

Effects of temperature on nutrient self-selection in the silverfish *Lepisma saccharina*

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Abstract. Nutrient self-selection represents an important behaviour that has been measured across many taxa. Despite the amount of research on this phenomenon, few studies report the evaluation of the effects of environmental variables such as temperature on nutrient selection by animals. In the present study, the nutrient selections of the silverfish *Lepisma saccharina* L. are measured across a range of temperatures (10, 15, 20, 25, 30 and 35 °C) using feeding arenas with three nutrient choices: carbohydrate (sucrose), protein (casein) and fat (lard). An overall preference for carbohydrates is shown across the range of temperatures, followed by protein, and then fat. However, the proportional consumption of each dietary component changes with temperature; the proportional carbohydrate consumption decreases dramatically with increasing temperature (>94% of the diet at 15 °C but <58% at 30 °C), whereas the proportional protein and lipid consumption increases with increasing temperature up to 30 °C. Changes in nutrient selection with temperature may be related to the dietary requirements of the insect at different temperatures.

Key words. Dietary self-selection, Lepismatidae, metabolism, nutrition, silverfish, Thysanura.

Introduction

Many organisms have the ability to select the quantity and type of nutrients they consume. This phenomenon is known as nutrient (diet) self-selection and has been observed and studied for almost a century (Evard, 1915). Organisms ranging from single-celled protists to vertebrates possess the ability to self-select an optimal diet, suggesting an early evolutionary origin for this phenomenon (Waldbauer & Friedman, 1991). Nutrient self-selection is particularly important in insects because of the potential impacts and benefits for integrated pest management (Waldbauer & Friedman, 1991). Insect taxa that have been examined for nutrient self-selection include ants (Dussutour & Simpson, 2009; Cook *et al.*, 2010), beetles (Waldbauer & Bhattacharya, 1973; Soares *et al.*, 2004), cockroaches (Cohen *et al.*, 1987), flies (Cangussu & Zucoloto, 1995), locusts (Simpson *et al.*, 1990) and moths (Waldbauer *et al.*, 1984). The majority of species investigated are herbivores, with only a few omnivorous or opportunistic feeders being studied.

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Despite these and other studies, little is known about the role of temperature in insect nutrient self-selection. Almost all of the species studied experience either daily or seasonal temperature fluctuations. Despite this, nutrient selection is usually evaluated at a single constant temperature. Coggan *et al.* (2011) demonstrate a direct relationship between the nutritional composition of fixed diets and thermoregulation in *Locusta migratoria*. Nevertheless, the effect of temperature on nutrient selection remains to be evaluated.

Shifts in the nutritional requirements of an organism with temperature are documented. Ants provide an example of a group that regularly shifts its feeding preference depending on the season and colony requirements (Cook *et al.*, 2012). In addition, metabolic studies comparing respiratory quotient ($RQ = CO_2/O_2$) across a range of temperatures by Vogt & Appel (1999) and DeVries & Appel (2013) suggest that metabolic substrate may change with temperature. However, it is currently unknown whether a change in metabolic substrate is directly related to a change in diet.

The silverfish *Lepisma saccharina* L. is an urban pest species that often encounters large fluctuations in temperature, both daily and seasonally. Silverfish are often found in close association with humans and can be found in bathrooms, basements and attics (Meek, 2011). Silverfish can survive a wide range of

temperatures for extended periods without feeding (Sweetman, 1939). They feed on a wide variety of foods with a general preference for starchy materials, although they are reported to feed on a number of different items, including sugars, starches, cellulose, glue (book bindings), linens, silk, other dead insects and even each other (Sweetman, 1939; Rust & Millard, 2009; Meek, 2011; Sims & Appel, 2012).

In response to the limited information on the effects of temperature on nutrient self-selection, a comprehensive study of the effects of temperature on nutrient self-selection is necessary. In the present study, silverfish consumption of three main nutrient classes (carbohydrates, protein, and fat) is measured across a range of temperatures (10, 15, 20, 25, 30 and 35 °C). The data obtained are used to compare the rate of consumption and the proportion of each nutrient in the diet across all temperatures.

Materials and methods

Experimental animals

Silverfish were obtained in 2010 from a laboratory colony where they had been reared for > 20 years. Colonies were housed in 19-L plastic containers (40 × 28 × 17 cm³; VWR International, Radnor, Pennsylvania) at 25 ± 2 °C and under an irregular photoperiod varying from 8 to 12 h of light per day. Colonies were fed dried oatmeal (The Quaker Oats Company, Chicago, Illinois) and pieces of Purina dog chow (Nestle Purina Pet Care, St Louis, Missouri). Each container was filled with shredded paper and corrugated cardboard (various types) along with two 70-mL glass water jars fashioned with lids and a water wick (Absorbal Inc., Wheat Ridge, Colorado). Silverfish weighing > 7 mg were selected at random for testing.

Nutrient self-selection

Nutrient self-selection experiments were conducted in smooth round aluminium pans with vertical sides (diameter 23 cm, height 5 cm). Within each pan were three hexagonal plastic weighing boats (64 × 51 mm; VWR International), two pieces of cardstock paper folded into tents for harbourage (20 cm²) and a piece of water wick (3 cm). Weighing boats were modified by removing one raised end and replacing this with a plastic straw, which was glued into place. This allowed silverfish to easily access each nutrient at the same time as preventing the nutrients from being tracked out of the weighing boats and throughout the pan. The water wick was wetted daily to ensure a continuous supply of water. Each weighing boat contained 100 mg of one of three diets: carbohydrate (sucrose; Walmart Stores Inc., Bentonville, Arkansas), protein (casein; VWR International) and fat (lard; ConAgra Foods, Omaha, Nebraska). Weighing boats with each nutrient were weighed before and after each experiment to determine the amount of each nutrient that was consumed. After the initial set-up, aluminium pans were placed into an incubator at the experimental temperature for 24 h

before the initial weight was taken. Weighing boats within the aluminium pan were then weighed to the nearest 0.01 mg using a Mettler-Toledo AX205 digital balance (Mettler-Toledo GmbH, Switzerland). After the weights were recorded, 20 silverfish weighing > 7 mg each were placed into the pan, and the pans were returned to an incubator at one of six temperatures (10, 15, 20, 25, 30 and 35 °C). Temperatures were tested in a completely randomized order, and 10 replicates were performed for each temperature along with two controls. Relative humidity ranged from 6% (35 °C) to 16% (10 °C). The controls were treated identically, except they did not contain any silverfish. Experiments were performed for various periods ranging from 4 to 21 days depending on temperature. All experiments were concluded once total consumption reached a minimum of 7 mg, except at 10 °C where no consumption could be detected after 21 days. Silverfish nutrient consumption was adjusted for any changes in mass measured in the controls for each nutrient.

Statistical analysis

The effect of temperature on total dietary consumption was determined by one-way analysis of variance and the least significant difference test to distinguish the means (SAS Institute, 1985). Individual nutrient consumption for each nutrient (carbohydrate, protein, or fat) was divided by total consumption and multiplied by 100. Using percentages, we compared nutrient selection among the diets at each temperature and among the temperatures for each nutrient using the Kruskal–Wallis analysis of variance on ranks, with individual means compared using the Student–Newman–Keuls method (SPSS, 2002).

Results

Effect of temperature on total consumption

Analysis of variance revealed that temperature had a significant effect on total dietary consumption (carbohydrate + protein + fat; $F_{5,52} = 51.5$, $P < 0.0001$). Total dietary consumption increased with temperature between 10 and 30 °C (Fig. 1). However, at 35 °C, consumption decreased and was significantly less than total consumption at 30 °C and significantly different from all other temperatures (Fig. 1).

Effects of temperature on proportional nutrient selection within temperatures

At 15 °C, proportional carbohydrate consumption was significantly greater than both protein and fat consumption, which were not significantly different from one another ($H_{2,27} = 20.9$, $P < 0.001$) (Table 1). At 20 °C ($H_{2,27} = 26.0$, $P < 0.001$), 25 °C ($H_{2,27} = 25.8$, $P < 0.001$), 30 °C ($H_{2,27} = 24.8$, $P < 0.001$) and 35 °C ($H_{2,27} = 23.5$, $P < 0.001$), proportional consumption was significantly different between all three nutrients (Table 1).

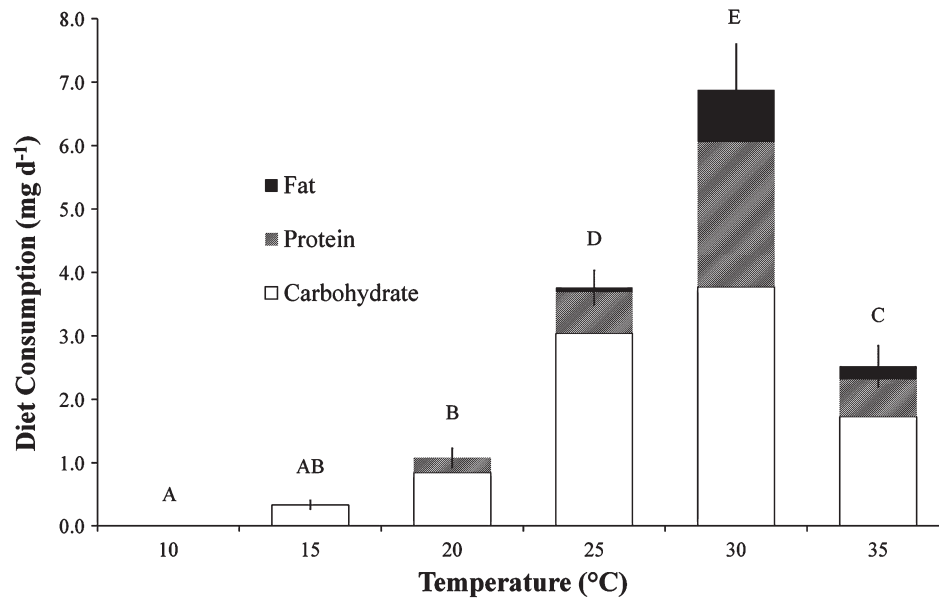


Fig. 1. Total diet consumption (mg day^{-1}) by *Lepisma saccharina* at several temperatures. Diet consumption is also divided into partitions representing each nutrient choice. Means that are significantly different according to the least significant difference test are indicated by different uppercase letters.

At these temperatures, carbohydrates represented the highest consumption, followed by protein, and then fat.

Effects of temperature on proportional nutrient selection across temperatures

Finally, the proportional consumption of each nutrient was compared individually across all temperatures. Despite carbohydrates being the predominant dietary component across all temperatures (>57% of diet at all temperatures), a significant difference in proportional consumption of carbohydrates across the measured temperature range was found ($H_{4,45} = 24.0$, $P < 0.001$). Proportional carbohydrate consumption was lowest at 30 °C (57.1%) and greatest at 15 °C (94.2%), with no significant difference at 20, 25 and 35 °C (Table 1). Proportional protein consumption also differed among temperatures ($H_{4,45} = 27.9$, $P < 0.001$). Proportional protein consumption was significantly different among all temperatures, except 20 and 25 °C (Table 1). The greatest proportional protein consumption occurred at 30 °C (32.1%) (Table 1), and the lowest

occurred at 15 °C (4.7%) (Table 1). Proportional fat consumption also differed among temperatures ($H_{4,45} = 28.9$, $P < 0.001$). Proportional fat consumption was significantly different among all temperatures, except 15 and 20 °C (Table 1). The greatest proportional consumption occurred at 30 °C (10.8%), and the lowest proportional consumption occurred at 20 °C (0.5%) (Table 1).

Discussion

Total nutrient consumption follows the expected pattern for ectothermic species, namely increasing with temperature (Scriber & Lederhouse, 1983; Reynolds & Nottingham, 1985; Levesque *et al.*, 2002). The pattern observed in total consumption correlates strongly with life-history data on silverfish (Sweetman, 1939). Sweetman (1939) reports the preferred temperature range of the silverfish to be between 22 and 27 °C, at the same time finding that survival and reproduction continued up to 32 °C, although at reduced rates. This suggests that thermal stress does not occur until above 32 °C, likely

Table 1. Mean \pm SE percentage consumption of carbohydrates (sucrose), protein (casein) and fat (lard) by the silverfish *Lepisma saccharina* at different temperatures.

Diet	Temperature (°C)					
	10	15	20	25	30	35
Carbohydrate	–	94.2 \pm 3.0 ^{A,a}	78.4 \pm 4.3 ^{B,a}	78.6 \pm 3.8 ^{B,a}	57.1 \pm 3.2 ^{C,a}	69.0 \pm 3.4 ^{B,a}
Protein	–	4.7 \pm 2.6 ^{A,b}	21.1 \pm 4.0 ^{B,b}	19.6 \pm 3.8 ^{B,b}	32.1 \pm 2.2 ^{D,b}	24.5 \pm 3.3 ^{C,b}
Fat/lipid	–	1.1 \pm 0.6 ^{A,b}	0.5 \pm 0.4 ^{A,c}	1.8 \pm 0.5 ^{B,c}	10.8 \pm 2.2 ^{D,c}	6.5 \pm 3.6 ^{C,c}

Ranks that differ significantly according to the Student–Newman–Keuls test are indicated by different uppercase letters for each nutrient across temperatures, and by different lowercase letters across nutrients within each temperature.

leading to the decreased consumption rates observed at 35 °C. Even though 30 °C falls outside of the thermal temperature preferences described by Sweetman (1939), it is still within the upper limits of reproduction and survival. Despite the peak in total consumption at 30 °C, the observed increase is still less than would have been expected based on the rate of increase of total consumption from 15 to 25 °C and the known rate of change in metabolism for a 10 °C change in temperature ($Q_{10} = 2.07$; DeVries & Appel, 2013). Therefore, it is possible that, despite the increase in total consumption, these silverfish are still experiencing a moderate amount of heat stress leading to a decrease in total consumption compared with that expected at 30 °C. It should also be noted that, at 10 °C, silverfish show several unique behaviours that are not observed at any other temperatures. These behaviours include little to no movement when agitated with a probe and random dispersal throughout the arena (not under the paper harbourages) (Z. DeVries, unpublished observations). This suggests that these silverfish may lack adaptations to cold temperatures (Zachariassen, 1985; Bale, 1996). It should also be noted that the relative humidity is lower than that preferred by silverfish; however, all insects have continual access to water throughout the experiments, making desiccation of little importance and reducing the impact of low relative humidity.

In addition to the observed changes in total consumption, the present results show that the ratio of nutrients selected changes with temperature. To our knowledge, a change in nutrient selection with temperature is not reported previously for insects. Also, when assessed alongside work by Coggan *et al.* (2011), these results demonstrate that insects not only thermoregulate in response to changes in the nutritional composition of a diet, but also can select the optimal nutrient composition of their diet for a specific temperature.

By assessing the life history and ecology of silverfish, the change in nutrient selection across temperatures can be better understood. At all temperatures, carbohydrates are the predominant dietary component. Carbohydrates are extremely useful for energy production and much easier to convert into energy (ATP) than either protein or fat as a result of the direct pathways of conversion (Chapman, 1998; Moyes & Schulte, 2008). At colder temperatures, such as 15 °C and below, silverfish may have limited needs for both protein and fats because they will have almost no growth (moulting), and reproduction will be extremely limited, with 15 °C estimated as the lower threshold for development (Sweetman, 1939). Selection of carbohydrates likely decreased in favour of protein and fat at 30 °C because of the increased use of these nutrients for growth, development and reproduction at this temperature. Selection of carbohydrates likely increases from 30 to 35 °C because growth, development and reproduction do not occur at temperatures >32 °C (Table 1) (Sweetman, 1939).

Protein is generally used to generate amino acids after digestion, and these in turn are used for future protein production (Chapman, 1998). Without proper protein consumption, basic insect biological functions, such as moulting, growth and development, would cease (Chapman, 1998). However, many of these functions are greatly reduced in silverfish at 15 °C, which is likely why protein consumption is only 4.75% at

this temperature. However, because temperature increases, protein consumption increases to a maximum at 30 °C, a temperature where rapid growth and development occurs (Table 1) (Sweetman, 1939). However, at 35 °C, there is a decline in protein consumption coupled with an increase in carbohydrate consumption, likely as a result of the decline in growth and development and the biological drive for silverfish to escape environments with temperatures >32 °C (Sweetman, 1939).

Fats are used for cell membrane construction and long-term energy storage, although they are not always essential for survival (Chapman, 1998). Although fats are not necessarily essential for survival, the fat provided experimentally (lard) also contains some cholesterol. Cholesterol forms the backbone of ecdysone, making it a required nutrient, especially during times of rapid growth and development (Chapman, 1998). The non-essential nature of fats/lipids and cholesterol at extreme temperatures where little growth, development or reproduction occurs likely leads to their relatively low consumption at these temperatures. The fat consumption pattern follows a similar pattern to that of protein, indicating that they are primarily utilized in growth, development and reproduction, comprising physiological processes that are limited at extreme temperatures.

The physiological mechanisms behind these switches are not yet understood; however, it is possible that the change in nutrient selection occurs in response to a change in enzyme activity levels. Different enzymes function at different optimum temperature levels (Chapman, 1998; Moyes & Schulte, 2008). Therefore, it is possible that the enzymes involved in metabolism of different nutrients (carbohydrates, proteins, fats) have adapted to different temperature ranges in which they are best suited to be active. This difference in enzyme functionality would ensure that energy is allocated only to those enzymes necessary for survival. In addition to this hypothesis, the changes in nutrient selection could also be linked to the activity of the microbial symbionts associated with silverfish. In a related thysanuran species, Woodbury & Gries (2013) report that the firebrat *Thermobia domestica* (Packard) is associated with two microbial symbionts (*Enterobacter cloacae* and *Mycotypha microspora*) providing a growth and development benefit to firebrats living under nutrient poor environments. Considering this, it is also likely that silverfish possess similar microbial symbionts, and thus silverfish nutrient preference may be linked to the temperature-dependent proliferation and food-processing performance of their symbionts.

Comparing the results of the present study with those of DeVries & Appel (2013) reveals that whole body metabolism apparently does not drive nutrient selection. Respiratory quotients measured by DeVries & Appel (2013) indicate an increased fat metabolism at colder temperatures; however, the results of the present study show a decrease in the proportion of the diet that fat comprises at colder temperatures. Several studies show that RQ changes with temperature, although the present study is the first to provide evidence showing that nutrient selection does not immediately change to match the observed changes in metabolic substrate (Vogt & Appel, 1999; DeVries & Appel, 2013). These results indicate that there are likely several

complicated metabolic reactions occurring, leading to changes in metabolic substrate that are not immediately accompanied by changes in nutrient selection. The present findings imply that nutrient selection is driven by whatever provides the organism with the greatest fitness benefit at a given temperature, namely energy and survival versus growth and reproduction.

In conclusion, the silverfish *L. saccharina* has the ability to change the nutrient composition of its diet with temperature. Switches in nutrient selection, such as those observed in silverfish, are important to consider when measuring dietary self-selection, especially when changes as small as 5 °C can lead to large changes in nutrient selection (>20% changes). The present study also describes the first example of a change in nutrient selection with temperature. Future studies should investigate the role of temperature and nutrient composition in silverfish control (baits). In addition, future studies should also aim to understand the role of daily temperature shifts, such as those occurring in an attic (i.e., a location where silverfish are often found), on nutrient selection.

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