Insect winter ecology

From Wikipedia, the free encyclopedia

Insect winter ecology entails the overwinter survival strategies of insects, which are in many respects more similar to those of plants than to many other animals, such as mammals and birds. This is because unlike those animals, which can generate their own heat internally (endothermic), insects must rely on external sources to provide their heat (ectothermic). Thus, insects sticking around in the winter, must tolerate freezing or rely on other mechanisms to avoid freezing. Loss of enzymatic function and eventual freezing due to low temperatures daily threatens the livelihood of these organisms during winter. Not surprisingly, insects have evolved a number of strategies to deal with the rigors of winter temperatures in places where they would otherwise not survive.

Contents

Survival strategies

Two major strategies for winter survival have evolved in the Class Insecta due to their inability to generate significant heat metabolically. The first, migration, is a complete avoidance of the temperatures that pose a threat. If an insect cannot migrate, then it must stay and deal with the cold temperatures in one of two ways. This cold hardiness is separated into two categories, **freeze avoidance** and **freeze tolerance**.

Migration

Migration in insects is different than in birds. Bird migration is a two-way, round-trip movement of each individual, whereas this is not usually the case with insects. The short lifespan of insects compared to birds means that the adult that made one leg of the trip will be replaced by a member of the next generation on the return voyage. As a result, invertebrate biologists have redefined migration for this group of organisms as consisting of three parts:

1. A persistent, straight line movement away from the natal area
2. Distinctive pre- and post-movement behaviors
3. Re-allocation of energy within the body associated with the movement

This definition allows for mass insect movements to be considered as migration. Perhaps the best known insect migration is that of the monarch butterfly. The monarch in North America migrates from as far north as Canada southward to Mexico and Southern California annually from about August to October. The population east of the Rocky Mountains overwinters in Michoacán, Mexico, and the western population overwinters in various sites in central coastal California, notably in Pacific Grove and Santa Cruz. The round trip journey is typically around 3,600 km in length. The longest one-way flight on record for monarchs is 3,009 km from Ontario, Canada to San Luis Potosí, Mexico. They use the direction of sunlight and magnetic cues to orient themselves during migration.

The monarch requires significant energy to make such a long flight, which is provided by fat reserves. When they reach their overwintering sites, they begin a period of lowered metabolic rate. Nectar from flowers procured at the overwintering site provides energy for the northward migration. To limit their energy use, monarchs congregate in large clusters in order to maintain a suitable temperature. This strategy, similar to huddling in small mammals, makes use of body heat from all the organisms and lowers heat loss.

Another common winter migrant insect, found in much of North America, South America, and the Caribbean, is the Green Darner. Migration patterns in this species are much less studied than those of monarchs. Green darners leave their northern ranges in September and migrate south. Studies have noted a seasonal influx of green darners to southern Florida, which indicates migratory behavior.[1] Little has been done with tracking of the green darner, and reasons for migration are not fully understood since there are both resident and migrant populations.[1] The common cue for migration southward in this species is the onset of winter.

Freeze avoidance

Lethal freezing occurs when insects are exposed to temperatures below the melting point (MP) of their body fluids; therefore, insects that do not migrate from regions with the onset of colder temperatures must devise strategies to either tolerate or avoid freezing of intracellular and extracellular body fluids. Surviving colder temperatures, in insects, generally falls under two categories: Freeze-tolerant insects can tolerate the formation of internal ice and freeze-avoidant insects avoid freezing by keeping the bodily fluids liquid. The general strategy adopted by insects also differs between the northern hemisphere and the southern hemisphere. In temperate regions of the northern hemisphere where cold temperatures are expected seasonally and are usually for long periods of time, the main strategy is freeze avoidance. In temperate regions of the southern hemisphere, where seasonal cold temperatures are not as extreme or long lasting, the main strategy is freeze tolerance.[2] However, in the Arctic, where freezing occurs seasonally, and for extended periods (>9 months), freeze tolerance also predominates.[3]

Freeze avoidance involves both physiological and biochemical mechanisms. One method of freeze avoidance is the selection of a dry hibernation site in which no ice nucleation from an external source can occur.[4] Insects may also have a physical barrier such as a wax-coated cuticle that provides protection against external ice across the cuticle.[5] The stage of development at which an insect over-winters varies across species, but can occur at any point of the life cycle (i.e., egg, pupa, larva, and adult).

Freeze-avoidant insects that cannot tolerate the formation of ice within their bodily fluids need to implement strategies to depress the temperature at which their bodily fluids will freeze. Supercooling is the process by which water cools below its freezing point without changing phase into a solid, due to the lack of a nucleation source. Water requires a particle such as dust in order to crystallize and if no source of nucleation is introduced, water can cool down to -42°C without freezing. In the initial phase of seasonal cold hardening, ice-nucleating agents (INAs) such as food particles, dust particles and bacteria, in the gut or intracellular compartments of freeze avoidant insects have to be removed or inactivated. Removal of ice-nucleating material from the gut can be achieved by cessation in feeding,[6] clearing the gut and removing lipoprotein ice nucleators (LPINs) from the haemolymph.[7]

And in some species, by the shedding of the mid-gut during moulting.[8]

Overwintering lesser stag beetle larva

In addition to physical preparations for winter, many insects also alter their biochemistry and metabolism. For example, some insects synthesize cryoprotectants such as polyols and sugars, which reduce the lethal freezing temperature of the body. Although polyols such as sorbitol, mannitol, and ethylene glycol can also be found, glycerol is by far the most common cryoprotectant and can be equivalent to ~20% of the total body mass.[9] Glycerol is distributed uniformly throughout the head, the thorax, and the abdomen of insects, and is in equal concentration in intracellular and extracellular compartments. The depressive effect of glycerol on the super cooling point (SCP) is thought to be due to the high viscosity of glycerol solutions at low temperatures. This would inhibit INA activity[10] and SCPs would drop far below the environmental temperature. At colder temperatures (below 0 °C), glycogen production is inhibited, and the breakdown of glycogen into glycerol is enhanced, resulting in the glycerol levels in freeze avoidant insects reaching levels five times higher than those in freeze tolerant insects[11] which do not need to cope with extended periods of cold temperatures.

Though not all freeze avoidant insects produce polyols, all hibernating insects produce thermal hysteresis factors (THFs). A seasonal photoperiodic timing mechanism is responsible for increasing the antifreeze protein levels with concentrations reaching their highest in the winter. In the pyrochroid beetle, ‘’Dendroides canadensis’’, a short photoperiod of 8 hours light and 16 hours of darkness, results in the highest levels of THFs,[12] which corresponds with the shortening of daylight hours associated with winter. These antifreeze proteins are thought to stabilize SCPs by binding directly to the surface structures of the ice crystals themselves, diminishing crystal size and growth.[10] Therefore, instead of acting to change the biochemistry of the bodily fluids as seen with cryoprotectants, THFs act directly with the ice crystals by adsorbing to the developing crystals to inhibit their growth and reduce the chance of lethal freezing occurring.

Freeze tolerance

Freeze tolerance in insects refers to the ability of some insect species to survive ice formation within their tissues. All insects are ectothermic, which can make them vulnerable to freezing. In most animals, intra- and extracellular freezing causes severe tissue damage, resulting in death. Insects that have evolved freeze-tolerance strategies manage to avoid tissue damage by controlling where, when, and to what extent ice forms.[13] In contrast to freeze avoiding insects that are able to exist in cold conditions by supercooling, freeze tolerant organisms limit supercooling and initiate the freezing of their body fluids at relatively high temperatures. Physiologically, this is accomplished through inoculative freezing, the production of ice nucleating proteins, crystalloid compounds, and/or microbes.[14]

Although freeze-avoidance strategies predominate in the insects, freeze tolerance has evolved at least six times within this group (in the Lepidoptera, Blattodea, Diptera, Orthoptera, Coleoptera, and Hymenoptera).[15] Freeze tolerance is also more prevalent in insects from the Southern Hemisphere (reported in 85% of species studied) than it is in insects from the Northern Hemisphere (reported in 29% of species studied). It has been suggested that this may be due to the Southern Hemisphere's greater climate variability, where insects must be able to survive sudden cold snaps yet take advantage of unseasonably warm weather as well. This is in contrast to the Northern Hemisphere, where predictable weather makes it more advantageous to overwinter after extensive seasonal cold hardening.[15]

Examples of freeze tolerant insects include: the woolly bear, *Pyrrharctia isabella;*[16] the flightless midge, *Belgica antarctica;* [17] and the alpine cockroach, *Celatoblatta quinquemaculata*.[18]

Dangers of freezing

With some exceptions, the formation of ice within cells generally causes cell death even in freeze-tolerant species due to physical stresses exerted as ice crystals expand.[19] Ice formation in extracellular spaces is also problematic, as it removes water from solution through the process of osmosis, causing the cellular environment to become hypertonic and draw water from the cell interiors. Excessive cell shrinkage can cause severe damage. This is because as ice forms outside the cell, the possible shapes that can be assumed by the cells are increasingly limited, causing damaging deformation.[20] Finally, the expansion of ice within vessels and other spaces can cause physical damage to structures and tissues.[20]

Ice nucleators

In order for a body of water to freeze, a nucleus must be present upon which an ice crystal can begin to grow. At low temperatures, nuclei may arise spontaneously from clusters of slow-moving water molecules. Alternatively, substances that facilitate the aggregation of water molecules can increase the probability that they will reach the critical size necessary for ice formation.[21]

Freeze-tolerant insects are known to produce ice nucleating proteins.[14] The regulated production of ice nucleating proteins allows insects to control the formation of ice crystals within their bodies. The lower an insects' body temperature, the more likely it is that ice will begin to form spontaneously. Even freeze-tolerant animals cannot tolerate a sudden, total freeze; for most freeze-tolerant insects it is important that they avoid supercooling and initiate ice formation at relatively warm temperatures.[22] This allows the insect to moderate the rate of ice growth, adjust more slowly to the mechanical and osmotic pressures imposed by ice formation.[14][23]

Nucleating proteins may be produced by the insect, or by microorganisms that have become associated with the insects' tissues.[14] These microorganisms possess proteins within their cell walls that function as nuclei for ice growth.[24]

The temperature that a particular ice nucleator initiates freezing varies from molecule to molecule. Although an organism may possess a number of different ice nucleating proteins, only those that initiate freezing at the highest temperature will catalyze an ice nucleation event. Once freezing is initiated, ice will spread throughout the insect's body.[14]

Cryoprotectants

The formation of ice in the extracellular fluid causes an overall movement of water out of cells, a phenomenon known as osmosis. As too much dehydration can be dangerous to cells, many insects possess high concentrations of solutes such as glycerol. Glycerol is a relatively polar molecule and therefore attracts water molecules, shifting the osmotic balance and holding some water inside the cells. As a result, cryoprotectants like glycerol decrease the amount of ice that forms outside of cells and reduce cellular dehydration.[23] Insect cryoprotectants are also important for species that avoid freezing; see description above

Intracellular freezing

Most freeze-tolerant species restrict ice formation to extracellular spaces. Some species, however, can tolerate intracellular freezing as well. This was first discovered in the fat body cells of the goldenrod gall fly *Eurosta solidaginis*.[25] The fat body is an insect tissue that is important for lipid, protein and carbohydrate metabolism (analogous to the mammalian liver).[26] Although it is not certain why intracellular freezing is restricted to the fat body tissue in some insects, there is evidence that it may be due to the low water content within fat body cells.[27]

Locations of hibernating insects

Insects are well hidden in winter, but there are several locations in which they can reliably be found. Ladybugs practice communal hibernation by stacking one on top of one another on stumps and under rocks to share heat and buffer themselves against winter temperatures.[28] The female grasshopper (family Tettigoniidae [long-horned]), in an attempt to keep her eggs safe through the winter, tunnels into the soil and deposits her eggs as deep as possible in the ground.[28] Many other insects, including various butterflies and moths also overwinter in soil in the egg stage. Some adult beetles hibernate underground during winter; many flies overwinter in the soil as pupae. Other methods of hibernation include the inhabitance of bark, where insects nest more toward the southern side of the tree for heat provided by the sun. Cocoons, galls, and parasitism are also common methods of hibernation.

Aquatic insects

Insects that live under the water have different strategies for dealing with freezing than do terrestrial insects. Many insect species survive winter not as adults on land, but as larvae underneath the surface of the water. Under the water many benthic invertebrates will experience some subfreezing temperatures, especially in small streams. Aquatic insects have developed freeze tolerance much like their terrestrial counterparts. However, freeze avoidance is not an option for aquatic insects as the presence of ice in their surroundings may cause ice nucleation in their tissues.[29]:148 Aquatic insects have supercooling points typically around – 3º to – 7°C.[29]:149 In addition to using freeze tolerance, many aquatic insects migrate deeper into the water body where the temperatures are higher than at the surface. Insects such as stoneflies, mayflies, caddisflies, and dragonflies are common overwintering aquatic insects. The dance fly larvae have the lowest reported supercooling point for an aquatic insect at – 22°C.[29]:149

See also

- Overwinter
- Cryobiology

References

1. May, Mike. "Dragonfly Migration". Dept. of Entomology Cook College Rutgers University.
2. Sinclair BJ and Chown SL (2005) Climatic variability and hemispheric differences in insect cold tolerance:

support from southern Africa. Functional Ecology 19:214-221

3. Danks, H.V. (1981). *Arctic Arthropods*. Ottawa, Canada: Entomological Society of Canada. p. 279. ISBN 0-9690829-0-8.
4. Marchand, Peter (1996). *Life in the Cold*. Hanover, NH: University Press of New England ISBN 978-0874517859
5. Duman JG (2001) Antifreeze and ice nucleator proteins in terrestrial arthropods. Annual Review Physiology 63:327-357
6. Olsen TM and Duman JG (1997) Maintenance of the supercooled state in the gut fluid of overwintering pyrochroid beetle larvae, Dendroides canadensis: role of ice nucleators and antifreeze proteins. Journal of Comparative Physiology 167: 114-122
7. Neven LG, Duman JG, Beals JM, Castellino FJ (1986) Overwintering adaptations of the stag beetle, Ceruchus piceus: removal of ice nucleators in the winter to promote supercooling. Journal of Comparative Physiology 156:707-716
8. Worland MR, Leinaas HP, Chown SL (2006) Supercooling point frequency distributions in Collembola are affected by moulting. Functional Ecology 20:323-329
9. Pfister TD and Storey KB (2006) Responses of Protein Phosphatases and cAMP-Dependent Protein Kinase in a Freeze-Avoiding Insect, Epiblema scudderiana. Archives of Insect Biochemistry and Physiology 62:43-54
10. Zachariassen KE (1985) Physiological Reviews: Physiology of Cold Tolerance in Insects. The American Physiological Society 65:799-832
11. Chapman RF (1998). The Insects Structure and Function 4th ed. Cambridge University Press 520-522
12. Horwath KL and Duman JG (1982) Involvement of the Circadian System in Photoperiodic Regulation of Insect Antifreeze Proteins. The Journal of Experimental Zoology 219:267-270
13. Ramlov H (2000) Aspects of natural cold tolerance in ectothermic animals. Human Reproduction 15:26-46
14. Lee RE and Costanzo JP (1998) Biological ice nucleation and ice distribution in cold-hardy ectothermic animals. Annual Review of Physiology. 60:55-72
15. Sinclair BJ, Addo-Bediako A, and Chown SL (2003) Climatic variability and the evolution of insect freeze tolerance. Biological Reviews 78:181-195
16. Layne JR, Edgar CL and Medwith RE (1999) Cold hardiness of the woolly bear caterpillar (Pyrrharctia Isabella Lepidoptera: Arctiidae. American Midland Naturalist 141:293-304

17. Hayward SAL, Rinehart JP, Sandro LH, Lee RE, and Denlinger DL (2007) Slow dehydration promotes desiccation and freeze tolerance in the Antarctic midge Belgica antarctia. Journal of Experimental Biology 210:836-844
18. Sinclair BJ (2001) Field ecology of freeze tolerance: interannual variation in cooling rates, freeze-thaw and thermal stress in the microhabitat of the alpine cockroach Celatoblatta quinquemaculata. OIKOS 93:286-293
19. Duman JG (2001) Antifreeze and ice nucleator proteins in terrestrial arthropods. Annual Review of Physiology. 63:327-357
20. Mazur P (1984) Freezing of living cells: mechanisms and implications. American Journal of Physiology. 247:C125-142
21. Lee RE, Warren GJ, and Gusta LV, eds. (1995) Biological ice nucleation and its applications. St. Paul, MN: The American Phytopathological Society.
22. Marchand PJ and Walker L (1996) Life in the Cold: An Introduction to Winter Ecology. Hanover, NH: University Press of New England
23. Storey KB and Storey JM (1988) Freeze tolerance in animals. Physiological Reviews 68:27-84
24. Costanzo JP and Lee RE (1996) Ice nucleation in freeze-tolerant vertebrates. Cryo-Letters 17:111-118
25. Salt RW (1959) Survival of frozen fat body cells in an insect. Nature 184:1426
26. Keeley LL (1985) Physiology and biochemistry of the fat body. In: Kerkut G.A., Gilbert L.I., editors. Comprehensive insect physiology biochemistry and pharmacology: integument, respiration and circulation. New York: Pergamon Press. p 211-248.
27. Davis DJ and Lee RE (2001) Intracellular freezing, viability, and composition of fat body cells from freeze-intolerant larvae of Sarcophaga crassipalpis. Archives of Insect Biochemistry and Physiology 48:199-205
28. "Prairie Insects in Winter". Fermilab. 1998-03-03.
29. Marchand, Peter (1996). *Life in the Cold*. Hanover, NH: University Press of New England.

External links

- Ennis, Bonnie (2007-01-15). "Winter Survival Strategies of Insects". CSU/Denver County Cooperative Extension Master Gardener.
- "Surviving the Freeze". Ducks Unlimited Canada.
- "Most Dreadful and Dangerous Insects". Azeem Shaukat.

- "Where Do Ants Go In The Winter?". TERRO.

Categories: Insect ecology | Insect physiology | Winter phenomena

---