



# Density-Dependent Foraging and Interference Competition by Common Gartersnakes are Temperature Dependent

William D. Halliday & Gabriel Blouin-Demers

Department of Biology, University of Ottawa, Ottawa, Ontario, Canada

## Correspondence

William D. Halliday, Department of Biology,  
University of Victoria, Victoria, British  
Columbia, Canada  
E-mail: whall075@uottawa.ca

Received: June 10, 2016

Initial acceptance: July 25, 2016

Final acceptance: September 2, 2016

(L. Ebensperger)

doi: 10.1111/eth.12562

**Keywords:** ideal free distribution, handling time, optimal foraging, patch selection, *Thamnophis sirtalis*, thermal reaction norm, thermal performance curve

## Abstract

The ideal free distribution (IFD) predicts that optimal foragers will select foraging patches to maximize food rewards and that groups of foragers should thus be distributed between food patches in proportion to the availability of food in those patches. Because many of the underlying mechanisms of foraging are temperature dependent in ectotherms, the distribution of ectothermic foragers between food patches may similarly depend on temperature because the difference in fitness rewards between these patches may change with temperature. We tested the hypothesis that the distribution of Common Gartersnakes (*Thamnophis sirtalis*) between food patches can be explained by an IFD, but that conformance to an IFD weakens as temperature departs from the optimal temperature because fitness rewards, interference competition and the number of individuals foraging are highest at the optimal temperature. First, we determined the optimal temperature for foraging. Second, we examined group foraging at three temperatures and three density treatments. Search time was optimized at 27°C, handling time at 29°C and digestion time at 32°C. Gartersnakes did not match an IFD at any temperature, but their distribution did change with temperature: snakes at 20°C and at 30°C selected both food patches equally, while snakes at 25°C selected the low food patch more at low density and the high food patch more at high density. Food consumption and competition increased with temperature, and handling time decreased with temperature. Temperature therefore had a strong impact on foraging, but did not affect the IFD. Future work should examine temperature-dependent foraging in ectotherms that are known to match an IFD.

## Introduction

The ideal free distribution (IFD; Fretwell & Lucas 1969) is an important framework within habitat selection theory (Morris 2003). The IFD predicts that individuals should choose the habitat offering the highest fitness reward and that these individual choices will lead to individuals being distributed between habitats so that, on average, individuals in each habitat achieve the same fitness (Fretwell & Lucas 1969). Although the IFD was originally developed as a model of habitat selection (Fretwell & Lucas 1969), it has been successfully applied to optimal foraging (reviewed in Kennedy & Gray 1993;

but see also Åström 1994 and Milinski 1994). An optimal forager should forage in the patch offering the highest food rewards, and groups of foragers will be distributed between food patches in proportion to the amount of food in those patches so that each individual, on average, obtains the same amount of food. The IFD assumes that individuals have perfect knowledge of the distribution of resources and of competitors between habitats, have the freedom to move between habitats with zero fitness costs and have equal competitive abilities. The assumptions of the IFD are too simplistic: individuals rarely have equal competitive ability, competitors are not omniscient and travel always comes at a cost. Yet, despite

the simplicity of its assumptions (Milinski 1988; Matsumura et al. 2010), the IFD has been used successfully to predict the distribution of several foraging animals, including fish (e.g. Milinski 1979; Godin & Keenleyside 1984; Dupuch et al. 2009), birds (e.g. Harper 1982; Díaz et al. 1998; van Gils et al. 2006) and insects (e.g. Dreisig 1995). The IFD has also been expanded to include interference competition and unequal competitors (the ideal despotic distribution; Fretwell & Lucas 1969), interspecific competition (Rosenzweig & Abramsky 1986; Morris 1988) and predation risk (Moody et al. 1996; Grand & Dill 1999).

Foraging by ectotherms is temperature dependent because of the functional relationship between temperature and both metabolism (e.g. Bergman 1987; Schulte et al. 2011) and energy assimilation (Angilletta 2001). While metabolic rate increases with temperature (e.g. Gillooly et al. 2001), energy assimilation is optimized within a narrow range of temperatures (Angilletta 2001). Similarly, locomotor performance is also temperature dependent and optimized within a narrow range of temperatures (e.g. Stevenson et al. 1985; Blouin-Demers et al. 2003; Halliday & Blouin-Demers 2015), which suggests that the ability of individuals to find and handle food can also be optimized within a narrow range of temperatures. Moreover, the intensity of intraspecific competition in ectotherms can be temperature dependent (Halliday & Blouin-Demers 2014; Halliday et al. 2015): negative density dependence is strongest at the optimal temperature for growth. The fitness reward for each food item consumed is highest at the optimal temperature for energy assimilation, and these fitness rewards decrease as temperature deviates from that optimal temperature. Therefore, food items may have little value to ectotherms when temperature is far from the optimal temperature because they cannot assimilate the energy from these food items. Competition for food should be strongest when food is most valuable; therefore, competition should be strongest at the optimal temperature. Because food passage rate is also fastest at the optimal temperature (Stevenson et al. 1985; Angilletta et al. 2002a), there should be more individuals foraging at the optimal temperature because ectotherms are more likely to have an empty digestive tract when food passage rate is higher. In ectotherms, therefore, concordance with the IFD should be most marked at the optimal temperature and should weaken as temperature deviates from the optimal temperature due to decreased competition for food and to fewer individuals foraging. Individuals that are not foraging should not be distributed

according to food availability, thus weakening concordance with the IFD.

In this study, we examine the hypothesis that the distribution of ectotherms between food patches can be explained by an IFD, but that conformance to an IFD weakens as temperature departs from the optimal temperature because fitness rewards, interference competition and the number of individuals foraging are highest at the optimal temperature. More specifically, we predict that the distribution of ectotherms foraging at suboptimal temperatures will not match an IFD, whereas the distribution of those foraging at the optimal temperature will match an IFD. We used foraging experiments with Common Gartersnakes (*Thamnophis sirtalis*) in the laboratory to test this prediction. First, we conducted foraging trials with single snakes across a range of temperatures to determine the optimal temperature for foraging and to confirm that handling time is minimized and that consumption is maximized at the optimal temperature. We then conducted group foraging trials with different numbers of snakes at three temperatures, one of which was the optimal temperature for foraging, and recorded the distribution of snakes between food patches that differed in food abundance. This is the first test, to the best of our knowledge, of ideal free foraging in reptiles, although a previous study (Calsbeek & Sinervo 2002) examined ideal despotic distributions in lizards competing over basking sites.

## Methods

### Study Animals

Our study species was the Common Gartersnake (*Thamnophis sirtalis*). Common Gartersnakes are common throughout North America, from Florida in the Southeast United States to the southern Northwest Territories in Northern Canada, with a relatively continuous distribution other than in tall mountain ranges and in deserts (International Union for the Conservation of Nature and Natural Resources 2016). Common Gartersnakes eat a variety of invertebrate and small vertebrate prey, with earthworms and frogs being their most common prey (reviewed in Halliday 2016).

We captured 18 adult (>40 cm snout-vent length), non-gravid female Common Gartersnakes (*Thamnophis sirtalis*) in fields and wetlands around Ottawa, Ontario, Canada, and transported them back to our laboratory at the University of Ottawa. We only used females for this experiment because pilot studies demonstrated that males were less willing to eat in

captivity than females (Halliday *unpublished data*). All snakes were acclimated to captivity for at least 1 wk prior to experiments. Snakes were housed in plastic containers (31 × 17 × 10 cm) in an environmental chamber that was on a 14 10-hour light dark cycle and temperatures of 25°C during the day and 10°C during the night to approximate seasonal conditions around Ottawa. Snakes were provided with *ad lib* water and a refuge, a hot spot for thermoregulation, and were fed two earthworms every 2–3 d. Following experiments, all snakes were released back at their point of capture. All methods were approved by the University of Ottawa Animal Care Committee (protocol BL-278), which follows the guidelines of the Canadian Council for Animal Care.

### Thermal Reaction Norms for Foraging

To determine the optimal temperature for foraging, we examined three metrics of foraging by adult female Common Gartersnakes ( $N = 8$ ) at six temperatures (10, 15, 20, 25, 30 and 35°C) in a randomized order. We allowed females to acclimate to the experimental temperature for at least two hours prior to the experiment. We placed individual female Common Gartersnakes in an arena (50 × 35 × 50 cm) for a one-minute acclimation period. Following one minute, we added one large earthworm to the centre of the arena and recorded the time it took the snake to bite the earthworm (search time) and the time it took the snake to swallow the earthworm (handling time). We gave the snake a maximum of five minutes with the worm. We recorded the entire trial with a video camera and measured search time and handling time from the video. Following each trial, we sprayed the arena with water and wiped every surface. The snake was maintained at the experimental temperature following the trial, and we counted the number of days it took until it defecated. Snakes were fasted for 2 d prior to this experiment to ensure that the faeces that they passed were from the worm eaten during the experiment. If the snake did not eat during a trial, we placed the snake back in its container with the worm. If the snake ate the worm within 24 h, we included its time to defecation. We fit nonlinear curves to each thermal reaction norm to estimate the optimal temperature ( $T_o$ ; Huey & Stevenson 1979) (see Appendix 1 for details).

### Optimal Foraging Experiments

We conducted foraging trials at three temperatures (20, 25 and 30°C).  $T_o$  for our three metrics of foraging

were 27, 29 and 32°C (Results). Therefore, our 30°C treatment approximated  $T_o$ , our 25°C treatment was just below  $T_o$  and our 20°C treatment was below  $T_o$ . We allowed snakes to acclimate to the treatment temperature for at least two hours prior to the experiment. We placed three, six or nine snakes in the centre of a large stainless steel rectangular enclosure (2.0 × 0.5 × 0.5 m) and replicated each density treatment three times for each temperature treatment. We determined trial order randomly, and we never used the same snake twice in 1 d. After one minute of acclimation, we added three earthworms to one end of the enclosure and one worm to the other end of the enclosure. We repeated the addition of worms after four and after seven minutes so that in total nine and three worms were added to the high and low food patches, respectively. We removed the snakes from the enclosure after ten minutes, and we counted the number of worms remaining on each side of the enclosure. We used a video camera to record the trial, and we used the video to determine the distribution of snakes between the two sides of the enclosure (low food or high food) throughout the experiment, the handling time for each foraging event (the amount of time for snake to bite and swallow a worm) and the amount of time spent competing over food items (the amount of time that two snakes were biting the same worm).

We calculated the distribution of snakes between the high and low food sides of the enclosure based on the location of the heads of the snakes. We included all snakes in this analysis, whether or not they were foraging, because foraging individuals likely assessed snake density in each patch based on the total number of potential competitors and not based just on the number of snakes currently foraging. We recorded the length of time (in seconds) that each distribution lasted during each trial. Thus, the sum of the distribution times for each trial equalled the total time in a trial (540 s). We calculated the mean distribution of snakes between the low and high food patch in each trial with the following equation:

$$D = \frac{\sum[(1 \times T_1) + (2 \times T_2) + \dots (i \times T_i)]}{540}$$

where  $D$  is the mean number of snakes in the high food patch during the trial,  $T$  is the total time during the trial when  $i$  snakes were in the high food patch and 540 s is the total time available during the trial when food was also available (the sum of  $T_1$  through  $T_i$ ).

We cleaned the enclosure with water and dried it between trials. We also alternated the side of the

enclosure receiving the low and the high food every trial. Snakes were allowed to rest at least 24 h between consecutive trials at 25 and at 30°C, and at least 48 h between trials at 20°C. These are the required times for snakes to digest and defecate food at each temperature (Results).

We tested the prediction that the distribution of snakes should match an IFD at  $T_o$  and should deviate from an IFD as temperatures deviate from  $T_o$  with two analyses. First, we examined the density-dependent distribution of snakes at each temperature using isodars (Morris 1988) built with geometric mean regression. Second, we examined the proportion of individuals using the high food patch using linear mixed effects models. We used two analyses because isodars are an effective tool for examining density-dependent effects in habitat selection, but methods in geometric mean regression have not been developed for comparison of multiple independent variables or random effects. We therefore used linear mixed effects models in the second analysis to specifically test whether the distribution of snakes overlapped with the IFD (distribution of 3:1).

We built isodars using geometric mean regression in R (package: `lmodel2`; function: `lmodel2`; Legendre 2014) with the mean number of snakes in the high food patch during a trial as  $y$  and the mean number of snakes in the low food patch during a trial as  $x$ . We built one isodar for each temperature treatment. We compared isodars by examining the 95% confidence intervals around their intercept and slope. An isodar with an intercept significantly different than zero demonstrates preference for a habitat (Morris 1988), or in this case a foraging patch, and a slope different than one demonstrates a habitat preference that changes with density (Morris 1988).

We examined the proportion of snakes in the high food patch with linear mixed effects models in R (package: `nlme`; function: `lme`; Pinheiro et al. 2014) with temperature, the number of snakes in a trial and their interaction as fixed effects, and the trial order nested within trial date as random effects. We compared models with Akaike's information criteria (package: `stats`; function: `AIC`; R R Core Team 2014) and considered the model with the lowest AIC to be the best model. We considered models within two AIC units of the best model to be competing models (Bozdogan 1987) and used model averaging amongst the competing models to determine final model estimates (Burnham & Anderson 2002). We used this model selection approach for all subsequent analyses.

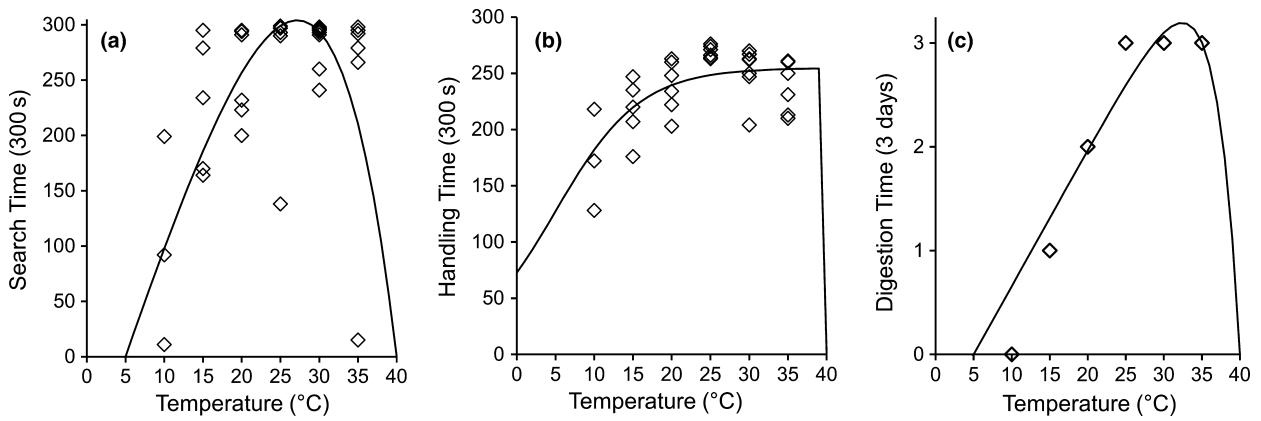
We tested the assumptions that fitness rewards, competition and the number of individuals foraging

are highest at the optimal temperature by examining the amount of food eaten in a trial, the effect of competitors on handling time and the number of competitive events during a trial. We examined the amount of food eaten during a trial using linear mixed effects models with the total number of worms eaten as the dependent variable, temperature, density and their interaction as fixed effects, and trial order nested within trial date as random effects. We also used linear mixed effects models to examine the amount of food eaten in a patch to directly assess the effect of competition on foraging at each temperature. We used the number of worms eaten in a patch as the dependent variable with temperature, the average number of snakes in that patch during the trial, the patch type (high or low food), and all interactions as fixed effects, and with trial order nested within trial date as random effects. We examined handling time for each foraging event in each density and temperature treatment with a linear mixed effects model with handling time as the dependent variable, and temperature, density, competition time (time spent competing with another snake) and all interactions as fixed effects. We used trial order nested within trial date as random effects. Finally, we examined the number of competitive events during each trial using linear mixed effects models with a Poisson distribution in R (package: `lme4`; function: `glmer`; family = `Poisson`; Bates et al. 2014) with the number of competitions within a trial as the dependent variable, temperature, density and their interaction as fixed effects, and trial order nested within trial date as random effects. We used a Poisson distribution for this analysis because the distribution of residuals was heavily right skewed and fit a Poisson distribution better than a normal distribution.

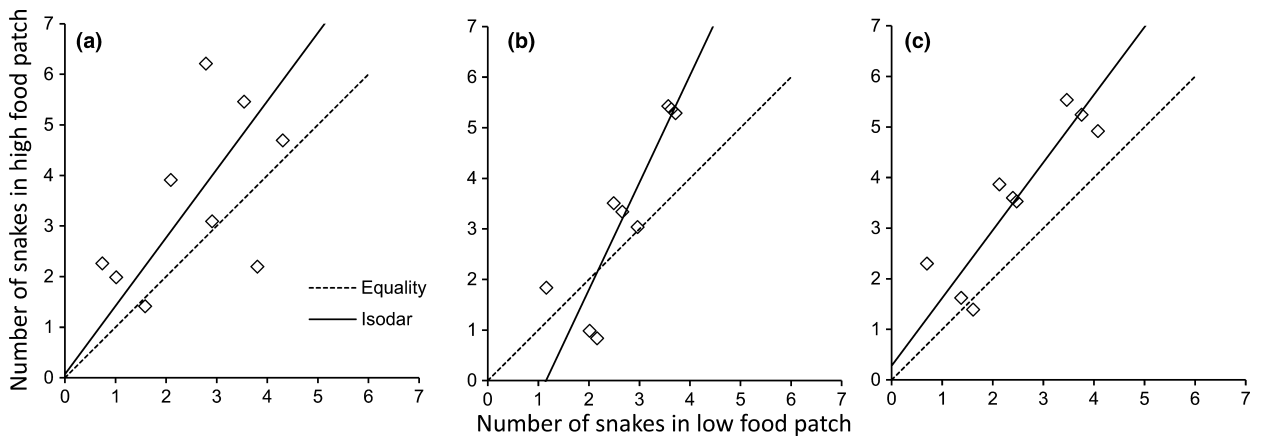
## Results

### Thermal Reaction Norms for Foraging

During individual foraging trials, three Common Gartersnakes ate worms at 10°C; five snakes ate at 15°C; six snakes ate at 20, 25 and 35°C and all eight snakes ate at 30°C. Search time of Common Gartersnakes was best described by a curve with a linear increase and an exponential decay (Fig. 1a, Appendix 1 Table A1). Gartersnakes that ate spent between 1 and 289 s searching for the worm ( $\bar{x} = 9.5$  s;  $\bar{x} = 55.6$  s). The  $T_o$  for search time was 27°C (Fig. 1a, Appendix 1 Table A2). Handling time of Common Gartersnakes was best described by a curve with a logistic growth and an exponential decay (Fig. 1b, Appendix 1



**Fig. 1:** Thermal reaction norms of Common Gartersnakes (*Thamnophis sirtalis*) for search time (a), handling time (b) and digestion time (c) across six temperatures. Each line of best fit represents the nonlinear curve selected (Appendix 1).



**Fig. 2:** Isodars for ideal free foraging between high food and low food patches by Common Gartersnakes (*Thamnophis sirtalis*) at 20 (a), 25 (b) and 30°C (c). The isodar (solid line) is based on the predicted equation from isodar analysis, equality (dotted line) represents no selection for either food patch and the IFD (ideal free distribution; dashed line) represents the distribution predicted based on food abundance in a patch.

Table A1). Gartersnakes took between 24 and 172 s to handle an earthworm ( $\bar{x} = 51.0$  s;  $\bar{x} = 61.6$  s). The  $T_o$  for handling time was 29°C (Fig. 1b, Appendix 1 Table A2). Digestion time of Common Gartersnakes was best described by a curve with a linear increase and an exponential decay (Fig. 1c, Appendix 1 Table A1). Gartersnakes took between 1 and 4 d to digest fully a worm ( $\bar{x} = 1$  d;  $\bar{x} = 2$  d). The  $T_o$  for digestion time was 32°C (Fig. 1c, Appendix 1 Table A2).

**Group Foraging**

Snakes in the 20°C treatment did not have a significant preference for either the low or high food patch (intercept  $\approx 0$ , slope  $\approx 1$ ), and the isodar was not statistically significant and explained relatively little

variance ( $R^2 = 0.30$ ,  $p = 0.13$ ; Fig. 2a, Appendix 2 Table A3). Snakes in the 25°C treatment showed preference for the low food patch at low density (intercept  $< 0$ ), but showed increasing preference for the high food patch as density increased (slope  $> 1$ ). The isodar for the 25°C treatment was statistically significant and explained a large amount of variance ( $R^2 = 0.75$ ,  $p < 0.01$ ; Fig. 2b, Appendix 2 Table A3). This isodar predicts that an equal number of snakes will be in each food patch at the lowest density and that more snakes will be in the high food patch than in the low food patch at the intermediate and high densities. Lastly, snakes in the 30°C treatment showed equal preference for both food patches across all densities (intercept  $\approx 0$ , slope  $\approx 1$ ), and the isodar was statistically significant and explained the largest amount of variance ( $R^2 = 0.79$ ,  $p < 0.01$ , Fig. 2c,



Appendix 2 Table A3). The mean proportion of snakes in the high food patch did not match an IFD for any temperature or density treatment (Fig. 3, Appendix 2 Table A4) and did not differ significantly between density or temperature treatments (Appendix 2 Table A4). The mean distribution of snakes across all density and temperature treatments was 0.56 in the high food patch.

The total number of worms eaten in a trial increased as the number of snakes in a trial increased (slope = 0.58,  $t_{15} = 3.55$ ,  $p < 0.01$ , Fig. 4a, Appendix Table A5) and as temperature increased (slope = 0.21,  $t_{15} = 2.15$ ,  $p = 0.049$ , Fig. 4b, Appendix 2 Table A5). The total number of worms eaten in a patch increased as the number of snakes in that patch increased and increased at a greater rate in the high food patch (slope = 1.02 worms eaten/snake,  $t_{41} = 5.56$ ,  $p < 0.01$ ) than in the low food patch (slope = 0.12 worms eaten/snake,  $t_{41} = 2.67$ ,  $p = 0.01$ , Fig. 4c, Appendix 2 Table A6). The total number of worms eaten in a food patch was unaffected by temperature (Fig. 4d, Appendix 2 Table A6).

Handling time of snakes in the foraging trials increased as the amount of time spent competing with another snake increased (slope = 0.006,  $t_{146} = 5.78$ ,  $p < 0.01$ ; Fig. 4e) and decreased as temperature increased (slope = -0.02,  $t_{146} = 4.45$ ,  $p < 0.01$ ; Fig. 4f, Appendix 2 Table A7). The number of competitive events increased as temperature increased (slope = 0.11,  $z_{23} = 1.99$ ,  $p = 0.047$ ; Fig. 5, Appendix 2

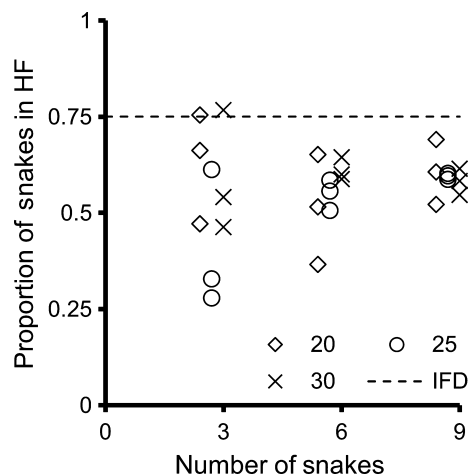
Table A8), but was unaffected by the number of individuals in a trial ( $z_{22} = 1.48$ ,  $p = 0.14$ ).

## Discussion

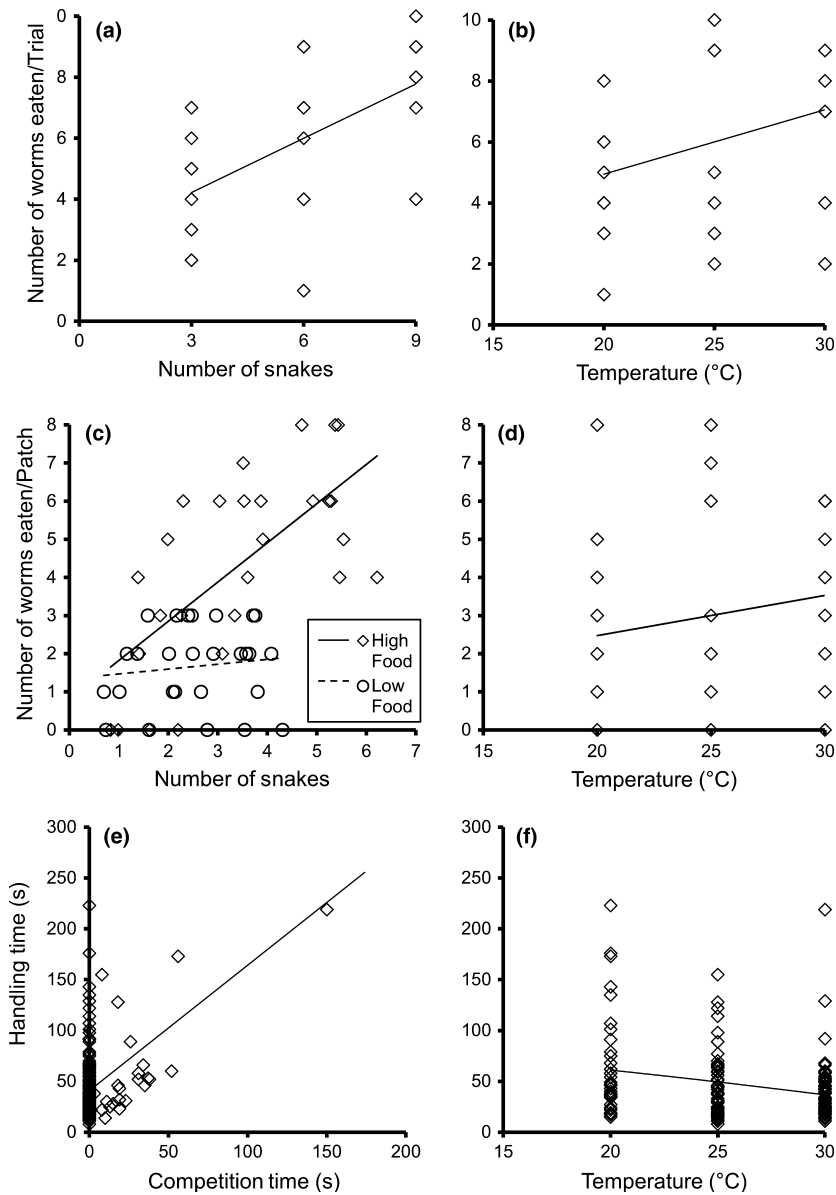
The IFD is a strong model for predicting the distribution of animals between habitats (Fretwell & Lucas 1969) and between foraging patches (Milinski 1979), yet no study has investigated how temperature affects ideal free foraging by ectotherms despite temperature being a key factor in all aspects of ectotherm life (Angilletta et al. 2002b). We found that Common Gartersnakes generally showed little preference for the high or low food patch, regardless of temperature or density. The strength of patch selection increased with temperature (increasing  $R^2$  values with temperature). In addition, both the number of worms eaten in a treatment and the number of competitive events increased with temperature. Although Common Gartersnakes did not achieve an IFD, they did eat worms according to an IFD (three times as many worms eaten in the high than in the low food patch).

The distribution of gartersnakes undermatched the IFD across all density and temperature treatments (mean distribution = 0.56, IFD = 0.75). Undermatching an IFD is common in foraging trials (Kennedy & Gray 1993) and is often due to high travel costs between foraging patches or to imperfect knowledge. Because our foraging enclosure was relatively small, the undermatching was likely due to imperfect knowledge rather than to travel costs. Alternatively or additionally, undermatching could have occurred because not all snakes foraged during a trial. Snakes that did not forage would be equally distributed between patches, thus pulling the distribution towards 0.5. Snakes that were not foraging were generally exploring the arena, but were likely still considered potential competitors by snakes that were foraging. Despite these deviations from an IFD according to snake distribution, food consumption did match an IFD, especially at higher density. As density increased, snakes tended to forage more in the high food than in the low food patch.

Although our study is the first in which the temperature dependence of group foraging by snakes in the laboratory was examined, several field studies of habitat selection and foraging by snakes in the field have been conducted. Many habitat selection studies in temperate climates have indicated that temperature is the most important factor affecting habitat selection by snakes (Blouin-Demers & Weatherhead 2001; Carfagno & Weatherhead 2006; Carfagno et al. 2006; Row & Blouin-Demers 2006; Halliday &



**Fig. 3:** The proportion of snakes using the high food patch (HF) at different temperatures (20, 25 and 30°C) and different numbers of snakes during foraging trials with Common Gartersnakes (*Thamnophis sirtalis*). The ideal free distribution, denoted by the dashed line, was 3:1 in this experiment based on the number of worms provided in each foraging patch.

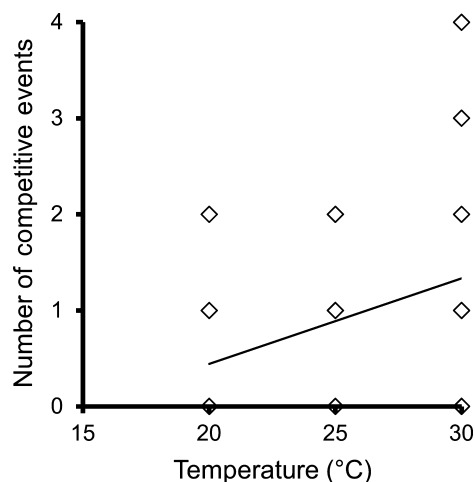


**Fig. 4:** The number of worms eaten per trial (a, b), the number of worms eaten in a patch (c, d) and handling time (e, f) for Common Gartersnakes (*Thamnophis sirtalis*) during foraging trials at 20, 25 and 30°C.

Blouin-Demers 2016). In the tropics, some studies have indicated that the location of prey can be very important and temperature less important in dictating patterns of habitat use by snakes (Madsen & Shine 1996; Shine & Madsen 1996), while others indicated that temperature is also very important (Luiselli & Akani 2002). Thus, overall, our laboratory results corroborate the large amount of evidence from the field that temperature is a key driver of habitat selection by snakes.

Although previous work has suggested that competition, as measured by negative density dependence of fitness, is temperature dependent (Halliday & Blouin-Demers 2014; Halliday et al. 2015), this is the first

study, to the best of our knowledge, to demonstrate that direct interference competition between individuals is temperature dependent. As temperature increased, more gartersnakes competed over worms. This competition appeared to be a form of interference competition because the aggressor bit onto the worm already being eaten by another individual. This increased competition may explain the reduced preference for the high food patch at 30°C because an increased number of competitive interactions in the high food patch may have caused individuals to move to the low food patch. An interesting observation is that snakes often engaged in competitive interactions even when other worms were available at the food



**Fig. 5:** The number of competitive events over food during foraging trials at 20, 25 and 30°C between Common Gartersnakes (*Thamnophis sirtalis*).

patch. It is unclear why snakes would try to eat a worm already being consumed by a conspecific when other worms are available, and this aspect deserves further study.

Handling time decreased with increasing temperature, which was expected because processes that rely on musculature such as locomotion (Stevenson et al. 1985; Blouin-Demers et al. 2003; Halliday & Blouin-Demers 2015) are temperature dependent. Food consumption increased with temperature, which could be due to energetic demands increasing with temperature (e.g. Schulte et al. 2011). In summary, therefore, foraging by ectotherms is a temperature-dependent process because its underlying components (foraging rate, handling time and competition) are temperature dependent. Future work should explore temperature-dependent foraging in ectotherms that are more likely to achieve an IFD at optimal temperatures and should be expanded to a wider range of ectothermic species. The temperature dependence of foraging should also be included in some of the other models of foraging, such as quitting harvest rates and giving-up densities (Brown 1988). This expansion would allow for a truly mechanistic approach to the study of foraging.

### Acknowledgements

We are grateful to P. Fassina, S. Karabatsos and M. Routh for their help collecting snakes in the field. Funding for this project was provided by the University of Ottawa and the Natural Science and Engineering Research Council of Canada through a post-graduate scholarship to WDH and a Discovery

Grant to GBD. All work was approved by the University of Ottawa Animal Care Committee under protocol BL-278. All snakes were collected with permission from the Ontario Ministry of Natural Resources and from the Québec Ministère des Ressources Naturelles.

### Literature Cited

- Angilletta, M. J. 2001: Thermal and physiological constraints on energy assimilation in a widespread lizard (*Sceloporus undulatus*). *Ecology* **82**, 3044–3056.
- Angilletta, M. J., Hill, T. & Robson, M. A. 2002a: Is physiological performance optimized by thermoregulatory behavior? A case study of the eastern fence lizard *Sceloporus undulatus*. *J. Therm. Biol.* **27**, 199–204.
- Angilletta, M. J., Niewiarowski, P. H. & Navas, C. A. 2002b: The evolution of thermal physiology in ectotherms. *J. Therm. Biol.* **27**, 249–268.
- Åström, M. 1994: Travel cost and the ideal free distribution. *Oikos* **69**, 516–519.
- Bates, D., Maechler, M., Bolker, B. & Walker, S. 2014: lme4: linear mixed-effects models using Eigen and S4. R package version 1.1-7.
- Bergman, E. 1987: Temperature-dependent differences in foraging ability of two percids, *Perca fluviatilis* and *Gymnocephalus cernuus*. *Environ. Biol. Fishes* **19**, 45–53.
- Blouin-Demers, G. & Weatherhead, P. J. 2001: Habitat use by black rat snakes (*Elaphe obsoleta obsoleta*) in fragmented forests. *Ecology* **82**, 2882–2896.
- Blouin-Demers, G., Weatherhead, P. J. & McCracken, H. A. 2003: A test of the thermal coadaptation hypothesis with black rat snakes (*Elaphe obsoleta*) and northern water snakes (*Nerodia sipedon*). *J. Therm. Biol.* **28**, 331–340.
- Bozdogan, H. 1987: Model selection and Akaike's information criterion (AIC): the general theory and its analytical extensions. *Psychometrika* **52**, 345–370.
- Brown, J. S. 1988: Patch use as an indicator of habitat preference, predation risk, and competition. *Behav. Ecol. Sociobiol.* **22**, 37–47.
- Burnham, K. P. & Anderson, D. R. 2002: Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. Springer, Berlin.
- Calsbeek, R. & Sinervo, B. 2002: An experimental test of the ideal despotic distribution. *J. Anim. Ecol.* **71**, 513–523.
- Carfagno, G. L. F. & Weatherhead, P. J. 2006: Intraspecific and interspecific variation in use of forest-edge habitat by snakes. *Can. J. Zool.* **84**, 1440–1452.
- Carfagno, G. L. F., Heske, E. J. & Weatherhead, P. J. 2006: Does mammalian prey abundance explain forest-edge use by snakes? *Ecoscience* **13**, 293–297.
- Díaz, M., Illera, J. C. & Atienza, J. C. 1998: Food resource matching by foraging tits *Parus* spp. during spring-summer in a Mediterranean mixed forest;



- evidence for an ideal free distribution. *The Ibis* **140**, 654–660.
- Dreisig, H. 1995: Ideal free distributions of nectar foraging bumblebees. *Oikos* **72**, 161–172.
- Dupuch, A., Dill, L. M. & Magnan, P. 2009: Testing the effects of resource distribution and inherent habitat riskiness on simultaneous habitat selection by predators and prey. *Anim. Behav.* **78**, 705–713.
- Fretwell, S. D. & Lucas, H. L. 1969: On territorial behavior and other factors influencing habitat distribution in birds: I. Theoretical development. *Acta Biotheoretica* **19**, 16–36.
- Gillooly, J. F., Brown, J. H., West, G. B., Savage, V. M. & Charnov, E. L. 2001: Effects of size and temperature on metabolic rate. *Science* **293**, 2248–2251.
- van Gils, J. A., Spaans, B., Dekinga, A. v & Piersma, T. 2006: Foraging in a tidally structured environment by red knots (*Calidris canutus*): ideal, but not free. *Ecology* **87**, 1189–1202.
- Godin, J. & Keenleyside, M. H. A. 1984: Foraging on patchily distributed prey by a cichlid fish (Teleostei, Cichlidae): a test of the ideal free distribution theory. *Anim. Behav.* **32**, 120–131.
- Grand, T. C. & Dill, L. M. 1999: Predation risk, unequal competitors and the ideal free distribution. *Evol. Ecol. Res.* **1**, 389–409.
- Halliday, W. D. 2016: Evidence of predation on nestling birds by Eastern Gartersnakes (*Thamnophis sirtalis sirtalis*). *The Canadian Field-Naturalist* **130**, 110–115.
- Halliday, W. D. & Blouin-Demers, G. 2014: Red flour beetles balance thermoregulation and energy acquisition via density-dependent habitat selection. *J. Zool.* **294**, 198–205.
- Halliday, W. D. & Blouin-Demers, G. 2015: A stringent test of the thermal coadaptation hypothesis in flour beetles. *J. Therm. Biol.* **52**, 108–116.
- Halliday, W. D. & Blouin-Demers, G. 2016: Differential fitness in field and forest explains density-independent habitat selection by gartersnakes. *Oecologia* **181**, 841–851.
- Halliday, W. D., Thomas, A. S. & Blouin-Demers, G. 2015: High temperature intensifies negative density dependence of fitness in red flour beetles. *Ecol. Evol.* **5**, 1061–1067.
- Harper, D. G. C. 1982: Competitive foraging in mallards: ‘Ideal free’ ducks. *Anim. Behav.* **30**, 575–584.
- Huey, R. B. & Stevenson, R. D. 1979: Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. *Am. Zool.* **19**, 357–366.
- International Union for the Conservation of Nature and Natural Resources. 2016: *Thamnophis sirtalis*. <http://www.iucnredlist.org/details/62240/0>. Accessed 8 August 2016.
- Kennedy, M. & Gray, G. 1993: Can ecological theory predict the distribution of foraging animals? A critical analysis of experiments on the ideal free distribution. *Oikos* **68**, 158–166.
- Legendre, P. 2014: lmodel2: Model II Regression. R package version 1.7-2.
- Luiselli, L. & Akani, G. C. 2002: Is thermoregulation really unimportant for tropical reptiles? Comparative study of four sympatric snake species from Africa. *Acta Oecologia* **23**, 59–68.
- Madsen, T. & Shine, R. 1996: Seasonal migration of predators and prey – a study of pythons and rats in tropical Australia. *Ecology* **77**, 149–156.
- Matsumura, S., Arlinghaus, R. & Dieckmann, U. 2010: Foraging on spatially distributed resources with sub-optimal movement, imperfect information, and traveling costs: departures from the ideal free distribution. *Oikos* **119**, 1469–1483.
- Milinski, M. 1979: An evolutionarily stable feeding strategy in sticklebacks. *Zeitschrift für Tierpsychologie* **51**, 36–40.
- Milinski, M. 1988: Games fish play: making decisions as a social forager. *Trends Ecol. Evol.* **3**, 325–330.
- Milinski, M. 1994: Ideal free theory predicts more than only input matching – a critique of Kennedy and Gray’s review. *Oikos* **71**, 163–166.
- Moody, A. L., Houston, A. I. & McNamara, J. M. 1996: Ideal free distributions under predation risk. *Behav. Ecol. Sociobiol.* **38**, 131–143.
- Morris, D. W. 1988: Habitat-dependent population regulation and community structure. *Evol. Ecol.* **2**, 253–269.
- Morris, D. W. 2003: Toward an ecological synthesis: a case for habitat selection. *Oecologia* **136**, 1–13.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & R Core Team. 2014: nlme: linear and nonlinear mixed effects models. R package version 3.1-118.
- R Core Team. 2014: R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rosenzweig, M. L. & Abramsky, Z. 1986: Centrifugal community organization. *Oikos* **46**, 339–348.
- Row, J. R. & Blouin-Demers, G. 2006: Thermal quality influences effectiveness of thermoregulation, habitat use, and behaviour in milk snakes. *Oecologia* **148**, 1–11.
- Schulte, P. M., Healy, T. M. & Fangue, N. A. 2011: Thermal performance curves, phenotypic plasticity, and the time scales of temperature exposure. *Integr. Comp. Biol.* **2011**, doi:10.1093/icb/icr097.
- Shine, R. & Madsen, T. 1996: Is thermoregulation unimportant for most reptiles? An example using water pythons (*Liasis fuscus*) in tropical Australia. *Physiol. Zool.* **69**, 252–269.
- Stevenson, R. D., Peterson, C. R. & Tsuji, J. 1985: The thermal dependence of locomotion, tongue flicking, digestion, and oxygen consumption in the wandering garter snake. *Physiol. Zool.* **58**, 46–57.

### **Supporting Information**

Additional supporting information may be found in the online version of this article at the publisher's web-site:

**Appendix 1.** Statistical methods for developing thermal reaction norms for foraging, including Tables A1 and A2.

**Appendix 2.** Statistical tables for analyses of temperature-dependent foraging by Common Garter-snakes, including Tables A3-A8.