Optimal foraging behavior and the thermal neutral zone of *Peromyscus leucopus* during winter: A test using natural and controlled ambient temperatures

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ABSTRACT

Endotherms foraging at temperatures outside of their thermal neutral zone (TNZ) pay an increased energetic cost. We asked if thermally-induced changes in foraging costs influence quitting harvest rate (QHR) of mice. We predicted that mice foraging during the winter would have a higher QHR in more costly colder conditions. We conducted our study with wild caught *Peromyscus leucopus* in an enclosure located in West Terre Haute, Indiana. We assayed changes in QHR using the forager's giving up density (GUD), which is the amount of uneaten seeds reaming in a tray after foraging activity. Each night from January 12th to March 13th, we assigned 4 trays as "cold trays" (at ambient temperature), and 4 trays as "hot trays" (trays with a ceramic heat element that increased the temperatures of feeding trays ca. 10–15 °C). GUDs (and therfore QHRs) increased as a function of decreasing ambient temperature. Furthermore there was an interaction between tray temperature and ambient temperature; namely, on cool nights mice had lower GUDs in the "hot trays", but on warm nights mice had lower GUDs in the "cold trays". The TNZ for *P. leucopus* actively foraging during winter may be closer to the environmental average temperature than typically measured in the laboratory. Overall, these results support the idea that QHR is related to an animal's foraging in thermally challenged conditions. We present a unique way of measuring an animal's TNZ in the field using behavioral indicators.

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1. Introduction

There are many models which demonstrate, or assume, that animals should be energy rate maximizers (McNamara et al., 2001). In these models an animal pays an energetic cost to harvest a resource, while gaining the benefit of the energy from that harvested resource. The best decision for an animal is to forage such that its net energetic gain during some time frame is maximized. By incorporating information on the environment into decision making processes, an optimal forager is able maximize its time and energy investment and ultimately its fitness. One environmental parameter that could influence optimal foraging decisions, but has not been thoroughly examined empirically, is ambient temperature (T_a).

Brown's (1988) giving up density (GUD) model can be used to predict an animal's patch use as a function of temperature. In the model animals have diminishing returns to energetic gain as food items are removed from a patch. These diminishing returns result from an increased search time per food item as resource density decreases. An animal should quit foraging a patch when its harvest rate equals the sum of the costs of (1) predation, (2) energetic expenditure, and (3) missed opportunity. The animal quits foraging at a given harvest rate referred to as the quitting harvest rate QHR (Charnov, 1976); the GUD is, therefore, a surrogate for a QHR. In Brown's (1988) model the energetic cost of foraging is the additional energetic costs (above and beyond its basic metabolic energetic cost) an animal incurs when being active. If we consider only energetic costs, an animal should quit foraging a patch when its energetic cost of foraging equals its energetic gain. Therefore, if an animal's energetic cost of foraging increases, the animal's net energetic gain decreases, and the model predicts that an animal should have a higher GUD.

Temperature can affect the energetic costs of foraging for an endotherm (Huey, 1991; McNab, 2002), and ambient temperatures during foraging are often above or below its thermal neutral zone (TNZ). At such temperatures the animal will incur additional

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bioenergetic costs stemming from thermoregulation. Therefore, when an endotherm is outside its thermal neutral zone its cost of foraging is higher and it should have a decreased net energetic gain per unit time. An endotherm foraging at temperatures further from its thermal neutral zone should quit foraging sooner (higher QHR) and have higher GUDs.

Many studies have evaluated the influence of temperature on foraging behavior (e.g. Webster and Dill 2007; Druce et al., 2006; Bacigalupe et al., 2003; Boziinovic and Vasquez, 1999; Huey, 1991). Yet few studies have done this in the context of optimal foraging and QHRs (Falcy and Danielson, 2013; Vickery et al., 2011; Orrock and Danielson, 2009; Druce et al., 2006; Kilpatrick, 2003; Meyer and Valone 1999; Kotler et al., 1993; Bowers et al., 1993).

We tested the energetic component of Brown's (1988) model. Specifically we predicted that *P. leucopus* GUDs would be negatively correlated with increasing ambient temperature for mice forging during winter. Also mice should have lower QHR in artificially warmer patches (ca. 10–15 °C) because the reduction in resting metabolic rate represents a ca. 25–40% decrease in the energetic cost of maintenance for *P. leucopus* (Deavers and Hudson, 1981).

2. Methods

This study was conducted at the Indiana State University Kieweg Woods Research Station in West Terre Haute, Indiana. The experiment was carried out from January 12th 2008 to March 13th 2008. During October 2007 we placed 14 wild-caught *P. leucopus* in 8 m × 9 m outdoor steel-walled enclosure located in the woods. The enclosure contained a large central brush pile, 16 nest boxes, and 4 wooden trellises (1 m tall, 1.33 m cover board). Eight of the nest boxes were heated with a small reptile heat rock to ensure that the mice had adequate locations for thermoregulation during the day. These 8 boxes did not get warmer than boxes where mice huddled (personal observation). One month prior to the start of the experiment the mice were fed (millet, small amounts of sunflower seeds, and peanuts) from seed trays located under the trellises. Two weeks prior to the start of the experiment we placed the seed trays in the experimental bins (see below). One week prior to the start of the experiment the diet was switched to millet only. *Peromyscus leucopus* (Lewis et al., 2001) and the closely related *Peromyscus maniculatus* (Vickery et al., 1994) eat about 2–3 g of food per day. The *P. leucopus* in this study ate about 3 g of millet per day (personal observation).

Each foraging station was located under a wooden trellis and consisted of 2 upside down opaque storage bins (dimensions 55 × 35 × 33 cm^3) with 3 entry holes at the bottom. The foraging stations were arranged in a square and each station was 2–3 m apart. The bins at each forging station were 10 cm apart. In each bin was a seed tray (a disposable metal turkey baking pan 50 × 31 × 9 cm^3) with 6.1 g of millet mixed evenly in 4 L of sand. The density of millet in sand was much lower than many other experiments using *Peromyscus* (references in Verdolin (2006)) and provided the mice with rapidly diminishing returns during foraging. Four of the bins were "hot" and 4 of the bins were "cold". The hot bins had a ceramic, "no-light", heat elements mounted to the interior of the bin roof, whereas the cold bins had a sham element mounted on the interior of the roof. The heating elements emitted no visible light but did emit in the infrared spectrum. To our knowledge there is no research demonstrating that mice can see in the infrared wavelength. During the experiment we used 2 tray distributions. In 1 instance each of the 4 stations had 1 hot tray and 1 cold tray. In the other instances 2 stations had 2 cold trays and the other 2 stations had 2 hot trays. Each station had a hot-hot, cold-cold, cold-hot, and hot-cold arrangement ∼15 times. (Note

that tray arrangement did not influence our results). The heat elements were turned on ca. 2 h before dusk every night by an automatic timer. 1 I-Button (Dallas Semiconductor TM) was placed on the side of each bin just above the height of the seed tray to record bin temperature. There were 4 I-Buttons located in the brush pile to measure ambient temperature. Temperatures were measured as the average temperature recorded every hour from 6:30 pm until 7:30 am. The heat elements on average increased the temperature of the hot tray I buttons by an average of 10.25 °C. On several occasions, when the experiment was not running, we placed a mouse sized copper model in the seed trays with and without heat elements for several hours. The models were placed on the surface of the sand in the center of the tray. The measurements taken with copper models suggest the increase in temperature for the mice may have been ca. 15 °C.

Each morning we sifted the remaining seeds and husk from the seed trays. The seeds were given a day to dry (to help remove any stuck sand), and the husks were removed before weighing. The mass of seeds collected was the GUD.

The experiment was run for 59 nights resulting in 472 GUDs (4 hot trays and 4 cold trays per night). For the analysis we natural log transformed GUD +1 values for normality. To avoid psudoreplication for each night we averaged the GUDs in the hot trays and the GUDs in the cold trays for analysis (118 total: 59 hot, 59 cold). Ambient temperatures from the four I-buttons were averaged to determine the nightly ambient temperature. All data were analyzed using JMP version 4.

3. Results

To test the GUD data we used a standard least squares model that included: ambient temperature, tray type (hot or cold), and ambient temperature*tray type (Table 1). We further evaluated these relationships with regressions. GUDs were negatively related to ambient temperature in cold (Log (Cold Tray GUD+1)=0.844–0.054*Average Ambient Temperature; $N=59$; $R^2=0.312$; DF=1,57; $P=0.0001$), and warm (Log (Warm Tray GUD+1)=0.646–0.022*Average Ambient Temperature; $N=59$; $R^2=0.076$; DF=1,57; $P=0.035$) trays (Fig. 1). There was not a significant effect of tray type because there was a significant interaction between tray type and ambient temperature (Table 1, Fig. 1). We explored the exact nature of this interaction by looking at how ambient temperature influenced the difference in GUDs between hot and cold trays on a given night. The interaction was such that as temperature increased, GUDs became relatively higher in the hot trays (Log (Hot Tray GUD+1)–(Log (Cold Tray GUD+1)=0.103–0.031*Average Ambient Temperature; $N=59$; $R^2=0.386$; DF=1,57; $P=0.0001$) (Fig. 2). This relationship is meaningful because on colder nights GUDs were lower in hot trays, but on hot nights GUDs were lower in cold trays.

4. Discussion

Our results support the energetic component of the Brown (1988) GUD model. The fact that mice had lower GUDs in warm

Table 1
General linear model for the listed effects on log GUD+1. See text for details.

Source	DF	SS	F ratio	Prob > F
Temperature Treatment	1,114	0.069	0.603	0.439
Nightly Ambient Temp	1,114	3.047	26.554	< 0.001
Temp Treat*Ambient Temp	1,114	0.522	4.549	0.035