

# Differential fitness in field and forest explains density-independent habitat selection by gartersnakes

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**Abstract** The ideal free distribution concept predicts that organisms will distribute themselves between habitats in a density-dependent manner so that individuals, on average, achieve the same fitness in each habitat. In ectotherms, environmental temperature has a strong impact on fitness, but temperature is not depletable and thus not density dependent. Can density-dependent habitat selection occur in ectotherms when habitats differ in thermal quality? We used an observational study of habitat selection by small snakes in field and forest, followed by manipulative habitat selection and fitness experiments with common gartersnakes in enclosures in field and forest to test this hypothesis. Snakes were much more abundant in the field, the habitat with superior thermal quality, than in the forest. Gartersnakes in our controlled experiment only used the forest habitat when snake density was highest and when food was more abundant in the forest; habitat selection was largely density independent, although there was weak evidence of density dependence. No female garter-snake gave birth in the forest enclosures, whereas half of the females gave birth in the field enclosures. Growth rates of females were higher in field than in forest enclosures. Overall, our data indicate that temperature appears to be the most important factor driving the habitat selection of

gartersnakes, likely because temperature was more limiting than food in our study system. Snakes, or at least temperate snakes, may naturally exist at population densities low enough that they do not exhibit density-dependent habitat selection.

**Keywords** Ideal free distribution · Giving-up density · Growth rate · Reproductive output · Thermal quality

## Introduction

The ideal free distribution (IFD; Fretwell and Lucas 1969) concept is the predominant framework for habitat selection theory (Rosenzweig 1981; Morris 2003). This theoretical framework predicts that organisms will distribute themselves between habitats in proportion to the suitability of the various habitats such that each individual obtains the same fitness (Fretwell and Lucas 1969). These authors defined habitat suitability as “the average potential contribution from that habitat to the gene pool of succeeding generations” (Fretwell and Lucas 1969), thus explicitly linking habitat suitability to mean potential fitness. Habitat suitability is determined by several factors, such as food abundance, interference competition (the ideal despotic distribution: Fretwell and Lucas 1969; Fretwell 1972; Morris 1988), interspecific competition (Rosenzweig and Abramsky 1986; Morris 1988), and predation risk (Moody et al. 1996; Grand and Dill 1999), the influence of most of which is density-dependent. Importantly, therefore, the IFD assumes that habitat suitability always decreases with density (Fretwell and Lucas 1969). Finally, the IFD assumes that individuals are ‘ideal’ in the sense that they select the habitat that will maximize their fitness and be ‘free’ in the sense that they can enter any habitat on an equal basis with

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all their conspecifics (Fretwell and Lucas 1969). The IFD has been tested extensively in birds (e.g., Shochat et al. 2002; Jensen and Cully 2005; Zimmerman et al. 2009), mammals (e.g., Morris 1988; Ovadia and Abramsky 1995; Lin and Batzli 2002; Tadesse and Kotler 2010), fish (e.g., Rodríguez 1995; Morita et al. 2004; Haugen et al. 2006; Knight et al. 2008), and invertebrates (e.g., Krasnov et al. 2003, 2004; Lerner et al. 2011) and has also been used to examine optimal foraging behavior (see Kennedy and Gray 1993 for a review). Despite the unrealistic ‘free’ and ‘ideal’ assumptions of the IFD (see review in Kennedy and Gray 1993; but see also Åström 1994 and Milinski 1994), the IFD remains an important and powerful theoretical framework to predict the habitat selection of organisms.

One important assumption of the IFD that has received less attention is whether habitat suitability always decreases as population density increases. In animals that are limited by depletable resources, such as food, the assumption of density dependence is reasonable. Yet food or other depletable resources are not always the most important limiting factor (Hutchinson 1959; Huey 1991; Buckley et al. 2012), especially for ectotherms that must regulate their body temperatures by selecting habitats with appropriate temperatures to perform maximally (Huey 1991; Calsbeek and Sinervo 2002; Buckley et al. 2012). Since, under most circumstances, temperature is not a depletable resource, thus violating the density-dependence assumption of the IFD, can the IFD still predict the distribution of organisms that are limited by temperature in addition to food? If individuals distribute themselves between habitats based on temperature alone, we should expect density-independent habitat selection unless access to preferred temperatures is limited by competition (e.g., Calsbeek and Sinervo 2002). If habitat suitability is dictated by the interacting effects of temperature and food abundance, however, then individuals should distribute themselves among habitats according to the combined effects of temperature and food abundance (Halliday and Blouin-Demers 2014).

Snakes are probably limited more by temperature than by food as they can go for weeks without eating due to their relatively slow metabolism (e.g., Shine 1986) and the typically large meals they ingest. It is often assumed that snakes select habitats independently of density, however to the best of our knowledge no study has yet tested whether this assumption is correct (e.g., Harvey and Weatherhead 2006). Habitat selection studies on snakes frequently show that thermal quality is very important in dictating patterns of habitat selection (e.g., Blouin-Demers and Weatherhead 2001; Row and Blouin-Demers 2006; Lelièvre et al. 2011; Weatherhead et al. 2012), and thermal quality can be more important than the availability of food in dictating patterns of habitat selection (Blouin-Demers and Weatherhead 2001). Snakes are therefore logical organisms for testing

whether the IFD can successfully predict the distribution of animals when habitat suitability is largely a function of thermal quality, and thus probably largely density independent contrary to a key assumption of the IFD.

In this study, we tested the hypothesis that habitat selection by snakes is not a function of conspecific density because the fitness of snakes is more tightly linked to thermal quality, a non-depletable resource, than to the availability of depletable resources. More specifically, we tested the predictions that snake habitat selection patterns are density independent and that variation in snake density across habitats is better explained by differences in thermal quality than by differences in food abundance. We tested this hypothesis with an observational study and with a manipulative study. For our observational study, we measured the abundance of small northern snakes, specifically common gartersnakes (*Thamnophis sirtalis*), red-bellied snakes (*Storeria occipitomaculata*), and Dekay’s brownsnakes (*Storeria dekayi*), in field and forest, two habitats with very different thermal qualities. In our study area, these habitats are dominant land covers that should be encountered commonly by snakes. We consider both land covers to be habitats for these species because, although previous studies have demonstrated that gartersnakes show a strong preference for open habitats (Carpenter 1952; Burger et al. 2004), forests are also used (see Results). We examined the habitat suitability of field and forest based on thermal quality (in relation to the preferred body temperature of most snakes) and based on prey abundance. For our manipulative study, we used enclosures that encompassed both the field and forest habitat and manipulated common garter-snake density and food abundance. We quantified habitat selection in response to variation in conspecific density and in food abundance, and we examined the foraging costs of selecting both habitats with giving-up densities. Finally, we examined the fitness consequences of habitat selection to confirm that the habitat selection choices of snakes were adaptive. We measured reproductive output and growth rate of female common gartersnakes living in enclosures in the field and the forest under two food regimes.

## Materials and methods

### Observational test of density-dependent habitat selection

We conducted an observational study of snake habitat selection at Queen’s University Biological Station (QUBS; 44°33’N, 76°21’W) in eastern Ontario, Canada. Although QUBS is home to nine species of snakes, we only obtained sufficient capture data for common gartersnakes (*Thamnophis sirtalis*), Dekay’s brownsnakes (*Storeria dekayi*), and

red-bellied snakes (*Storeria occipitomaculata*). All three species have relatively generalized diets, but *T. sirtalis* eats invertebrates and small amphibians, whereas *S. dekayi* and *S. occipitomaculata* only eat invertebrates.

We set up five 50 × 100-m study plots that each encompassed 50 % field and 50 % forest. All of the fields were cut once per year and were thereby maintained as a mixed grass and forb community. Forests were mixed hardwood, mainly sugar maple (*Acer saccharum*), ironwood (*Ostrya virginiana*), and American beech (*Fagus grandifolia*). We placed sixteen 60 × 60-cm plywood cover boards on each grid (4 rows of 4 boards spaced every 25 m) to act as snake refuges (Halliday and Blouin-Demers 2015), with half of the boards placed in the field and half placed in the forest. We surveyed field and forest habitats twice a day (0900 and 1400 hours) for 3 days every 2 weeks from 5 May 2013 to 16 July 2013. These 3-day periods represent one sampling period, for a total of six sampling periods throughout the study. During each survey, we walked across the plots at a constant pace and checked under every cover board. We hand-captured each snake that we encountered and gave each individual a unique mark by branding its ventral scales using a medical cautery unit (Bovie Aaron Low-Temp Reusable Cautery Unit, Bovie Medical Corp. Clearwater, FL; technique and rationale for branding described in Winne et al. 2006). We then released each individual at its point of capture.

The abundance of each snake species was estimated during each 3-day sampling period by counting the number of individual snakes caught on each plot during the sampling period. We only counted snakes found under cover boards (snakes captured under cover boards represented 94 % of the 132 snakes captured in the field and 2 of the 3 snakes captured in the forest) because our ability to detect snakes in field outside of the cover boards may have decreased as the season progressed due to vegetation growth.

We estimated the abundance of amphibian prey in each habitat of each plot by counting the number of amphibians encountered during each sampling period while surveying for snakes. We identified each amphibian to species. We mostly encountered northern leopard frogs (*Lithobates pipiens*) in the field and American toads (*Anaxyrus americanus*) in the forest, but we also encountered wood frogs (*Lithobates sylvaticus*), spring peepers (*Pseudacris crucifer*), blue-spotted salamanders (*Ambystoma laterale*), and eastern newts (*Notophthalmus viridescens*) on occasion.

Invertebrate prey density was monitored in both habitats at 2-week intervals from 21 May 2013 to 16 July 2013. For this purpose, we built 1-m drift fences using 10-cm wide tin material and dug 15-cm-deep pitfall traps at both ends of each drift fence. Each pitfall trap contained a plastic cup into which we poured approximately 200 ml of soapy water. We built three traps in each habitat in each plot and

emptied the traps every 2 weeks. The invertebrates from each habitat of each plot were identified to group level (Annelida, Arachnida, Coleoptera, Diplopoda, Lepidoptera, Mollusca, Orthoptera, and other), and the wet mass of all invertebrates in each group was weighed. Although it is unlikely that snakes eat all of these invertebrates, they likely all consume a subset of these prey items. For example, both red-bellied snakes and Dekay's brownsnakes are known to eat molluscs and earthworms (Rossman and Myer 1990), and common gartersnakes are successfully fed earthworms in captivity (see fitness experiments).

We monitored the temperature that could be achieved by snakes in each habitat (environmental temperature,  $T_e$ ) using copper snake models. These models were made of 30-cm-long copper pipe (diameter 1.9 cm) with a cap soldered on one end; they were filled with water and sealed on the other end with a rubber stopper. The models were approximately the same size as the most common snake species in our study, the common gartersnake. We placed an iButton (Maxim Integrated, San José, CA) inside the model, which measured temperature every 30 min, and then placed one copper model under a cover board and one outside of a cover board in all five forest plots and in four of the five field plots.

To assess thermal quality of the two habitats, we determined the thermal preference of the common gartersnakes, the most abundant snake in our samples, by placing individual snakes ( $n = 49$ ) in a thermal gradient ranging from 15 to 40 °C. The thermal gradient was a wooden box (length × width × height = 170 × 74 × 35 cm) with two lanes (30 cm wide), heated at one end by heat pads and cooled at the other end by coiled tubes of cold well water. After an acclimation period of 1 h, we recorded the skin temperature of each snake at its head, mid body, and tail using an infrared thermometer (Raytek Corp., Santa Cruz, CA) every hour for 6 h. We then averaged these three measurements for each hour to obtain six measures of mean body temperature for each snake. Snakes used in this experiment were not part of the habitat selection experiment but had been captured in fields and wetlands within 5 km of the study plots. All snakes fasted in captivity for at least 24 h before being placed in the thermal gradient. We calculated the thermal preference ( $T_{set}$ ) of all individuals as the 25th to 75th percentiles of the selected body temperatures (Hertz et al. 1993). The  $T_{set}$  of common gartersnakes ( $n = 49$ ) ranged from  $25.5 \pm 0.4$  °C to  $27.4 \pm 0.3$  °C.

We assessed the thermal quality of habitats by calculating the absolute deviations of  $T_e$  from  $T_{set}$  ( $d_e$ ; Hertz et al. 1993), where a lower  $d_e$  indicates a higher thermal quality. We used  $T_{set}$  of common gartersnakes as a proxy for  $T_{set}$  of Dekay's brownsnakes and red-bellied snakes because common gartersnakes made up ~55 % of the individuals caught in our study (71 common gartersnakes, 34

red-bellied snakes, 24 Dekay's brownsnakes), and the thermal preference of common gartersnakes is very similar to the mean thermal preference of other snakes in a thermal gradient (average  $T_{\text{set}}$  of other snakes =  $26.8 \pm 0.9$  °C to  $30.7 \pm 0.8$  °C; see Electronic Supplementary Material).

Habitat selection data of each species were assessed using a linear mixed effects model in R (package: nlme; function: lme; Pinheiro et al. 2012). We used the abundance of each species as the response variable, habitat type as the fixed effect, and plot nested within sampling date as random effects. The differences between field and forest habitat were quantified in terms of thermal quality and prey abundance using a multivariate analysis of variance (MANOVA; package: stats; function: aov; R Core Team 2012), where the response variables were thermal quality ( $d_e$ ), invertebrate biomass, and amphibian abundance, and the independent variable was habitat with sample period as a repeated measure. We only used  $d_e$  from daylight hours (0800–2000 hours) because snakes in our region are mostly diurnal (e.g., Weatherhead et al. 2012). We repeated this analysis with a subset of the invertebrate data that only included the biomass of molluscs and earthworms because these two groups have been confirmed in the diets of the three species in our study (e.g., Rossman and Myer 1990).

### Experimental test of density-dependent habitat selection

An enclosure experiment was designed to test whether the choice of habitat between field and forest by common gartersnakes is density dependent. These experimental enclosures, which were  $8 \times 16$  m with 1.3-m-high walls, were built on a property owned by the Nature Conservancy of Canada in Pontiac County, Québec, Canada. The bottoms of the walls were partially buried into the ground to prevent snakes from escaping. The frames of the enclosures were built with lumber, and the walls were constructed with polyethylene vapor barrier. Half of each enclosure was in field ( $8 \times 8$  m) and the other half was in forest. The forest habitat consisted mostly of trembling aspen (*Populus tremuloides*) with minimal understory growth, while the field was typical old field habitat with common grasses and flowering plants, such as goldernrod (*Solidago* sp.), milkweed (*Asclepias* sp.), purple loosestrife (*Lythrum salicaria*), and vetch (*Vicia cracca*).

We placed three  $60 \times 60$ -cm wooden cover boards and one feeding station in each habitat within each enclosure. Each feeding station consisted of a  $10 \times 30 \times 7$ -cm plastic container inserted into the ground that was filled three-quarters full with soil and covered by a  $30 \times 30$ -cm wood cover with a 5-cm gap between the top of the container and the wood cover. These feeding stations were used to add large earthworms to the habitat to supplement the natural

food sources. We moistened the soil with water whenever it became dry.

We created three food treatments and three density treatments in the enclosures in a fully factorial design, with two replicates of each food  $\times$  density treatment. Each replicate lasted 7 days. The food treatments consisted of ten earthworms in the field, ten earthworms in the forest, or five earthworms in each habitat. These worms were added on day 1 of the replicate and then counted and replenished on days 2, 4, 6, and 7 of each replicate. Common gartersnakes were collected from different source populations around Ottawa (Ontario) and Pontiac (Québec) to populate our enclosures [snout–vent length (SVL) range 271–617 mm; approx. equal sex ratio]. The snakes were added to the enclosures at three densities (3, 6, or 9 snakes per enclosure), with the aim to ensure an approximately even distribution of body sizes and equal sex ratio. These numbers translate to 234, 468, and 702 snakes per hectare. The highest density of snakes that we found during the observational study was 24 snakes per hectare. Therefore, these experimental densities represent unnaturally high densities that should allow an effect of competition to be detected should such an effect be present. We released snakes in the edge habitat in each enclosure (interface between field and forest) on day 1 of the replicate and then counted the number of snakes in each habitat on days 2, 4, 6, and 7. For counting, we entered the enclosure as quietly as possible and quickly moved to the edge habitat in the enclosure. We caught all snakes in the edge habitat and then systematically checked each habitat and looked under all covers in each habitat and caught every snake that we encountered. As soon as a snake was caught, we measured its body temperature using an infrared thermometer.

We analyzed the experimental habitat selection data by building isodars (Morris 1988) for each food treatment using geometric mean regression in R (package: lmodel2; function: lmodel2; Legendre 2013), with the number of snakes in the field as the dependent variable and the number of snakes in the forest as the independent variable. We calculated the number of snakes in each habitat on each day of data collection. Snakes found in the edge were assigned to either the field or forest for this analysis depending on their body temperature, with snakes having temperatures closer to those experienced by snakes in the field being assigned to the field habitat, and vice versa. We then calculated the mean distribution of snakes between the field and forest within each replicate of each treatment (mean distribution across 4 days of data collection). Each isodar was therefore built using six data points (three density treatments, two replicates per treatment). Isodars for each treatment were compared with 95 % confidence intervals (CI) around the intercepts and slopes. This analysis served to test the density-dependence prediction of the IFD. Statistically



significant isodars indicate density dependence, intercepts significantly different than zero indicate a strong preference for a habitat, and a slope steeper than one combined with an intercept higher than zero indicate strong habitat preference across all densities (Morris 1988).

The number of worms remaining in a feeding station was used as a metric of giving-up density (GUD; Brown 1988), a parameter which has frequently been used as an index of the cost of foraging (Brown 1988; Kotler et al. 2010; Halliday and Morris 2013; Halliday et al. 2014; Morris 2014). By comparing GUDs in the two habitats, we were able to assess the foraging cost of using a habitat, which can be considered one of the fitness costs of habitat selection (Brown 1988; Morris 2014). We analyzed GUDs in the field versus forest with linear mixed effects models. The GUDs from the equal food treatment (five worms in each habitat) were analyzed separately from the other two treatments (10 worms in a single habitat). We used the number of worms remaining at a feeding station as the dependent variable, habitat of the feeding station, density treatment, number of snakes found in the habitat with the feeding station, and all interactions as fixed effects, and day into the experiment nested within replicate as a random effect.

### Fitness consequences of field and forest habitat selection

The fitness consequences of living in the field or forest habitat was assessed by placing female common gartersnakes in six small enclosures in each habitat. For this experiment, we built small enclosures ( $2.67 \times 2.67 \times 1.3$  m) as described above for the habitat selection enclosures. To populate our enclosures, we captured female common gartersnakes between late April and early June 2014 in a field and a wetland within 10 km of our enclosures and then placed ten females in the field enclosures and ten females in the forest enclosures, with up to two snakes per enclosure. We ensured that each female had the opportunity to mate before the experiment was started by placing each female in a large container for 30 min with three adult male common gartersnakes from the same population. Females in each habitat were assigned to one of two feeding treatments. Females were assigned randomly to habitat and food treatment, but body size was taken into account to obtain an approximately even distribution of body sizes within each treatment. Females assigned to the high food treatment were fed one large earthworm four times per week, while females in the low food treatment were fed one large earthworm two times per week. We fed snakes by isolating each snake within their enclosure and dropping an earthworm in front of their head. This normally elicited a feeding response where the snake either struck the earthworm immediately or began flicking its tongue

at the worm. We also measured the SVL and mass of each female once per week throughout the experiment. We continued this experiment until the beginning of September to allow for all births to occur. A few snakes escaped or were eaten during our experiment, making the final sample size in each habitat six snakes (one low food and five high food females in the field habitat, three females in each treatment in the forest habitat).

We examined the growth rate of female common garter-snakes for SVL and mass. First, we regressed the SVL and mass for each individual by time (the number of weeks that the snake was in the experiment), calculated the slope for each measure, and used these slopes as the growth rate for each individual for each measure. Using the slopes of the regressions allowed us to include females that escaped the enclosures or were eaten before the end of the experiment. We then used MANOVA in R (package: stats: function: manova) to examine differences in growth rate between habitat and food treatments. We used growth rate for SVL and mass as dependent variables, and habitat, food treatment, and their interaction as independent variables.

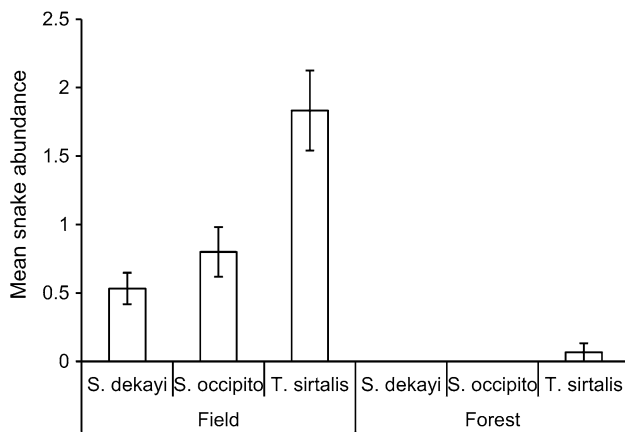
The reproductive output of females by habitat and food treatment was examined using an ANOVA in R (package: stats; function: aov). We used the number of offspring per female as the dependent variable, with habitat, food treatment, and their interaction as independent variables.

## Results

### Observational test of density-dependent habitat selection

All three species of snakes exhibited a strong and significant preference for field habitat. More specifically, almost all common gartersnakes were captured in the field (mean abundance in field  $1.83 \pm 0.29$ ; mean abundance in forest  $0.07 \pm 0.07$ ;  $t_{1,29} = 6.31$ ;  $p < 0.0001$ ; Fig. 1), and all red-bellied snakes and all Dekay's brownsnakes were captured in the field (mean Dekay's brownsnake abundance in field  $0.53 \pm 0.11$ ;  $t_{1,29} = 4.98$ ;  $p < 0.0001$ ; mean red-bellied snake abundance in field  $0.80 \pm 0.18$ ;  $t_{1,29} = 4.55$ ;  $p < 0.0001$ ).

Diurnal thermal quality was higher in the field than in the forest (mean diurnal  $d_e$  in field and forest  $5.0 \pm 0.2$  °C and  $6.2 \pm 0.5$  °C, respectively;  $F_{1,31} = 7.12$ ,  $p = 0.01$ ). Invertebrate biomass was higher in the field than in the forest (mean biomass in field and forest  $85.1 \pm 9.0$  and  $43.7 \pm 6.3$  g, respectively;  $F_{1,31} = 19.13$ ,  $p < 0.001$ ). When we restricted the analysis of invertebrate prey to earthworms and molluscs (known prey items of all three snake species), the difference in biomass between the field and forest disappeared ( $F_{1,31} = 1.83$ ,  $p = 0.19$ ).

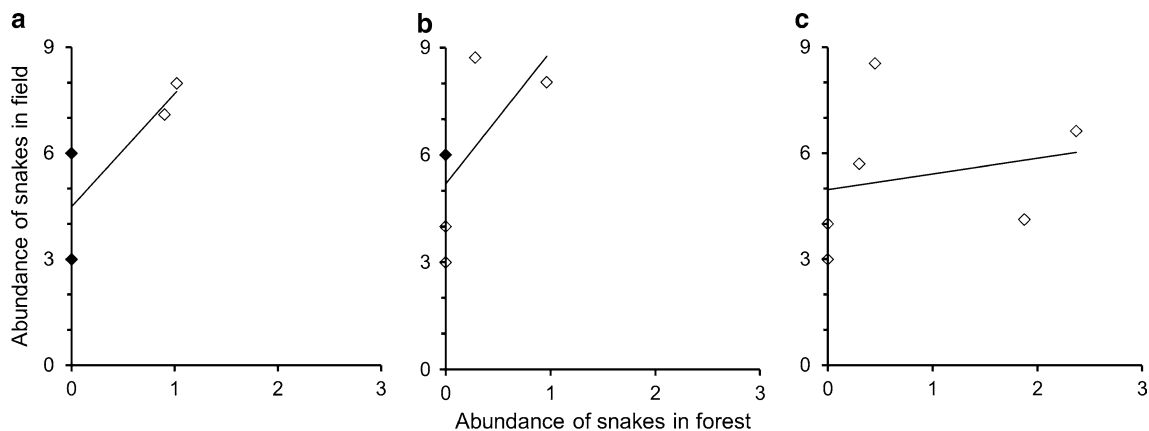


**Fig. 1** Mean number of individuals of three species of snakes detected in the field and forest habitats at Queen's University Biological Station, Ontario, Canada. *S. dekayi* = *Storeria dekayi* (Dekay's brownsnake), *S. occipito* = *Storeria occipitomaculata* (red-bellied snake), *T. sirtalis* = *Thamnophis sirtalis* (common gartersnake). Each bar was calculated using the number of individuals of each snake species caught on each of five 50 × 50-m grids across six sampling periods (each bar  $n = 30$ ). Each bar = mean value, error bars = standard error around the mean (SEM). Note that no *S. dekayi* or *S. occipitomaculata* were detected in the forest habitat

Amphibian abundance was not different between the field and forest (mean abundance in field and forest  $5.9 \pm 2.3$  and  $2.5 \pm 2.0$ , respectively;  $F_{1,31} = 0.84$ ,  $p = 0.37$ ). According to the habitat-matching prediction of the IFD, snakes should have been twofold more abundant in the field than in the forest based on total invertebrate biomass and equally abundant in the field and forest based on their main invertebrate prey (worms and molluscs) or on amphibian abundance. Contrary to the habitat-matching prediction, all red-bellied snakes and all Dekay's brownsnakes were caught in the field habitat, as were the majority of common gartersnakes (field:forest ratio = 26:1).

### Experimental test of density-dependent habitat selection

Common gartersnakes always preferred field over forest, regardless of the food treatment or of density (Fig. 2; Table 1). The preference for field habitat was strong across all densities when food was higher in the field than in the forest (isodar equation: snakes in field =  $4.77 + 5.72 \times$  snakes in forest) or when food



**Fig. 2** Isodars for an experimental test of density-dependent habitat selection with common gartersnakes (*Thamnophis sirtalis*) between field and forest habitats in enclosures straddling both habitats when food was equal between habitats (a), when food was higher in the

field (b), and when food was higher in the forest (c). Filled symbols = Two overlapping points, lines = predicted intercepts and slopes from a geometric mean regression

**Table 1** Isodars (calculated via geometric mean regression) for habitat selection by common gartersnakes (*Thamnophis sirtalis*) between field and forest in experimental enclosures that straddled each habitat

Treatment <sup>a</sup>	Intercept	Intercept CI <sup>b</sup>	Slope	Slope CI <sup>b</sup>	$R^2$	$p$
Equal	4.17	2.50–4.92	4.20	1.87–9.42	0.58	0.04
Field	4.77	2.98–5.49	5.72	2.27–14.37	0.42	0.08
Forest	3.68	0.31–4.79	1.99	0.65–6.04	0.05	0.33

<sup>a</sup> Each model refers to different food treatments, where Equal is equal food in each habitat, Field is high food availability in the field, and Forest is high food availability in the forest

<sup>b</sup> 95 % Confidence interval around the intercept and slope, respectively

abundance was equal between the field and forest (isodar equation: snakes in field =  $4.17 + 4.20 \times$  snakes in forest). The preference for field habitat was weakest when food was higher in the forest than in the field (isodar equation: snakes in field =  $3.68 + 1.99 \times$  snakes in forest) and when density was high (Fig. 2; Table 1). Habitat selection was partly density dependent: snakes in all food treatments used the forest at the highest population density, but not at the lowest population density (Fig. 2). However, the isodars for the high food treatment in the field and high food treatment in the forest were non-significant ( $p = 0.08$  and  $0.33$ , respectively), which indicates density independence or low statistical power. The isodar for the equal food treatment was significant ( $p = 0.04$ ), which indicates density dependence.

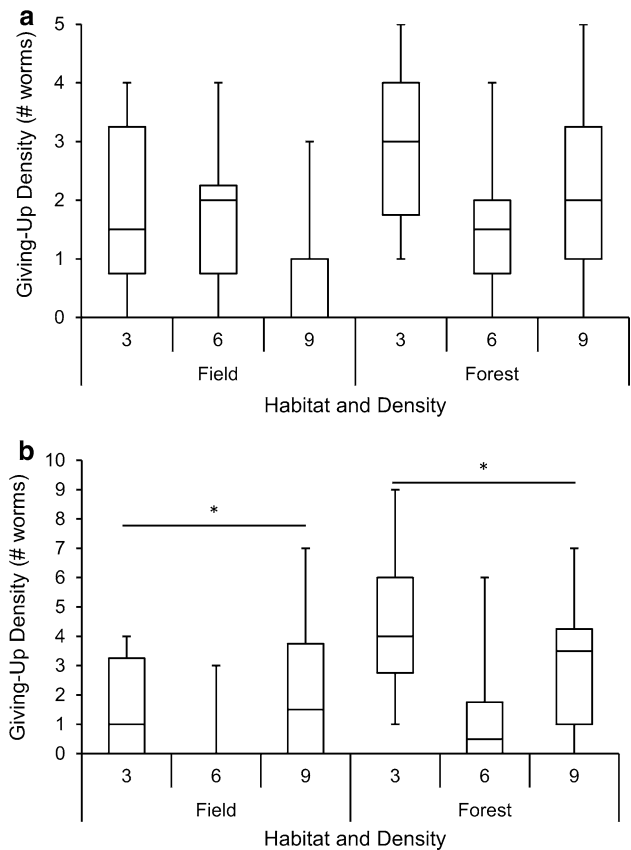
Snakes ate more worms (lower GUD) in the field than in the forest when we considered the two treatments in which food was provided only in one habitat (on average, 3 more worms eaten in the field than the forest;  $p < 0.01$ ; Fig. 3a). When food was provided equally in the two habitats, the GUDs again were lower in the field than in the forest, but this trend was not statistically significant ( $p = 0.08$ ; Fig. 3b). GUDs were lower when overall snake density was high and when snake density was high in the habitat considered ( $p = 0.02$ ). More snakes in the forest decreased the GUD in the forest (more worms were eaten), but more snakes in the field did not decrease the GUD in the field ( $p < 0.01$ ).

### Fitness consequences of field and forest habitat selection

None of the six female common gartersnakes in the forest gave birth, whereas three females out of six in the field gave birth (Table 2). The growth rate (based on mass or SVL) of female common gartersnakes was higher in the field than in the forest (Table 2). Females in the field gained mass and increased in SVL, whereas snakes in the forest increased in SVL, but lost mass (Table 2). As predicted, therefore, fitness was higher in the habitat with the higher thermal quality. Contrary to our prediction, however, food abundance had no effect on fitness (reproduction:  $F_{1,14} = 0.10$ ,  $p = 0.76$ ; mass:  $F_{1,14} = 0.08$ ,  $p = 0.78$ ; SVL:  $F_{1,14} = 0.07$ ,  $p = 0.80$ ).

### Discussion

We found some support for our hypothesis that habitat selection by snakes is not a function of conspecific density, but rather a function of thermal quality. Although our isodar analysis did provide some evidence of density-dependent habitat selection, this evidence was weak. We



**Fig. 3** Box-plot of giving-up densities (GUD), measured as the number of earthworms remaining at a feeding station, for an experimental test of density-dependent habitat selection with common gartersnakes (*Thamnophis sirtalis*) between field and forest habitats in enclosures straddling both habitats when food was equal between habitats (**a** five worms in each habitat) and when food was provided in a single habitat (**b** 10 worms in one habitat). Boxes = Interquartile range, lines within boxes = median, whiskers = minimum and maximum values, respectively. Asterisk = Statistically significant differences

also found that the habitat with the highest thermal quality provided the greatest fitness rewards, regardless of food abundance. We found no evidence of density-dependent habitat selection in our observational test: all red-bellied snakes and all Dekay's brownsnakes were found in field, as were the vast majority of common gartersnakes. Perhaps the natural density of snakes in our study area was too low to create competition for food; density dependence may only occur when densities are so high that food becomes limiting. In our manipulative experiment, in which snake densities were much higher than those in our observational study (maximum of 24 common gartersnakes/ha compared to  $>200$  common gartersnakes/ha), we found that gartersnakes continued to prefer the field over the forest, regardless of food abundance. We found weak evidence for density dependence in only one of three treatments. Overall, our results provide weak evidence for density-dependent

**Table 2** Reproductive output (number of offspring) and growth rates of female common gartersnakes (*Thamnophis sirtalis*) kept in enclosures in field and in forest

Reproductive output/growth rates <sup>a</sup>	Field		Forest		<i>F</i>	<i>p</i>
	Mean	CI <sup>b</sup>	Mean	CI <sup>b</sup>		
Number of offspring	4	0–8	0	NA	6.07	0.03
Mass (g/week)	1.3	0.8–1.8	–0.2	–0.6 to 0.2	21.9	<0.001
Snout–vent length (mm/week)	2.3	1.4–3.2	0.9	0.3 to 1.5	6.21	0.03

NA Data not available

<sup>a</sup> Number of offspring was used as a marker of reproductive output; mass and snout–vent length were used as markers of growth rates

<sup>b</sup> CI refers to the 95 % confidence interval around the mean for each metric

habitat selection by snakes when habitats differ in thermal quality, but they do provide clear evidence that thermal quality is extremely important in the habitat selection of snakes and that it can lead to largely density-independent habitat selection at naturally low snake population densities. Although we only found weak evidence for density-dependent habitat selection between the field and forest, it is possible that snakes exhibit density-dependent habitat selection between other habitat pairs. For example, density dependence could be stronger between habitat pairs of equivalent thermal quality, such as old fields and wetlands. Gartersnakes may be present at higher densities in wetlands than in fields (W.D. Halliday, unpublished data). Future studies should examine the density dependence of habitat selection between multiple habitat pairs.

We found unambiguous support for our prediction that snakes should prefer the habitat with the highest thermal quality (field). We also confirmed that choosing the habitat with the highest thermal quality translated to increased fitness, in terms of both reproductive output and growth rate. This leads to the obvious question: Why would snakes ever use forest? Possible explanations include (1) the use of forest habitat by free-ranging snakes while moving between patches of their preferred field habitat and (2) the use of forest by snakes for foraging only, with a return to the preferred field habitat for thermoregulation. Indeed, in our habitat selection experiment, worms were consumed in the forest although we rarely found snakes in the forest. In our manipulative experiment, common gartersnakes were only found in the forest at high densities, and more often when more food was provided in the forest. It is also possible that forest represents a sink habitat (Pulliam 1988) since snakes in the forest did not grow and did not give birth. It remains unclear whether population density affects fitness in snakes because we did not test for the effect of density on fitness, only for its effect on proximate measures of fitness. Snake species that are exceptionally abundant in nature should be used to test for the presence of density dependence.

Our study focused on snakes because our aim was to determine whether density-dependent habitat selection could occur for a species that was likely more limited by

temperature than by food. Repeating this study with a different ectotherm could yield very different results, simply because other taxa may have stronger responses to food availability, different levels of competition, and/or higher natural densities. Gartersnakes did not appear to compete for access to basking sites because we often found them coiled together. We have observed gartersnakes apparently competing over food items, however, where two snakes were attempting to eat the same earthworm. Therefore, we would not expect territoriality over thermal habitats in gartersnakes, but possibly over foraging patches. In a similar study on red flour beetles, we demonstrated strong density-dependent habitat selection between habitats differing in thermal quality, with the pattern of density-dependent habitat selection changing with changes in the abundance of food in each habitat (Halliday and Blouin-Demers 2014). Flour beetles clearly respond strongly to both temperature and food availability. A study on lizards demonstrated strong territoriality over basking patches, where dominant individuals defended the patches with the highest thermal quality, forcing subordinates to use patches with lower thermal quality (Calsbeek and Sinervo 2002). Increased competition for resources that are limiting can increase the strength of density dependence.

Thermal quality was a strong predictor of snake habitat selection in our study, but we worked in an area that is thermally challenging for snakes. At our study site, snakes are only active 6–7 months of the year and, based on the temperatures of our snake models, preferred body temperatures were only available, on average, for 1.2 h per day in the field during our observational study. It is therefore possible that snakes living at more temperate or at tropical latitudes are not as limited by temperature. For example, Weatherhead et al. (2012) demonstrated that ratsnakes (*Pantherophis* sp.) changed their habitat preferences and activity times at different latitudes. Gray ratsnakes (*Pantherophis spiloides*) in Ontario (at our observational study site) preferred forest edges and were diurnal, gray ratsnakes (*Pantherophis spiloides*) in Illinois preferred forests and were diurnal, and western ratsnakes (*Pantherophis obsoletus*) in Texas preferred forest, but were nocturnal (Weatherhead



et al. 2012). Ratsnakes used the thermally superior edge habitat in more northern latitudes and switched to forest further south. These findings suggest that the strong preference for field in our study could change for gartersnakes at more southern latitudes where factors other than thermal quality may be more important.

Use of forest was so limited that one may question whether it can really be considered a habitat for gartersnakes. According to Morris (2003), a habitat can be defined as a “spatially-bounded area, with a subset of physical and biotic conditions, within which the density of interacting individuals, and at least one of the parameters of population growth, is different than in adjacent subsets”. This definition is commonly used in studies of habitat selection; it allows for habitats to be species specific, and it allows for common land cover types on the landscape to be different or to be the same habitats for a species. For example, if common gartersnakes maintained identical densities and fitness in two adjacent land cover types (e.g., wetland and field), then these two land cover types would be considered to be the same habitat for gartersnakes. In our study, gartersnakes were present at different densities in the field and forest, and they achieved different fitness in these two land cover types. We can therefore confidently say that field and forest are distinct habitats for gartersnakes. Other definitions for habitat exist. For example, the Merriam–Webster dictionary (2015) defines habitat as simply “the place or type of place where a plant or animal naturally or normally lives and grows”. Based on this less specific definition, forest might not be considered a habitat because common gartersnakes use forest much less frequently than open habitats. We favored the more specific definition used in studies of habitat selection (Morris 2003). In addition, radio-telemetry studies in the same study area revealed that ratsnakes and milksnakes do use forest, albeit less frequently than open habitats (Blouin-Demers and Weatherhead 2001; Row and Blouin-Demers 2006). Had we used radio-telemetry instead of surveys in our observational study, we may have been able to document gartersnakes using forest habitat more frequently.

Previous studies have demonstrated that environmental temperature is a very strong predictor of habitat selection in snakes (e.g., Blouin-Demers and Weatherhead 2001; Burger et al. 2004; Carfagno and Weatherhead 2006; Row and Blouin-Demers 2006), yet that food can also be important (e.g., Reinert 1984; Robertson and Weatherhead 1992; Diller and Wallace 1996). To the best of our knowledge, however, our study is the first to examine explicitly density-dependent habitat selection in snakes. Using both observational and experimental approaches, we found evidence that habitat selection can be density dependent at unnaturally high snake densities, but that habitat selection was density independent at natural snake densities. Future

studies could more fully examine the fitness effects of habitat selection, for instance by obtaining data on survival in addition to growth and reproductive output. Understanding how competition (density dependence) affects the habitat selection of snakes is crucial since density dependence is an assumption of several important ecological models [e.g., Lotka-Volterra equation (Volterra 1926); Ricker equation (Ricker 1954); IDF (Fretwell and Lucas 1969)]. If density dependence does not apply to snakes, then do these ecological models apply to snake populations, and to ectotherms more generally? This is a fruitful avenue for future research.

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**Author contribution statement** WDH and GBD designed the project, WDH conducted all research and statistical analyses, and WDH and GDB wrote the manuscript.

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