



# Balancing of lipid, protein, and carbohydrate intake in a predatory beetle following hibernation, and consequences for lipid restoration



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## ABSTRACT

Carnivorous animals are known to balance their consumption of lipid and protein, and recent studies indicate that some mammalian carnivores also regulate their intake of carbohydrate. We investigated macronutrient balancing and lipid restoration following hibernation in the ground beetle *Anchomenus dorsalis*, hypothesizing that carbohydrates might be important energy sources upon hibernation when predator lipid stores are exhausted and prey are equally lean. We recorded the consumption of lipid, protein, and carbohydrate over nine days following hibernation, as the beetles foraged to refill their lipid stores. Each beetle was given the opportunity to regulate consumption from two semi-artificial foods differing in the proportion of two of the three macronutrients, while the third macronutrient was kept constant. When analyzing consumption of the three macronutrients on an energetic basis, it became apparent that the beetles regulated lipid and carbohydrate energy interchangeably and balanced the combined energy intake from the two macronutrients against protein intake. Restoration of lipid stores was independent of the availability of any specific macronutrient. However, the energetic consumption required to refill lipid stores was higher when a low proportion of lipids was ingested, suggesting that lipids were readily converted into lipid stores while there were energetic costs associated with converting carbohydrate and protein into stored lipids. Our experiment demonstrates that carbohydrates are consumed and regulated as a non-protein energy source by *A. dorsalis* despite an expectedly low occurrence of carbohydrates in their natural diet. Perhaps carbohydrates are in fact an overlooked supplementary energy source in the diet of carnivorous arthropods.

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## 1. Introduction

While the concepts of herbivores and carnivores are clear, the assignment of particular animal species to these categories has become increasingly difficult in recent years. Not only are there many species that regularly eat both plant and animal food; it is now recognized that many animals previously considered predators often include plant material in their diet and thus are better considered omnivores (Coll and Guershon, 2002; Wäckers et al., 2005). Many “predators” benefit from including plant material in their diet (Coll and Guershon, 2002; Eubanks and Styrsky, 2005), and this may include species previously seen as strict predators. Thus, feeding strategies may now better be considered a continuum of mixed plant-animal feeding with pure predators

and pure herbivores as the end points, and probably with most species in between. The position of a particular species along the continuum depends on its behavioural and metabolic adaptations and likely varies depending on the availability of plant and animal resource types. This study analyses some of the metabolic adaptations that may allow a predatory carabid beetle to extensively include plant-derived energy sources in its diet and thus contributes to the ongoing reevaluation of predator feeding strategies.

Protein and lipids are the main macronutrient constituents of carnivore diets, and studies of macronutrient balancing in carnivorous animals have therefore almost exclusively focused on these (Mayntz et al., 2005, 2009; Raubenheimer et al., 2007; Jensen et al., 2011, 2012). However, although carbohydrates are ingested in relatively low amounts by strict carnivores, recent studies on cats, dogs, and mink indicate that carbohydrate intake may be regulated independently in addition to lipid and protein intake in these species (Hewson-Hughes et al., 2011, 2013; Jensen et al.,

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2014). Little is known about how invertebrate predators handle carbohydrates relative to lipid and protein, and even in omnivorous animals the effects of the three macronutrients on intake balancing and post-consumptive utilization are little studied. In baboons, carbohydrates and lipids are presumably ingested as substitutable energy sources relative to protein, suggesting that non-protein energy requirements may be fulfilled by either of the two groups of macronutrients or any mix of them (Johnson et al., 2013). However, silverfish were found to vary the proportional self-selection of all three macronutrients substantially depending on temperature, with lipids constituting an increasingly higher proportion of the total energy intake as consumption increased with increasing temperature (DeVries and Appel, 2014).

As animal tissues do contain carbohydrates, the diet of strict carnivores will not be completely devoid of it, and in some cases carbohydrates may provide a substantial supplement to their energy consumption. Raubenheimer and Rothman (2013) found that some insects contain significant amounts of carbohydrate, and obligate insectivores including some carabid beetles would thus have access to significant amounts of carbohydrate in their diet even though it consists of insect prey alone. This carbohydrate could occur as glycogen or as trehalose in the hemolymph (Hahn, 2005). There is also the possibility that insect prey contains undigested carbohydrates in their gut at the point of capture and consumption. This may be the case for sap-sucking and nectarivorous insects like aphids, diptera and others, all of which are potential carabid prey. Unless predators carefully avoid consuming the gut content of their prey they would be likely to ingest carbohydrates that way. As predators are often found to be food limited, these supplements of carbohydrate in the prey may be important contributions to the overall energy budget of predators, although this has received very little attention so far.

The nutritional demands of animals that emerge from hibernation may differ from those at other life-history phases. Before hibernation, animals build up considerable lipid stores, which depending on temperature may be more or less depleted by the end of the winter (Leather et al., 1993). During summer, the lipid store functions as a buffer against starvation and makes the animal more robust against fluctuating food availabilities (Lee and Jang, 2014). Refilling lipid stores therefore has high priority during the first foraging bouts after hibernation (Raubenheimer et al., 2007), while other demands receive increasing priority secondarily as the fat body is restored (Raubenheimer et al., 2007; Jensen et al., 2012). Thus, Raubenheimer et al. (2007) found that with unlimited access to both lipid-rich and protein-rich foods, the predaceous carabid beetle *Anchomenus dorsalis* Pontoppidan strongly selected the lipid-rich food during the first two days of feeding, after which the preference changed.

Carabid beetles are mainly predatory or scavenging carnivores, but several species supplement their diet with small amounts of plant material (Toft and Bilde, 2002). The nutritional benefits accrued by ingesting plant material are uncertain and believed to be due only to attaining water and simple sugars (Toft and Bilde, 2002). However, some carabid clades have specialized as seed predators, i.e. a substantial part of their energy is likely to come from carbohydrates, although some seeds largely consist of lipid and protein. Even predominantly predacious species produce glucosidases (Terra 1990; Terra et al., 1996). Therefore, even if carbohydrates constitute only a small proportion of the diet of predatory carabids, they may possibly be important metabolites for survival during prey scarcity, and carbohydrate consumption by these predatory arthropods might be an overlooked phenomenon.

We analyzed nutrient self-selection and lipid deposition in the ground beetle *A. dorsalis* upon emergence from hibernation, using semi-artificial diets that included both carbohydrates and lipids as non-protein energy sources. Individual beetles were allowed

to self-select their dietary nutrient composition from two available foods in a total of 15 possible dietary combinations. One macronutrient was kept constant within each pair of foods, while the other two macronutrients varied between the two foods. We hypothesized a nutritional role for carbohydrate as a supplementary energy source. We did not expect the beetles to have an independent demand for this macronutrient, and predicted that they would rebuild their lipid stores from carbohydrates and protein with lower efficiency than from lipids. Our results show that *A. dorsalis* in addition to regulating lipid and protein intake also regulate and incorporate carbohydrates in their non-protein vs. protein energy budgets. They also show that the beetles are able to refill their lipid stores from all three macronutrient sources although seemingly at higher metabolic costs when building lipids from carbohydrates or protein than from lipids.

## 2. Methods

### 2.1. Beetles

*A. dorsalis* individuals were collected at Stjær and Løgten near Aarhus, Denmark, during September 2009. The species is a spring-breeder that occurs abundantly in agricultural fields. In autumn adults of the year's generation migrate to aggregate at field edges below stones, where they spend some time (approximately a month) before going deeper into the ground to hibernate. We collected beetles that had aggregated but not yet started hibernation. The animals were kept at 2–3 °C in humid soil but without food in a refrigerator for 1.5–2 months until the experiment started in mid-November. This period was meant to make up for hibernation, so that the animals in our experiment were considered to be in the post-hibernation (and pre-reproductive) phase of their life cycle. Previous studies on nutrient balancing in the species used animals in the same life-history phase (Mayntz et al., 2005; Raubenheimer et al., 2007) or extended experiments into the subsequent reproductive phase (Jensen et al., 2012).

### 2.2. Experimental foods

We prepared semi-artificial foods with different macronutrient ratios based on locust (*Locusta migratoria*) powder (50% of total food mass), which we mixed with varying relative amounts of lipid, protein, and carbohydrate. We used commercial lard as the lipid addition, casein as the protein addition, and an equal mixture of sucrose and dextrin as the carbohydrate addition. The macronutrient contents of all diets are displayed in Table 1. The locust powder was dried, pulverized and sieved through a fine mesh before pure macronutrients were added, and ingredients were then mixed thoroughly to make it impossible for the beetles to pick out certain fractions when feeding. The locusts used as the food basis were reared in a gregarious culture on seedling wheat grass and wheat germ at the Department of Zoology, University of Oxford, and contained approximately 17.8% lipid and 74.5% protein (Raubenheimer et al., 2007; Jensen et al., 2012). The carbohydrate content was estimated to 3.11% by the Anthrone test (van Handel, 1985).

### 2.3. Experimental procedures

The experiment consisted of three series of treatments, one for each of the macronutrient pairs (L vs. P, C vs. P, and L vs. C). All series had five treatments in which the five foods were combined in a standardized way: 1 vs. 3; 1 vs. 4; 1 vs. 5; 2 vs. 5; 3 vs. 5 (Table 1). Due to the different food combinations between treatments the ingested nutrient composition would differ between treatments

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