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The importance of fat accumulation and reserves for insect overwintering

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Winter is a challenging season for ectothermic species such as insects. In addition to thermal stress imposed by cold temperatures, food scarcity during winter can lead to starvation and energy drain. In preparation for winter, most insects accumulate lipid (fat) reserves, which are the principal source of energetic fuel during overwintering. In this review, we highlight the most recent literature on lipid metabolism in response to cold. We first discuss how lipid metabolism is affected by biotic and abiotic environmental changes in preparation for winter. We then highlight how lipid dynamics are affected during winter, including physiological and (epi)genetic mechanisms. We end our review emphasizing the importance of remaining fat reserves in spring and how climate change can negatively impact lipid metabolism and fitness.

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Introduction

As ectotherms, insect body temperature fluctuates with the temperature of the surrounding environment. During winters in temperate, continental, or polar regions, temperatures can decrease below the range that insects can tolerate, leading to cold injuries that can compromise biological functions [1,2]. Acclimation and adaptations to cold exposure can mitigate potential injuries (e.g. cryoprotectant accumulation, homeoviscous adaptation to maintain proper cell membrane fluidity) [2,3], including dormancy [4,5]. Dormancy responses vary in intensity, obligatory status, and developmental stage and are characterized by a decreased metabolic

activity [4,5]. Diapause, a programmed developmental arrest entered in anticipation of harsh environmental conditions, is common in insects [4]. Diapause is usually associated with physiological changes promoting cold tolerance [2,5,6] and increased lipid reserves through synthesis and accumulation [4,7]. Starvation poses an additional physiological challenge provoked by cold winter temperatures because food is generally scarce; hence, sufficient fat reserves are needed for winter survival. Cold exposures, and particularly winter conditions, thus represent a critical period for insects with strong selective pressures on energy metabolism.

Adequate responses to winter conditions require substantial energetic investment [8,9]. In insects, most energetic reserves are available in the fat body in the form of a lipid (fat) depot. Fat reserves also serve as energetic fuel during periods of food scarcity, and are, therefore, critical for winter survival in many insects. Here, we use lipid and fat interchangeably as synonyms for triacylglycerols. We make a distinction between fatty acid synthesis, with fatty acids being precursors for lipid synthesis, and the buildup of fat stores through accumulation of triacylglycerols (as defined in Ref. [10]). Lipid metabolism has already received attention from the thermal biology community [3,4,7,9]. In this review, we build upon this knowledge highlighting the most recent findings (< 5 years) in the field, focusing on the role of fat reserves for overwintering. Our review is divided into three parts: Preparation for winter, including fat synthesis and accumulation in response to abiotic and biotic cues; Overwintering, including lipid dynamics and underlying physiological and genetic mechanisms; Resumption of activity in spring, including the consequences of remaining fat reserves for fitness.

Accumulation of fat reserves to prepare for winter

Considering the key role fat reserves play for survival during winter, as well as reproduction at the onset of spring (see below), fat content of many insects is expected to increase in anticipation of winter (Table 1). Diapause induction, local adaptation, variation in seasonal conditions (for nondiapausing or field-collected insects), acclimation, and developmental temperature were indeed previously found to lead to substantial fat accumulation (Table 1 and Figure 1).

Table 1
Recent studies investigating fat content and changes in fat reserves in relation to temperature, photoperiod, and diapause in insects.

Factor under study	Environmental cue	Species	Stage	Changes in fat reserves	Reference
Diapause preparation	Photoperiod	<i>Hyphantria cunea</i> (Lepidoptera: Arctiidae)	Pupae	Increase	[11]
Diapause preparation	Temperature + photoperiod	<i>Coccinella septempunctata</i> (Coleoptera: Coccinellidae)	Adults (females)	Increase	[12]
Diapause preparation	Photoperiod	<i>Pieris napi</i> (Lepidoptera: Pieridae)	Larvae and prepupae	No change	[13]
Diapause maintenance	Photoperiod	<i>Aedes aegypti</i> (Diptera: Culicidae)	Egg	Increase	[14]
Diapause maintenance	Photoperiod	<i>Aedes albopictus</i> (Diptera: Culicidae)	Egg	Increase	[15]
Diapause maintenance	Photoperiod	<i>Culex pipiens</i> (Diptera: Culicidae)	Adults (females)	Increase	[16]
Diapause maintenance	Temperature + photoperiod	<i>Enallagma cyathigerum</i> (Odonata, Coenagrionidae)	Larvae	Increase during simulated winter conditions	[17]
Diapause maintenance	Temperature	<i>Rhagoletis indifferens</i> (Diptera: Tephritidae)	Pupae	Increase with increasing cold exposure duration	[18]
Whole diapause program	Temperature + photoperiod (field-collected insects)	<i>Gomphoceris sibiricus</i> (Orthoptera: Acrididae)	Egg	Stable during winter	[19]
Whole diapause program	Temperature + photoperiod (field-collected insects)	<i>Eurytoma plotnikovi</i> (Hymenoptera: Eurytomidae)	Larvae	Increase and then decrease during winter	[20]
Whole long-term diapause program	Temperature + photoperiod (field-collected insects)	<i>Cephalcia chuxiongica</i> (Hymenoptera: Pamphiliidae)	Larvae	Increase and then decrease during diapause	[21]
Whole diapause program	Temperature + photoperiod (field-collected insects)	<i>Culex pipiens</i> (Diptera: Culicidae)	Adults (females)	Increase and then decrease during winter	[22]
Whole diapause program	Temperature + photoperiod (field-collected insects)	<i>Dendrolimus tabulaeformis</i> (Lepidoptera: Lasiocampidae)	Larvae	Increase during winter and increase at spring	[23]
Whole diapause program	Temperature + photoperiod	<i>Leptinotarsa decemlineata</i> ; <i>Chrysolina polita</i> ; <i>Agelastica alni</i> (Coleoptera: Chrysomelidae)	Adults (males and females)	Decrease	[24]
Whole diapause program	Temperature + photoperiod (field-collected insects)	<i>Halyomorpha halys</i> (Hemiptera: Pentatomidae)	Adults (males and females)	Stable during winter	[25]
Local adaptation to colder (northern) environment	Different latitudes	<i>Aphelinus mali</i> (Hymenoptera: Aphelinidae)	Larvae	Increase	[26]
Local adaptation to colder environment	Different altitudes	<i>Canthon rutilans cyanescens</i> and <i>Dichotomius sericeus</i> (Coleoptera: Scarabaeidae)	Adults	Increase	[27]
Natural changes between microclimates	Temperature + photoperiod (field-collected insects)	<i>Belgica Antarctica</i> (Diptera: Chironomidae)	Larvae	Does not change with temperature	[28]
Natural seasonal changes	Temperature + photoperiod (field-collected insects)	<i>Streltziella insularis</i> (Lepidoptera: Cossidae)	Larvae	Increase and then stable during winter	[29]
Natural seasonal changes	Temperature + photoperiod (field-collected insects)	<i>Evergestis extimalis</i> (Lepidoptera: Pyralidae)	Larvae	Stable during winter and increase at spring	[30]
Natural seasonal changes	Temperature + photoperiod (field-collected insects)	<i>Acanthococcus lagerstroemiae</i> (Hemiptera: Ericococcidae)	Nymphs	Increase in autumn and then decrease during winter	[31]
Acclimation	Temperature	<i>Orius majusculus</i> (Hemiptera: Anthocoridae)	Adults (females)	Increase	[32]
Acclimation	Temperature	<i>Gaeolaelaps aculeifer</i> (Acari: Mesostigmata: Laelapidae)	Adults (females)	Increase	[32]
Acclimation	Temperature + photoperiod	<i>Drosophila suzukii</i> (Diptera: Drosophilidae)	Adults (females)	Increase	[33]

Table 1 (continued)

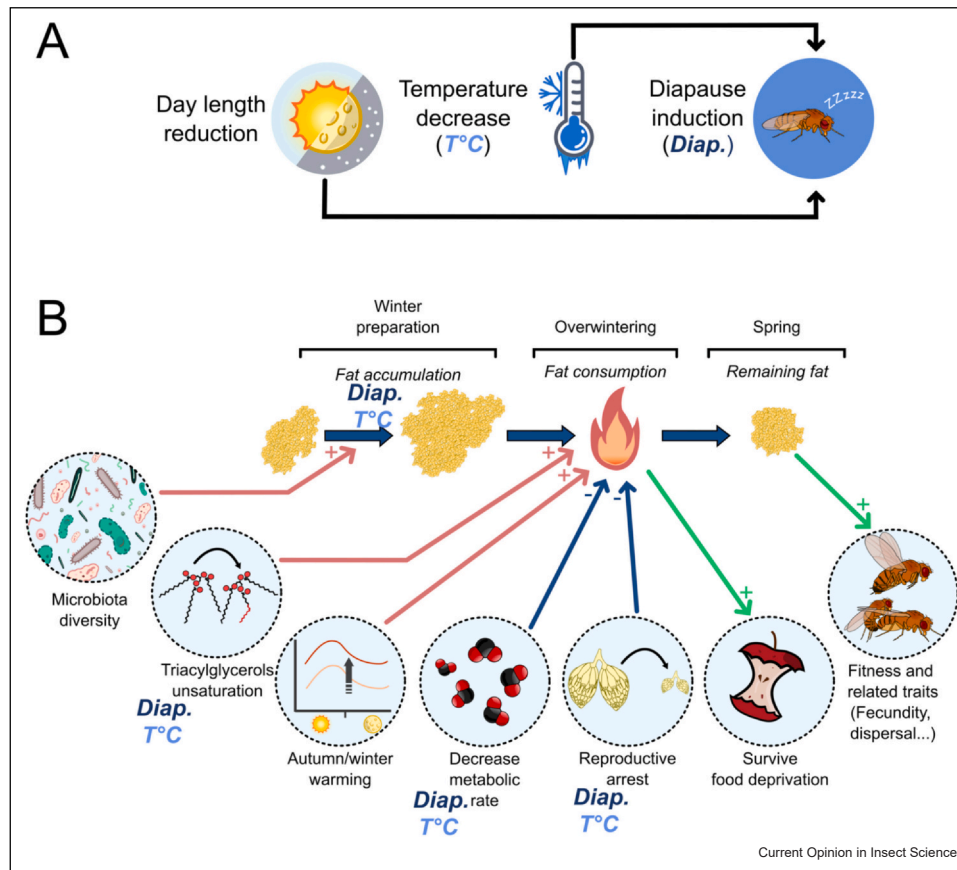
Factor under study	Environmental cue	Species	Stage	Changes in fat reserves	Reference
Developmental temperature	Temperature + photoperiod and geographic origin of the population	<i>Aphidius ervi</i> (Hymenoptera: Braconidae)	Adults (males and females)	Increase	[34]
Developmental temperature	Temperature	<i>Acyrtosiphon pisum</i> (Hemiptera: Aphididae)	Adults (females)	Increase	[35]
Developmental temperature	Temperature + photoperiod	<i>Aphidius platensis</i> (Hymenoptera: Braconidae)	Adults (males and females)	Increase	[36]

Several genes and enzymes are involved in lipid synthesis and accumulation before overwintering (Table 2). In the ladybird beetle *Coccinella septempunctata*, for example, expression of four genes involved in fatty acid metabolism was found to be the highest during the diapause preparation phase, while lowering near the end of diapause. These genes are involved in fatty acid synthesis, oxidation, and elongation and by knocking down their expression (using RNA interference) fat accumulation before diapause decreased [37]. A substantial increase in fatty acid synthesis can further be indicative of triacylglycerol synthesis and accumulation, as in *C. septempunctata* [12,37]. This may, however, not always be the case [10], for example, when fatty acids are synthesized in insufficient quantities for use in triacylglycerol synthesis. In the aphid *Acyrtosiphon pisum*, differences in fat accumulation were not associated with acetyl-CoA carboxylase activity (initiating the first committed step of fatty acid synthesis) nor with fatty acid synthase activity [35]. The increase in lipid reserves in diapausing aphids could rather result from energetic sparing due to arrest of reproductive functions [35] (Figure 1).

In addition to temperature, many insects use photoperiod to anticipate stressful conditions. In the cabbage beetle *Colaphellus bowringi*, for example, proteomics revealed that diapause induction in response to photoperiod led to an increase in enzymes associated with lipid metabolism. Fatty acid-binding protein levels, involved in lipid trafficking and signaling, were higher in diapause-destined females. Knockdown of the associated gene indeed reduced lipid accumulation, and, interestingly, decreased expression of two heat-shock proteins [38]. This could suggest a link between lipid metabolism and more general responses to thermal stress. Overall, the genes and enzymes listed in Table 2 belong to a variety of metabolic pathways highlighting that insects can have different metabolic strategies to achieve the same goal: fat synthesis and accumulation to prepare for overwintering.

Factors other than temperature or photoperiod can affect fat accumulation. In female *Culex pipiens* mosquitoes, endosymbiotic interactions were found to be essential for fat accumulation during diapause preparation. When microbiota diversity and quantity were lowered (almost absent), fat accumulation and the buildup of reserves were impeded, even though the expression of fatty acid synthesis genes was not [43] (Figure 1). Another example is the Antarctic midge, *Belgica antarctica*, where changes in fat content depend on microhabitat conditions. These changes are not driven, however, by microclimatic conditions in terms of temperature. Instead, food abundance, which can vary greatly between microhabitats, is the main driver of fat metabolism, where midges from food-rich habitats generally have a higher fat content [28]. These two examples emphasize that

Figure 1



Graphical representation of recent research (< 5 years) on fat metabolism in relation to cold temperatures and diapause. **(a)** Fat metabolism can be directly impacted by cold temperatures, but also by dormancy, which is initiated in response to changes in photoperiod, temperature, or both (see Table 1 for an overview of recent studies). **(b)** Fat reserves are accumulated in preparation for winter and serve as energetic fuel during prolonged cold exposures for the maintenance of biological functions. Red arrows indicate how biotic and abiotic factors affect lipid metabolism before and during overwintering. Blue lines show phenotypic responses of the insect that reduce lipid consumption during overwintering. Green arrows show how fat reserves affect other phenotypic traits of the insect. Genes and enzymes involved in lipid synthesis and accumulation in response to cold are presented in Table 2.

complex biotic interactions can impact insect lipid accumulation in preparation for winter.

Among insects, parasitoids that feed on other arthropods during development have a unique lipid metabolism in terms of fat accumulation because most species do not accumulate fat as adults [10]. If no fat can be accumulated to anticipate harsh winter conditions, how do adult parasitoids manage to survive until spring? As overwintering is costly in terms of fat reserves (see below), only the fattest parasitoids are expected to survive. In anticipation of winter, parasitoids could thus carry over larger amounts of fat from their host, for example, by exploiting larger hosts or through more efficient lipid scavenging. In aphid parasitoids, several studies indeed revealed that more fat is carried over from the host in response to colder temperatures, such as in *Aphidius ervi*

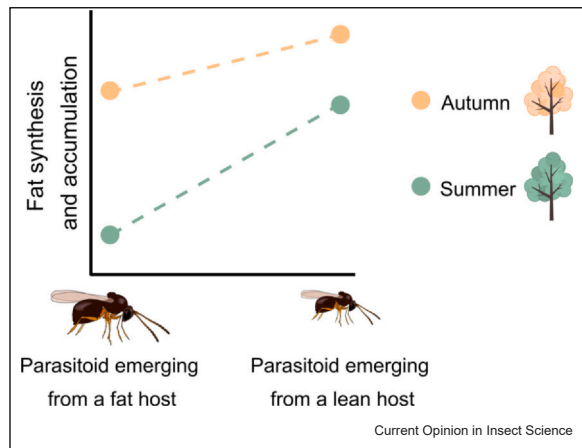
[34] and *Aphidius platensis* [36]. Although the latter species did not seem to go into diapause, individuals originating from locations with the coldest winter conditions were the largest and contained most fat. This suggests potential local adaptation and plasticity in response to winter climatic conditions [36].

Fat synthesis and accumulation of the amber wasp *Leptopilina heterotoma* depend, as in most insects, on the environmental temperature. Females accumulate more fat as an adult when reared at a lower developmental temperature (20 compared with 23°C) [44]. What distinguishes *L. heterotoma* from other insects and most parasitoids is that this species shows extreme plasticity in fat synthesis and accumulation [10,45]. When development occurs on a fat host (i.e. a *Drosophila* larva), adults emerge with high fat reserves and generally do

Table 2
Studies focusing on genes and enzymes involved in the lipid metabolic response to diapause or changes in temperature.

Adaptation	Gene/enzyme	Species	Stage	Changes in fat reserves	Metabolic role	Reference
Diapause induction	Lipases (enzymes)	<i>Hyphantria cunea</i> (Lepidoptera: Arctiidae)	Pupae	Increase	Increased fat content in diapause-destined larvae is associated with increased lipase activity (involved in acylglycerol catabolism).	[11]
Diapause induction	<i>Cathepsin L</i> (gene)	<i>Coccinella septempunctata</i> (Coleoptera: Coccinellidae)	Adult	Increase	<i>Cathepsin L</i> expression increases during diapause preparation. Involved in lipid accumulation through regulation of <i>fatty acid synthase 2</i> .	[12]
Diapause induction	Acetyl-CoA carboxylase (Acc); long-chain fatty acid-CoA ligase (AclI); elongase of very-long-chain fatty acids (Elo); very-long-chain 3-oxoacyl-CoA reductase (Kar) (genes)	<i>Coccinella septempunctata</i> (Coleoptera: Coccinellidae)	Adult	Increase	Knockdown decreases fat accumulation.	[37]
Diapause induction	Fatty acid-binding protein (FABP) (enzyme)	<i>Colaphellus bowringi</i> (Coleoptera: Chrysomelidae)	Adult	Increase	Knockdown decreases fat accumulation.	[38]
Diapause maintenance	Desaturase1 (<i>Desat1</i>); lipid storage droplet proteins 1 and 2 (<i>Lsd1</i> , <i>Lsd2</i>); fatty acyl-CoA reductase 1 (<i>Far1</i>); <i>fatty acid hydroxylase domain-containing protein 2</i> ; <i>3-hydroxyacyl-CoA dehydrogenase type-2</i> ; <i>acyl-coa-binding protein</i> ; <i>fatty acid synthase (Fas)</i> ; <i>acetyl-CoA carboxylase (Acc)</i> ; <i>sterol O-acyltransferase 1</i> ; <i>stearoyl-Coa desaturase 5</i> ; <i>fatty acid synthase-like</i> ; <i>fatty acyl-Coa reductase</i> ; very-long-chain fatty acid — CoA ligase <i>bubblegum (bgm)</i> ; <i>acetyl-CoA carboxylase X1</i> and <i>2 (Acc X1; Acc X2)</i> ; <i>acetyl-CoA acetyltransferase (Acat8)</i> (genes)	<i>Trichogramma dendrolimi</i> (Lepidoptera: Tortricidae)	Prepupae	Increase	RNAseq revealed 17 genes involved in lipid metabolism were upregulated in response to diapause.	[39]
Diapause maintenance	Par domain protein 1 (<i>Pdpr1</i>) (gene)	<i>Culex pipiens</i> (Diptera: Culicidae)	Adult	Increase	Regulates circadian clock genes to and <i>noc</i> and is involved in fat accumulation.	[16]
Diapause maintenance	Lipid storage droplet protein 2 (<i>Lsd2</i>) (gene)	<i>Leptinotarsa decemlineata</i> (Coleoptera: Chrysomelidae)	Adult	Increase	Involved in lipid droplet assemblage.	[40]
Diapause maintenance	Acetyl-CoA carboxylase (Acc); lipid storage droplet proteins 1 and 2 (<i>Lsd1</i> ; <i>Lsd2</i>) (genes)	<i>Chrysoperla nipponensis</i> (Neuroptera: Chrysopidae)	Adult	Increase	Diapause is associated with differential expression of more than 2000 genes (RNAseq).	[41]
Diapause maintenance	Glycogen synthase (GlyS) (enzyme)	<i>Culex pipiens</i> (Diptera: Culicidae)	Adult	Increase	Catalyzes glycogen formation. Knockdown results in decreased fat accumulation in diapausing females.	[42]
Acclimation	Acetyl-CoA carboxylase (ACC) (enzyme) Fatty acid synthase (FAS) (enzyme)	<i>Acyrtosiphon pisum</i> (Hemiptera: Aphididae)	Adult	Decrease No change	No link was found with fat accumulation.	[35]

Figure 2



Expected changes in reaction norms of fat synthesis and accumulation in parasitoids subjected to summer (green) or autumn (orange) conditions, when development occurs on fat or lean hosts.

not synthesize and accumulate fat at all. When development occurs on a lean host, adult parasitoids emerge with low fat reserves and synthesize and accumulate substantial lipids *de novo* [45]. Female *L. heterotoma* overwinter as quiescent adults [46]; hence, we expect females to synthesize and accumulate sufficient fat reserves during autumn to prepare for winter (Figure 2). Plasticity is thus expected to decrease, mostly irrespective of host lipid quality (poor or rich), as females should synthesize and accumulate fat to be able to survive during winter, but this remains to be empirically tested.

Metabolism of fat reserves during winter

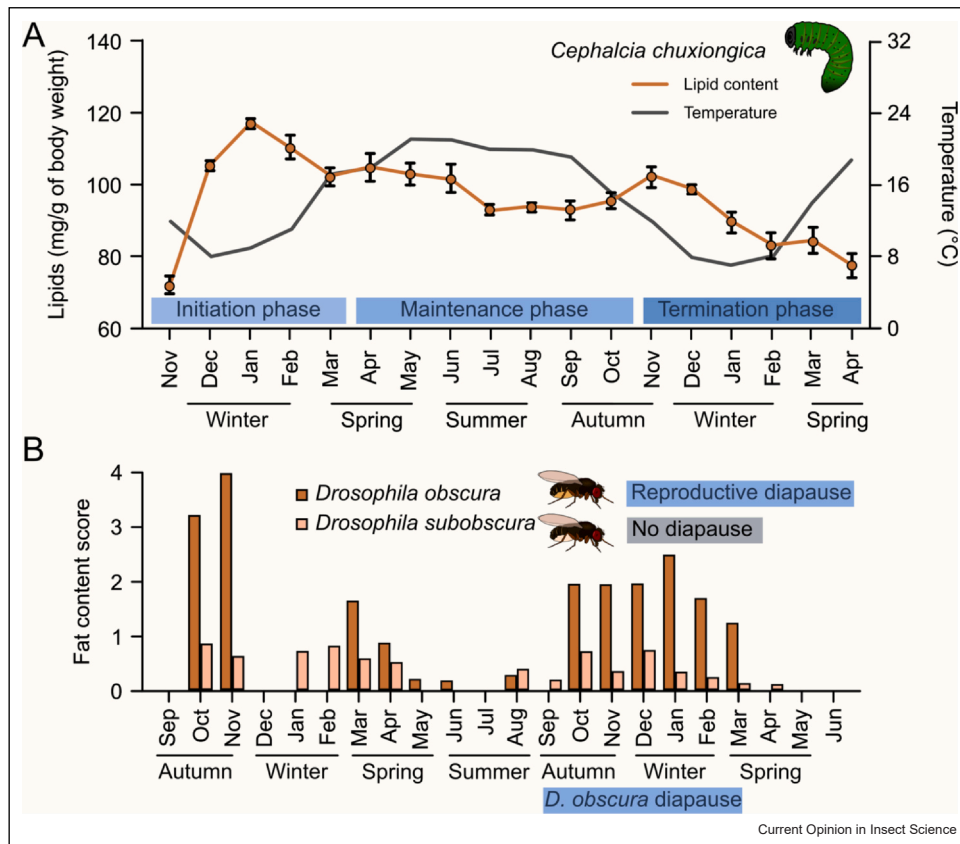
Once fat has been accumulated, reserves are then gradually consumed during winter even if cold exposures are typically characterized by a decreased metabolic rate [9,25,22] (Table 1; Figures 1 and 3). In diapausing species, fat reserves are slowly consumed during diapause maintenance when metabolic activity is the lowest (Figure 3). During the termination phase, metabolic activity increases using lipid stores as fuel [4]. The flesh fly *Sarcophaga crassipalpis* needs to overcome a long diapause period in the pupal stage that is characterized by alternating periods of metabolic suppression and high metabolic activity. Chen et al. [47] showed that such metabolic bursts are regulated by reactive oxygen species (ROS) levels: decreased ROS levels trigger metabolic bursts. Periods of high metabolic activity are characterized by aerobic metabolism of lipids, indicated by an increase in L-acetylcarnitine with carnitine being involved in lipid mobilization (but see Ref. [15] where diapausing mosquito eggs have reduced carnitine levels). Another line of evidence for aerobic lipid metabolism is that the fatty acid palmitate is oxidized via acetyl-CoA during metabolic bursts [47]. ROS likely acts on

adenosine-5'-monophosphate-activated protein kinase, a master regulator of lipid metabolism. In some insects, however, fat levels barely change during winter (Table 1), suggesting that only few lipids are used as metabolic fuel. A drastic lowering of metabolic rate in response to low temperature generally observed in insects [9,25,22] could explain why fat usage is lower during winter in these species (Figure 1).

Epigenetic factors, such as microRNAs (miRNAs), were also found to play a role in lipid metabolism during diapause. miRNAs are major post-transcriptional regulators of gene expression. Batz et al. [49] identified seven miRNAs that were differentially regulated in diapausing pharate larvae of the mosquito *A. albopictus*. Particularly, *miR-14-5p* was downregulated that typically regulates the accumulation of lipids in insects. In another study, Meuti and colleagues [50] showed that in diapausing female *C. pipiens*, 3 miRNAs (*miR-305-5p*; *miR-277-3p*; *miR-14-3p*) linked with fat accumulation were downregulated. As miRNAs are decreasing gene expression, their downregulation during diapause could be linked with an increased activity of lipid metabolic genes. We are only beginning to understand the role of epigenetic factors in regulating lipid metabolism, representing an important avenue for future research.

Many recent studies monitoring the gradual consumption of fat reserves during winter have focused on diapause (Table 1). Numerous insect species do not, however, rely on a true diapause response, but undergo overwintering in a quiescent state, for example, several *Drosophila* flies [48] or parasitoids such as *L. heterotoma* (see above, Figure 2; [46]). Quiescent insects facing cold exposures also rely on fat reserves. In nondiapausing larvae of the lepidopteran *Spodoptera litura*, for example, a shift to a colder temperature (from 27 to 13°C) leads to a concomitant shift in macronutrient usage from carbohydrates to lipids. This decrease in temperature also led to an increase in diacylglycerols, products of triacylglycerol catabolism and the form in which lipids are generally mobilized and transported in insects [51]. The dynamics of fat accumulation and consumption may differ in quiescent compared with diapausing species (Figure 3). As diapause termination is associated with high metabolic activity to resume development, more fat would be depleted during the termination phase of diapause, compared with the end of a quiescent state (Figure 3). For example, the moth *Streltzoviella insularis* does not seem to overwinter in a diapausing state [52] and fat content of overwintering individuals does not seem to vary much [29]. Data showing fat content levels in quiescent species during winter are, however, mostly lacking. It would be interesting to fill this gap of knowledge by tracking fat accumulation patterns in relation to overwintering in more quiescent species. Field-collected *Drosophila* species would be ideal study

Figure 3



Dynamic changes in fat content between an obligatory diapausing species (*Cephalcia chuxiongica* larvae, (a); data from Ref. [48]) and two species showing other types of dormancy (*Drosophila obscura* and *D. subobscura*, (b); data from Ref. [57]). (a) In diapausing species, fat accumulation typically occurs during the initiation phase. Fat reserves are then slowly consumed during diapause maintenance when metabolic activity is the lowest. During the termination phase, metabolic activity increases, using lipid stores as fuel; hence, the increased rate of fat reserve depletion. *C. chuxiongica* larvae go through a prolonged diapause program (20 months), but this pattern can also be observed in species diapausing during a single season (e.g. [10]). (b) In *Drosophila* flies, diapause status differs between species with some species showing developmental diapause, some showing reproductive diapause, and others no diapause at all [54]. *D. obscura* overwinters in reproductive diapause, while *D. subobscura* overwinters as quiescent adults. In these two species, fat reserves increase in preparation for winter, and then decrease at the end of winter and at spring. Diapausing adults from *D. obscura* contain more fat than quiescent adults from *D. subobscura* [57]. Of note is that this older study uses a 'fat content score' to quantify lipid reserves, which may not be as accurate as currently more common colorimetric/gravimetric measures.

systems to link ecological conditions to fat reserves, survival, and reproduction, as *Drosophila* species show a range of different dormancy statuses [48,53] (Figure 3).

Cold temperatures typically rigidify adipocytes in the fat body containing the insect's fat reserves. Fat deposit rigidification can decrease triacylglycerol accessibility by enzymes, thereby hindering lipid metabolism. Consequently, modifications such as homeoviscous adaptation occur also in fat reserves in response to cold temperatures or following diapause induction (Figure 1). Specifically, an increase in unsaturation of fatty acid chains from triacylglycerols has been observed [54,55]. Interestingly, increased unsaturation of triacylglycerols in response to diapause in the moth *Ostrinia nubilalis* was correlated with a decrease in the melting temperature of

the lipid pool [55]. This suggests an increased fluidity of fat reserves at cold temperatures that could be indicative of increased lipid mobilization.

The importance of remaining fat reserves in spring, and putative consequences of climate change

In insects, fat reserve quantities are correlated with fitness and related traits, including fecundity and dispersal: fatter females generally produce more offspring and can disperse further [56]. In the mosquito *C. pipiens*, fat reserves are not entirely consumed during overwintering and actually exceed fat quantities observed in summer females [22]. These fat reserves may be critical to resume activity and reproduction in spring. In the gall fly, *Eurosta solidaginis*, females with the highest energetic

reserves in spring also had the highest fecundity [57]. We know surprisingly little about the conditions under which individuals emerge following winter, even though we can expect intense selection for fatter and more fecund females. More studies on the effect of overwintering conditions on fat reserves and fitness consequences in spring are now needed.

The current climate crisis will have a major impact on insects, where lipid metabolism to changing temperatures could be of critical importance. As temperatures increase during autumn or winter, metabolic rates are expected to increase that could accelerate the depletion of fat reserves, compromising winter survival and fitness in spring (Figure 1). For example, CaraDonna et al. [58] manipulated the nesting temperature of wild diapausing *Osmia ribifloris* bees. By artificially increasing or decreasing the nest temperature in the field, they simulated current and future climatic conditions. While current climatic conditions did not have a major effect on bees, future climatic conditions decreased fat content at emergence at the end of the diapausing period (but see Ref. [59] for an opposite trend in a butterfly). Similarly, in the Antarctic midge *B. antarctica*, simulating a 2°C increase of winter temperature decreased fat content during overwintering [60]. Considering the rate of temperature changes during autumn and winter due to global changes, studying the effects of warmer temperatures on fat reserves will be of importance for predicting species responses to climate change.

Conclusions

Fat reserves are the fuel for insect overwintering; hence, most species build up considerably fat stores in preparation for winter in response to temperature or dormancy induction (Table 1). Several genes and enzymes belonging to diverse metabolic pathways affect lipid metabolism before and during winter in diapausing insects (Table 2), suggesting that different metabolic strategies can be used to regulate fat synthesis and accumulation. Much research effort has been dedicated to diapausing species, but we know only little about the lipid dynamics during overwintering of species with other dormancy strategies (e.g. quiescence, reproductive diapause). Fat accumulation is also affected by factors other than temperature and dormancy, such as microbiota abundance [43] or food abundance among microhabitats [28]. Multiple biotic factors and potential stressors thus interact to affect lipid metabolism for overwintering. We expect that fat reserves at the onset of spring are a major determinant of fitness, but more empirical work is needed to quantify this. Current global changes may fasten fat consumption during autumn and winter following warming [58,60], with negative consequences for insect survival during overwintering and reproductive fitness in spring.

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Data Availability

No data were used for the research described in the article.

Declaration of Competing Interest

No conflict of interest.

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