Journal of Thermal Biology 54 (2015) 5–11

Contents lists available at ScienceDirect

Journal of Thermal Biology

journal homepage: www.elsevier.com/locate/jtherbio

Review

Linking energetics and overwintering in temperate insects ☆

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ARTICLE INFO

Article history:
Received 6 June 2014
Received in revised form
16 July 2014
Accepted 20 July 2014
Available online 24 July 2014

Keywords:
Cold tolerance
Jensen's inequality
Fat reserves
Triglycerides
Metabolic suppression
Diapause

ABSTRACT

Overwintering insects cannot feed, and energy they take into winter must therefore fuel energy demands during autumn, overwintering, warm periods prior to resumption of development in spring, and subsequent activity. Insects primarily consume lipids during winter, but may also use carbohydrate and proteins as fuel. Because they are ectotherms, the metabolic rate of insects is temperature-dependent, and the curvilinear nature of the metabolic rate-temperature relationship means that warm temperatures are disproportionately important to overwinter energy use. This energy use may be reduced physiologically, by reducing the slope or elevation of the metabolic rate-temperature relationship, or because of threshold changes, such as metabolic suppression upon freezing. Insects may also choose microhabitats or life history stages that reduce the impact of overwinter energy drain. There is considerable capacity for overwinter energy drain to affect insect survival and performance both directly (via starvation) or indirectly (for example, through a trade-off with cryoprotection), but this has not been well-explored. Likewise, the impact of overwinter energy drain on growing-season performance is not well understood. I conclude that overwinter energetics provides a useful lens through which to link physiology and ecology and winter and summer in studies of insect responses to their environment.

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1. Introduction

Insects and other ectotherms that overwinter in temperate environments must overcome multiple challenges including low temperatures, water deficit, and energetic drain (Williams et al., in press). Because they are inactive and generally do not feed, the energy stores with which insects enter dormancy must fuel the mechanisms that protect against cold and desiccation, as well as provide for basal metabolism throughout the period when the insect is dormant – which may include parts of autumn and spring, as well as winter (Fig. 1). In the case of insects that metamorphose or develop prior to feeding in the spring, the energy stores remaining after winter must also fuel that development. If the adult stage does not feed (or has restricted nutrition),

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☆This article belongs to the Special Issue dedicated to Prof. Ken Bowler for on-going, long-term contributions to thermal biology : What sets the limit? how thermal limits, performance and preference in ectotherms are influenced by water and energy balance.

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http://dx.doi.org/10.1016/j.jtherbio.2014.07.007
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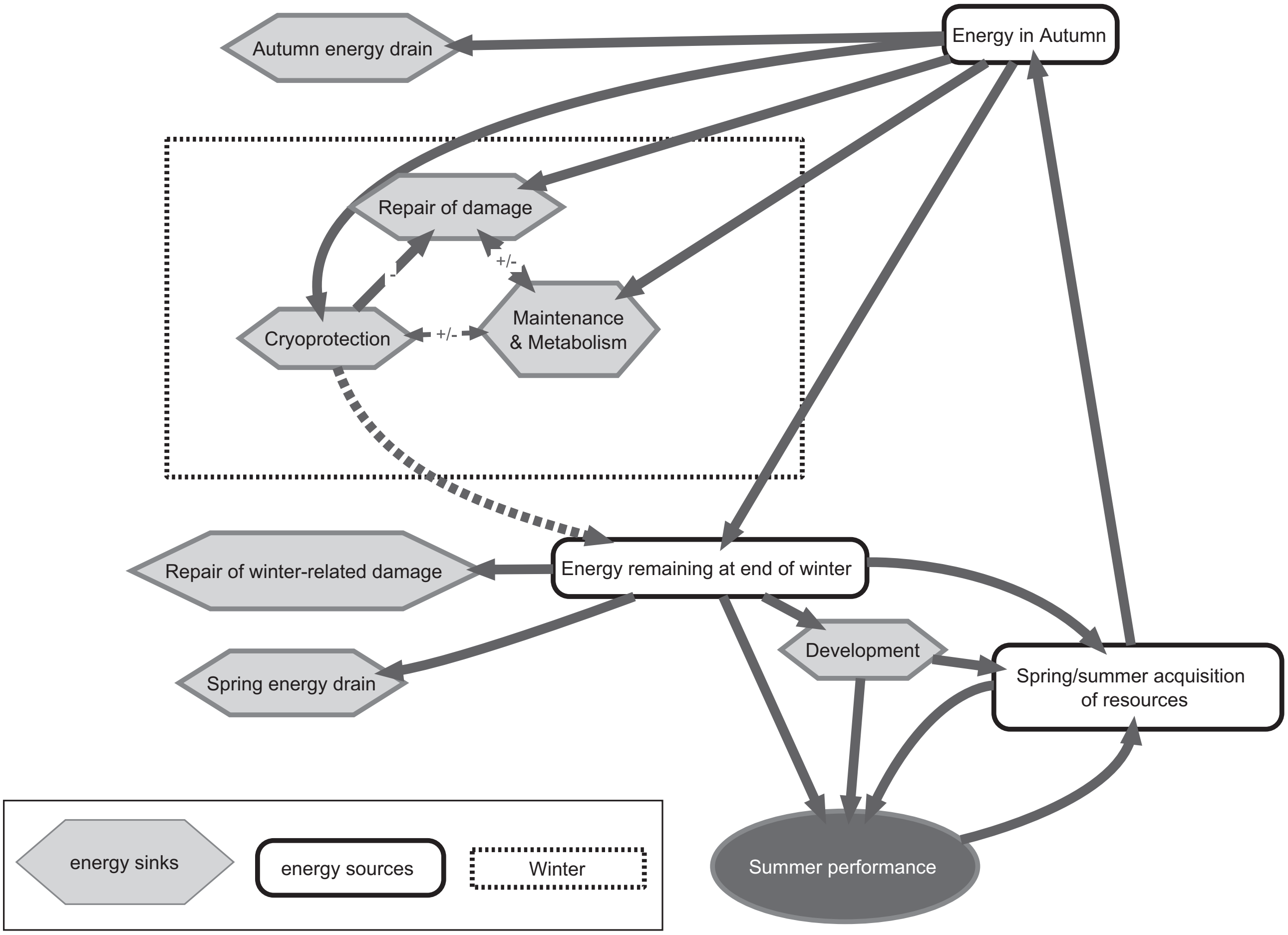

Fig. 1. Schematic of sources and sinks of energy before, during, and after wintering in insects, and how they might link to summer performance (which encompasses reproductive output and fitness). Winter-specific processes are outlined with a dotted box; the dashed arrow from cryoprotection to energy remaining reflects the use of cryoprotectants as a fuel at the end of winter.

remaining energy stores may represent all, or the majority of, the energy available for reproduction. Because ectotherm metabolism is temperature-dependent, the energy remaining at the end of the dormant period is determined by the thermal conditions experienced during winter (and the adjacent portions of autumn and spring), and energy conservation is thus a general requirement of overwintering that transcends variation in microhabitat, cold tolerance strategy and developmental stage. In this mini-review, I will explore the factors that affect overwinter energy use and conservation by temperate insects, with a view to exploring how growing-season fitness might be determined by dormant-season energy use and conservation.

2. Overwinter energy stores

The juvenile stages of many insects have been selected to maximise growth, energy acquisition, and storage to maximise the success of the adult stage (Boggs, 2009). Indeed, pupal mass is often used as a proxy for fitness because larger females are generally more fecund (Honek, 1993). In preparation for winter dormancy, many insects utilise specific energy storage strategies, reviewed in detail elsewhere (Hahn and Denlinger, 2007, 2011). The stores used to fuel metabolism are generally divided between lipid (usually fats in the form of triglycerides) and carbohydrate (often as glycogen, but also as smaller molecules such as the disaccharide trehalose). Many insects also utilise storage proteins (Burmester, 1999); however, although storage proteins do have a role in diapause (Hahn and Denlinger, 2007), they do not appear to be a primary source of energy for overwinter metabolism, and may instead be a route for transfer of amino acids between larval and adult stages (e.g. O'Brien et al., 2002).

Lipids offer the most energy-dense storage, and empirical measurements of body composition support the assumption that most non-feeding insects are consuming lipid (Sinclair et al., 2011). However, insects that are frozen, encased in ice, or in an otherwise hypoxic environment will likely rely on carbohydrate-fuelled anaerobic metabolism (Storey and Storey, 1986). Some species, such as the spruce budworm *Choristoneura fumiferana* rely on carbohydrates over the winter, even when unfrozen (Han and Bauce, 1993), while others switch from lipids to other energy sources mid-winter, possibly cued by diapause cessation (e.g. Adedokun and Denlinger, 1985; Yocum et al., 2005). Insects may shift their fuel use for other reasons; overwintering insects are also water-stressed (Danks, 2000), and could therefore shift to carbohydrate metabolism to liberate water hydrogen-bound to glycogen, as is seen in desiccation-tolerant *Drosophila* (Marron et al., 2003).

3. How do winter conditions drive energy use?

Below the thermal optimum, there is usually a curvilinear relationship between enzyme-mediated biological reactions and temperature (Schulte et al., 2011). Thus, warmer temperatures yield higher rates of activity, development, growth, and

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