Preface

Tiny, wingless snow flea freezes
overnight as stiff as tin.
Does he mind or even notice
just what sort of state he's in?
Things warm up and – leaping lizards! –
Snow flea's jumping as before,
none the worse for being frozen
on the icy Arctic shore.

(Eileen Spinelli, 2007 *Snow Flea*)

Although the tilt of the earth's axis is only a little over 23°, this is enough to provide the dramatic contrast between the heat of summer and the cold of winter as our planet rotates around the sun. These pronounced seasonal changes in temperature dictate the seasonal patterns that dominate the temporal patterns of life on earth. On a much shorter timescale, the daily rotation of the earth on its axis, yielding the day/night cycle, adds the important dimension of thermoperiodism that generates daily variation in the number of heat units that reach the earth's surface.

Certainly all animals are influenced by daily and seasonal cycles of temperature, but it is perhaps ectotherms, such as insects, that are most severely affected. With, at best, limited abilities to regulate their own body temperature, insects are at the mercy of the prevailing temperatures. Insects commonly use seasonal shortening in day length (photoperiod) as an environmental token to reliably signal the advent of inimical temperatures. For many insects these photoperiodic cues are used to program diapause, a period of developmental arrest used to wait out the winter months. And others, such as the Monarch butterfly, couple long-distance migration with entry into a reproductive diapause at a protected hibernaculum. Though entry into a dormant state is a key component for winter survival, dormancy by itself does not assure low-temperature survival. To this must be added a suite of physiological adaptations that enable the insect to survive at temperatures that are often well below zero. Adaptations for low-temperature survival are not restricted to overwintering species. Such adaptations are common, even among species that lack the capacity for diapause, as well as in non-diapausing stages of species that possess the capacity for diapause. Nearly all species are also confronted with daily changes in temperature that demand finely tuned physiological adaptations that enable the insect to function effectively over a wide temperature range. Fluctuations in temperature are particularly important during warm seasons when insects are especially active and thus need to make fine adjustments in their physiology to respond to daily temperature swings that frequently exceed 10–20 °C. And, even in tropical regions of the world, temperatures during the night can drop precipitously.

It is the goal of this book to outline the mechanisms used by insects to survive and respond to low temperature, then to reflect upon how these adaptations are expressed in a broader ecological and evolutionary context, particularly with respect to global climate change, and finally to examine practical applications that can be derived from low-temperature studies of insects.

In many ways this volume has its origin in our earlier book, *Insects at Low Temperature*, published in 1991. But, it's not exactly a revision, because the earlier book covered a number of topics not discussed here. In this book we focus on topics that have emerged or significantly grown since 1991. In many respects the field has blossomed, matured and diversified in the nearly two decades that have elapsed since the original book was published. The tools of molecular biology enormously enhance our understanding of mechanisms of cold-hardiness, and such updates are emphasized herein. We have not included chapters here that were well covered in the 1991 book and remain timely, thus readers will still find the earlier book to be a good source for literature on water relationships, the biochemistry of cryoprotectants, the effects of cold on morphogenesis, the relationship between diapause and cold-hardiness, thermoperiodism and numerous accounts of species' (e.g. fresh-water invertebrates, honey bees, silk moths) adaptations to low temperature.

Readers are introduced to the fundamentals of low-temperature insect biology in Chapter 1 (Lee) and the remainder of the first section of the book focuses on physiological and molecular responses to low temperature, including a discussion of rapid cold-hardening (Lee and Denlinger), antifreeze proteins and ice nucleators (Duman *et al.*), lessons from genomics, proteomics and metabolomics (Michaud and Denlinger), cell structural modifications (Kostal), oxidative stress (Storey and Storey) and cross-tolerance between cold, desiccation and environmental toxins (Holmstrup *et al.*). The second section of the book examines ecological and evolutionary responses to low temperature and includes chapters on a macroscale perspective of cold-hardiness (Chown and Sinclair), fitness consequences of low temperature (Huey), consequences of global climate change (Bradshaw and Holzapfel), genetic variability in the evolution of cold-tolerance (Overgaard *et al.*), and life-history adaptations to polar and alpine environments (Convey). A brief final section captures two important practical aspects of low-temperature biology. The one chapter documents advances in insect cryopreservation (Leopold and Rinehart), and the final chapter discusses the implications of cold-tolerance for insect pest management (Bale).

As editors of this volume, we are especially grateful for the participation of the contributing authors, who enthusiastically joined in this effort. Thanks also to Chris Hudson, Dominic Lewis and Caroline Brown from Cambridge University Press for their assistance with this project. We gratefully acknowledge the National Science Foundation, the National Institutes of Health and the United States Department of Agriculture for their support of research in our laboratories.

David L. Denlinger
Columbus, Ohio

Richard E. Lee, Jr.
Oxford, Ohio
October 2009