Morris, Dupuch and Halliday, 2012; birds: Rodenhouse et al., 2003; fish: Hixon and Carr, 1997; lizards: Massot et al., 1992).

Density-dependent habitat selection is a special case of density dependence and it arises because of the negative density dependence of fitness (Fretwell and Lucas, 1969; Rosenzweig, 1981; Morris, 1988). If individuals are selected to maximize fitness via habitat choice, then patterns of habitat selection should change with density (Morris, 2011). At low density, individuals should live in the highest quality habitat (Fretwell and Lucas, 1969; Morris, 1988). Habitat quality is determined by the factors that influence fitness, such as food availability and safety from predators (Fretwell and Lucas, 1969). As density increases in a habitat, mean per capita fitness decreases because at least some of the resources in

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the habitat are depletable, such as food, and per capita resource availability decreases as density increases (Fretwell and Lucas, 1969; Rosenzweig, 1981). The highest quality habitat eventually will offer the same fitness rewards as lower quality habitats because of the high population density in the highest quality habitat. At this point, it becomes beneficial for some individuals to live in the lower quality habitats at low density because the same mean per capita fitness can be achieved (Morris, 1988). Therefore, individual habitat selection choices should change as population density changes because of the negative density dependence of fitness. Under an ideal free distribution (Fretwell and Lucas, 1969), individuals use the habitat offering the highest fitness rewards, and individuals are distributed between habitats such that the mean fitness is the same in all habitats. The ideal free distribution has three main assumptions: 1) individuals have perfect knowledge of the quality of all available habitats and of the distribution of competitors between those habitats; 2) all competitors are equal; and 3) individuals are free to move between habitats and there is no travel cost associated with moving between habitats (Fretwell and Lucas, 1969). Although the ideal free distribution was proposed nearly half a century ago, and although its assumptions are unrealistic (reviewed by Kennedy and Gray, 1993), the ideal free distribution is still commonly used as the foundation for theoretical advances in habitat selection (e.g., Krivan, 2014; Cressman and Tran, 2015; Matthiopoulos et al., 2015). The null hypothesis for density-dependent habitat selection is density-independence where individuals occupy their preferred habitat regardless of changes in population density; habitat selection is density-dependent when individuals change their use of the available habitats as density changes.

Temperature is one of the most important environmental drivers (e.g., Buckley, Hurlbert and Jetz, 2012; Sunday, Bates and Dulvy, 2012; Araújo et al., 2013), yet its modulating effect on density dependence has only recently been established (Zamani et al., 2006; Englund et al., 2011; Halliday and Blouin-Demers, 2014; Halliday, Thomas and Blouin-Demers, 2015). The vast majority of animals are ectotherms and, by definition, do not maintain their internal body temperature via metabolism. Instead, most ectotherms use behavioural thermoregulation to regulate their body temperature. Because physiological processes depend on temperature, the performance and fitness of ectotherms is tightly linked to their body temperature (Bennett, 1980; Huey and Kingsolver, 1989; Angilletta, Niewiarowski and Navas, 2002; Halliday and Blouin-Demers, 2015a). For

example, red flour beetles can survive between 5 and 40°C, but they can only successfully reproduce between 23 and 35°C (Halliday, Thomas and Blouin-Demers, 2015). Within this range of temperatures over which reproduction is possible, red flour beetles produce the most eggs at 30°C (Halliday and Blouin-Demers, 2014, 2015a; Halliday, Thomas and Blouin-Demers, 2015). If ectotherms are unable to maintain their body temperature within the optimal range for performance, then density dependence weakens due to the reduced ability of individuals to assimilate energy (Halliday, Thomas and Blouin-Demers, 2015).

Snakes are ectotherms that are considered to exhibit weak density dependence (see Nowak, Theimer and Schuett 2008 for an example with vipers). Snakes may even select habitats independently of density (Harvey and Weatherhead, 2006; Halliday and Blouin-Demers, 2016). For example, we found that Common Gartersnakes (*Thamnophis sirtalis*) had a strong density-independent preference for field habitat (Halliday and Blouin-Demers, 2016), but it remains unknown whether this was caused by density independence in fitness (Halliday, Gilmour and Blouin-Demers, 2015; Halliday and Blouin-Demers, 2016). Because negative density dependence of fitness is caused by increased competition for depletable resources (often food) as density increases, Nowak, Theimer and Schuett (2008) postulated that functional and numerical responses by viperid snakes should be much weaker than for endothermic predators because of the low energetic requirements of snakes, and because of the generally much longer time between meals for viperids. The same reasoning should apply to many colubrids because they have low energetic requirements, especially compared to endotherms. For example, female long-tailed snakes (*Philodryas chamissonis* [Wiegmann, 1834]) in Chile require approximately one 30 g rodent per week throughout the 24-week reproductive season, which corresponds to approximately 16% of their body mass every week (Bozinovic and Rosenmann, 1988). These energetic requirements are half that of a similar sized endothermic predator (Bozinovic and Rosenmann, 1988). Given that snakes have low energetic requirements and apparently do not compete for food, changes in population density may not affect their rates of energy acquisition, and ultimately their fitness. If density does not affect fitness in snakes, then density should similarly have no effect on habitat selection.

In this study, we examine density dependence in growth (as a proxy for fitness) and habitat selection in Common Gartersnakes (*Thamnophis sirtalis* [Linnaeus, 1758]).

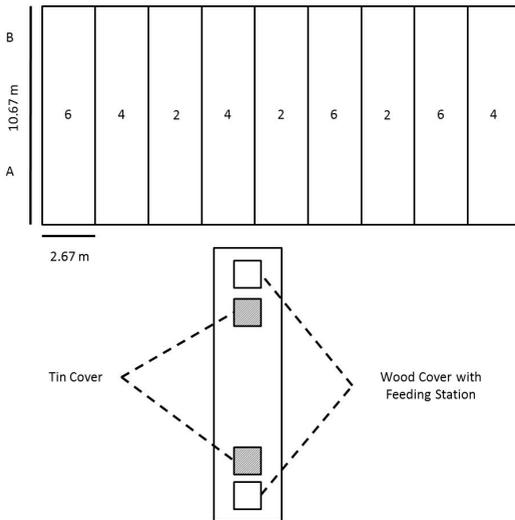


Figure 1. Design schematic for an experiment examining the effect of population density on fitness and habitat selection for Common Gartersnakes (*Thamnophis sirtalis*) in Pontiac County, Québec. Rectangles at the top of the figure represent the experimental enclosures, and the numbers within the rectangles represent the density of Common Gartersnakes within each enclosure. A and B represent the two ends of each enclosure. The rectangle at the bottom demonstrates the locations of cover objects and feeding stations within each enclosure.

We test the hypothesis that gartersnakes select habitats independently of density because their low energetic requirements should make their fitness independent of density. We used experimental enclosures in which we manipulated gartersnake density and food abundance. We monitored growth and documented habitat selection. We used population densities much higher than those typical under natural conditions to elicit a strong effect of density; if density does not affect fitness or habitat selection at these unnaturally high experimental densities, then it cannot be expected to have an effect at lower natural densities.

Materials and Methods

We collected all gartersnakes for this experiment in late May and early June 2015 at a wetland in Pontiac County, Québec. We used active searches and cover boards to capture snakes (Halliday and Blouin-Demers, 2015b). We marked each snake with ventral scale

branding (Winne et al., 2006) and transported them to our experimental enclosures. Following the experiment, we released all snakes back at their capture site.

We built nine experimental enclosures in an old field in Pontiac County, Québec. The dominant vegetation in this old field included grasses (*Poa* spp.), goldenrod (*Solidago* sp.), milkweed (*Asclepias* sp.), and vetch (*Vicia* sp.). We built frames with lumber and walls with polyethylene sheeting; we buried the bottom 10 cm of each wall in the ground. Each enclosure was 1.3 m tall, 2.7 m wide, and 10.7 m long. We surrounded the enclosures with an electric fence and placed nylon mesh (2 cm spacing) over the enclosures to keep predators out. We created one foraging patch at each end of each enclosure by digging a 30 x 10 x 7 cm plastic container into the ground, filling half the container with soil, and adding a 60 x 60 cm plywood cover. We placed six earthworms in one foraging patch and none in the other. Based on pilot trials, worms were unable to escape these foraging patches. We alternated the patch receiving food every two weeks for eight weeks. We also added one 60 x 60 cm piece of tin to each end of the enclosure as cover.

We created three density treatments with three replicates of each by adding two, four or six Common Gartersnakes to each enclosure (Fig. 1), for a total of six snakes in the low density treatment, 12 snakes in the medium density treatment, and 18 snakes in the high density treatment. We systematically placed individuals in each enclosure according to their snout-vent length (SVL) and sex so that enclosures had similar distributions of SVL and sex-ratios. Once per week, we measured the SVL and mass of each snake to monitor growth. Thrice per week at 0900h, we counted the number of snakes in each half of the enclosure and then replenished the worms. Once per week, we repeated the snake counts every hour between 0900h and 1400h, but the distribution of snakes was unaffected by the timing of the count (Halliday, unpublished data). Snakes occasionally managed to escape enclosures, either by climbing over (large snakes) or burrowing under the walls (small snakes). We replaced snakes that disappeared during the experiment with individuals of the same sex and approximate size to maintain the density treatment in each enclosure throughout the experiment. These snakes were collected as required from the same wetland as the original snakes. We replaced three snakes from the low density treatment, nine snakes from the medium density treatment, and five snakes from the high density treatment. We only used growth data for snakes if they were in the experiment for at least four weeks

to ensure that snakes had sufficient time to be affected by our treatments (based on our previous experiments (Halliday and Blouin-Demers, 2016), four weeks is sufficient to detect growth in our study population). This resulted in a final sample size of six snakes in the low density treatment, 17 snakes in the medium density treatment, and 19 snakes in the high density treatment.

We monitored the natural abundance of worms and slugs in each enclosure, as well as at four locations just outside of the enclosures with pitfall traps. At each sampling location, we dug three holes in the ground in a triangle with 30 cm between holes, placed a plastic cup (7 cm diameter, 15 cm height) in each hole, and half-filled each cup with soil. Pitfall traps in the enclosures were placed in the centre to avoid biasing the distribution of snakes to either end of the enclosure, although we never found snakes entering these pitfall traps. Once per week, we counted and removed all slugs and worms from each cup.

Growth Rate. We calculated the growth rate for mass for each snake in each enclosure by regressing mass by time. We used the slope of this regression for each individual as their growth rate. For gravid females, we calculated mass growth rate up until the week before they gave birth. We tested for density dependence of growth with linear mixed effects models in R (package: nlme; function: lme; Pinheiro et al., 2015). We used mass growth rate as the dependent variable, density, reproductive status (male, gravid female, non-gravid female), initial mass, and number of weeks that the snake was in the experiment as fixed effects, and enclosure as a random effect. We included reproductive status, initial size, and weeks into the experiment as control variables. We only had a single non-gravid female in the lowest density treatment, and its mass growth rate was an outlier. We therefore removed this outlier and re-analyzed the data. We used bias-corrected Akaike's information criteria (AICc; package: qpcR; function: AICc; Spiess, 2015) for model selection, and considered the model with the lowest AICc to be the best model. We considered models to be competing if they were within two AICc units of the best model (Bozdogan, 1987).

Foraging. Snakes had access to the worms we provided in foraging stations and to the food naturally available in the enclosures. Thus, we tested for the effect of snake density on natural food abundance (worms and slugs) with linear mixed effects models. We conducted two analyses with different dependent variables: total number of worms or total number slugs in the three pitfall traps at each monitoring location. For each

analysis, we used snake density (two, four, or six snakes/enclosure), days since last collection of the potential prey (which varied early in the experiment), and weeks into the experiment as fixed effects, and the ID of the trap station as a random effect. We assigned a snake density of zero to pitfall traps outside of the enclosures. Although there were certainly some snakes outside of the enclosures, their density would be much lower compared to densities in our enclosures. Density in our enclosures ranged from 700 to 2100 gartersnakes/ha, whereas the highest natural density that we have measured in the same habitat was 24 gartersnakes/ha (Halliday and Blouin-Demers, 2016).

Habitat Selection. We used isodar analysis (Morris 1988) to compare the abundance of snakes on one end of the enclosure versus snakes on the other end of the enclosure in relation to the location of food provisioning. We built isodars using geometric mean regression in R (package: lmodel2; function: lmodel2; Legendre, 2014), with the number of snakes on the end of the enclosure with food supplementation as y and the number of snakes on the end of the enclosure without food supplementation as x . To build the isodar, we took the mean distribution of snakes in each enclosure during each two-week period of the experiment ($n = 36$). We compared the isodar intercept to zero and slope to one with their 95% confidence intervals. An isodar with an intercept significantly different from zero demonstrates preference for a habitat, and a slope that is significantly different from one demonstrates that habitat preference changes with population density (Morris, 1988). An isodar with an intercept of zero and a slope of one demonstrates equal preference for two habitats that is constant across population densities. Statistically significant isodars are considered evidence of density dependence in habitat choice, and the R^2 represents the strength of density dependence (Morris 1988). Non-significant isodars or isodars with slopes not different from zero or infinity are considered evidence of density-independent habitat selection. We conducted all analyses in R version 3.2.1 (R Core Team, 2015).

Results

Growth Rate. When we included the outlier in our analysis, non-gravid females gained less mass as density increased ($t_{30} = 2.87, P < 0.01$), but this effect disappeared when we removed the outlier ($t_{30} = 0.14, P = 0.89$; Fig. 2, Appendix Table A1). Based on the analysis without the outlier, reproductive females gained more mass (4.0 ± 0.7 g/week, $t_{31} = 5.89, P < 0.01$) than males (0.2 ± 0.8

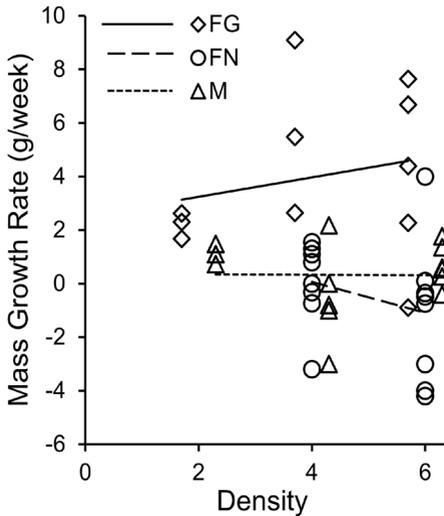


Figure 2. Mass growth rate for Common Gartersnakes (*Thamnophis sirtalis*) in different reproductive classes living in experimental enclosures at different population densities in Pontiac County, Québec. FG = gravid female, FN = non-gravid female, M = male.

g/week, $t_{31} = 4.92$, $P < 0.01$), and non-gravid females lost mass (-0.3 ± 0.8 g/week; $t_{31} = 5.53$, $P < 0.01$; Fig. 2A, Table A1). An analysis on SVL yielded qualitatively similar results; however, we do not report these results due to increased measurement error associated with measuring the length of snakes (Blouin-Demers, 2003).

Foraging. Fewer worms were caught in the pitfall traps as snake density increased ($t_{102} = 2.61$, $P = 0.02$; Appendix Table A2). On the other hand, the abundance of slugs was unaffected by snake density ($t_{102} = 0.21$, $P = 0.84$; Appendix Table A3).

Habitat Selection. Gartersnakes had an equal preference for both ends of the enclosure (intercept = 0.18, 95% CI = -0.54 – 0.71), and this equal preference was constant across all densities (slope = 1.03, 95% CI = 0.75 – 1.42). The isodar was statistically significant ($P = 0.02$, $R^2 = 0.15$; Fig. 3) indicating that habitat selection was density-dependent.

Discussion

Density dependence is prevalent in most animal taxa, and our experiment suggests that it also occurs in snakes. We found no evidence for density dependence of growth rate in Common Gartersnakes but, surprisingly,

we still found evidence of density dependence in habitat selection. Researchers have suggested that density dependence is not important for at least some snakes, either because snakes naturally live at population densities that are too low to detect density dependence (Harvey and Weatherhead, 2006) or because their energetic requirements are too low for competition to be important (Nowak, Theimer and Schuett, 2008). The highest density of gartersnakes that we have measured in the field was 24 snakes/ha (Halliday and Blouin-Demers, 2016), but to maximize our chances of detecting density dependence we used gartersnake densities between 700 and 2100 snakes/ha in our experiment. It appears likely that snakes rarely reach natural densities high enough for density dependence to be important, but our experiment provides evidence that under some circumstances density dependence can be important for snakes, at least in habitat selection. Density dependence may also affect gartersnakes in other situations. Many temperate snakes congregate at

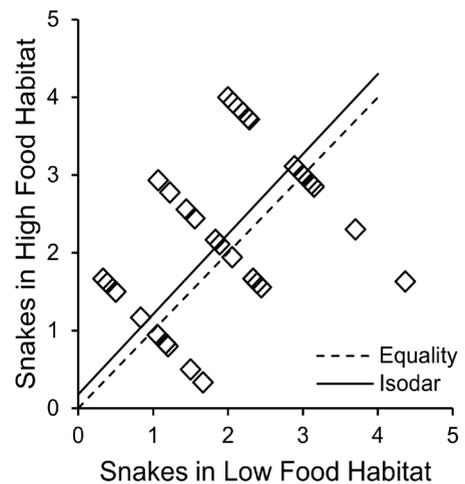


Figure 3. An isodar representing the number of Common Gartersnakes (*Thamnophis sirtalis*) in the end of the enclosure with food supplementation versus the number of Common Gartersnakes in the end of the enclosure without food supplementation for snakes living in experimental enclosures in Pontiac County, Québec. Points represent the average distribution of snakes in each enclosure over each two week period in the experiment. The solid line represents the isodar, calculated using geometric mean regression. The dashed line (equality) represents an isodar with an intercept of zero and a slope of one, which would demonstrate no preference between habitats.

communal hibernacula where densities can get very high. For example, red-sided gartersnakes (*Thamnophis sirtalis parietalis* [Say, 1823]) hibernacula in Manitoba, Canada, can contain over 20,000 individuals (Shine et al., 2001). Even though snakes generally do not feed at hibernacula, snakes dispersing from hibernacula will experience a decrease in density as they disperse away from the hibernacula, and their foraging and habitat selection strategies during dispersal may therefore be affected by these changes in density.

Gartersnakes demonstrated equal preference for both ends of our enclosures at all densities, regardless of the location of food supplementation. Snakes often ate all worms at feeding stations, it is therefore possible that we did not provide enough worms to successfully bias the distribution of snakes to one end of the enclosures. It is also possible that our food supplementation was relatively small compared to the naturally available worms in our enclosures. The fact that we captured fewer worms in our pitfall traps when snake density was high does indicate that snakes were depleting their naturally available prey population. Thus, it is possible that snakes in our enclosures were competing for the naturally available worms, that we presume were equally distributed in our enclosures given the homogeneous habitat, but that competition for our supplemental worms was short-lived because they were rapidly exhausted. If that inference is correct, it would explain why we found evidence of density dependence in habitat selection (a statistically significant isodar), but no preference for the end of the enclosure containing supplemental worms (an intercept not statistically different from 0). Future studies could use higher levels of food supplementation to assess if habitat preference is based on the distribution of food, but food saturation could equally lead to the inability to detect density dependence. A natural experiment in a system with patchily distributed food could be used to examine habitat preference based on the location of food, but natural snake densities would have to be high enough for competition to occur. Therefore, testing for density dependence in snakes will remain a challenge.

We detected no density dependence in growth. Again, it is possible that our food supplementation was relatively small compared to the naturally available worms in our enclosures, and that the food supply may have been high enough to suppress competition. Given the functional relationship between energy acquisition (foraging) and fitness (Morris, 2014), it appears likely that snakes in high-density enclosures still managed to eat enough worms to have fitness equal to that of

snakes in low-density enclosures. If that were the case, the density-dependent habitat selection we observed was not driven by density dependence of foraging rate. Density dependence can also occur in other aspects of fitness that are not related to energetics. For example, predation risk can increase as density increases because predators are attracted to habitats with a high density of prey (e.g., Rangeley and Kramer, 1998), or because prey are more conspicuous when aggregated. Thus, snakes in our enclosures could have been attempting to reduce predation risk by being distributed equally in the enclosure because a clumped distribution could have increased predation risk. Conversely, it is possible that high snake density did cause competition for food in our experiment, but that we were unable to detect it. Although our experiment lasted for eight weeks during the peak of growth for temperate snakes, it is possible that a longer experiment would have been required to detect density dependence in growth, especially if growth at least partly depends on accumulated energy reserves (Bonnet et al., 1998). Finally, given the high variance inherent to size measurements of snakes (Blouin-Demers, 2003), maybe an increased sample size would have been required to detect negative density dependence in growth.

One potential issue with our experiment is that the low density treatment had a small sample size ($n = 6$). The larger sample sizes in the medium ($n = 17$) and high density ($n = 19$) treatments demonstrated that growth rates were very variable among individuals, and almost completely overlapped between these two treatments. For mass growth rate, the 95% confidence interval (CI) was 1.1–2.2 g/week at low density, –0.5–2.3 g/week at medium density, and –0.6–2.2 g/week at high density. In a previous experiment (Halliday and Blouin-Demers, 2016), we found significant differences in growth rate between gartersnakes living in enclosures in field and in enclosures in forest over a similar period of time. We therefore feel that our experimental design was appropriate for detecting differences in growth rate if they were present. Although some studies have suggested that density dependence is not important for temperate snakes due to naturally low population densities and low energetic requirements (Harvey and Weatherhead, 2006; Halliday and Blouin-Demers, 2016), it is possible that density dependence is important for snakes closer to the tropics due to increased energetic requirements induced by higher body temperatures. For example, Weatherhead et al. (2012) demonstrated that habitat selection patterns of ratsnakes changed across their geographic range as

the thermal quality of the environment changed. Porter and Tracy (1974) suggested that the weekly energetic requirements of gartersnakes increase for snakes farther south in their range. Snakes closer to the tropics are able to maintain optimal body temperatures for longer than temperate-zone snakes. For this reason, snakes in the tropics may have higher energetic demands, which would make them more likely to compete over food than temperate-zone snakes. In fact, Nowak, Theimer and Schuett (2008) suggested that tropical viperids that eat frequently would be good models to look for density dependence. Future work could examine density dependence in wide ranging species to determine if density dependence is more prevalent in southern versus northern populations.

In summary, Common Gartersnakes showed evidence of density-dependent habitat selection, but no evidence of negative density dependence in growth rate. Although we used gartersnake population densities much higher than those typically observed in nature, our experiment revealed, for the first time, that density dependence can occur in snakes. The next steps are to determine if and when density dependence occurs in free ranging snakes, which is especially important given that density dependence is an important assumption in basic models of population growth and regulation (e.g., Lotka-Volterra equation (Volterra, 1926); Ricker equation (Ricker, 1954)).

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