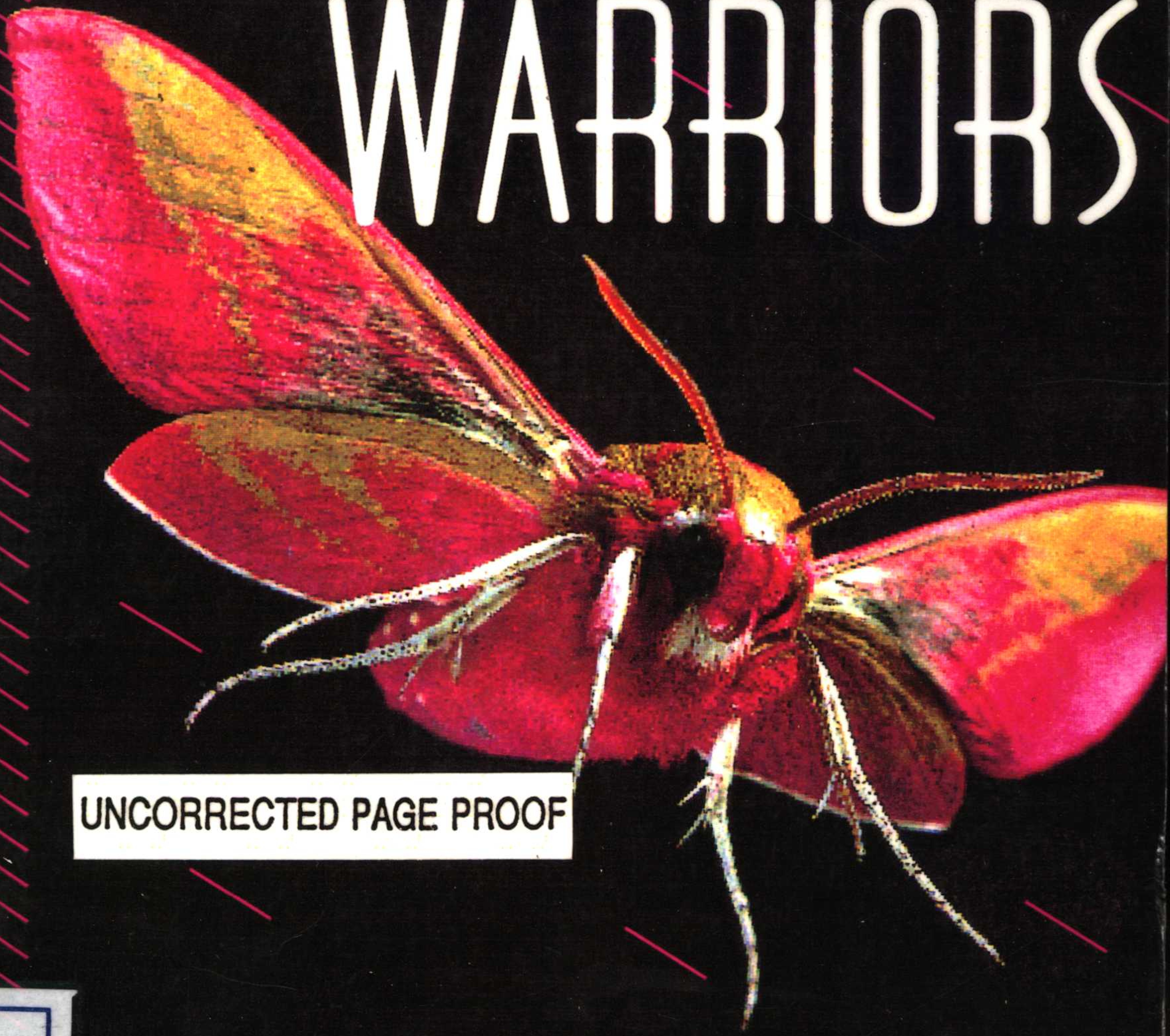
BERND HEINRICH

THE THERMAL WARRIORS



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STRATEGIES OF INSECT SURVIVAL

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Preface

We believe that it requires great enthusiasms to deal accurately with little things; and that it is, consequently, impossible to meet with a reasonable or sober entomologist.

$\frac{1}{M}$*Edinburgh Review*, 1822

On a spring day in the mid-1970s, the sports page of the Boston *Globe* ran a picture of a runner in full stride. The runner was Jack Fultz, on his way to victory in the Boston Marathon, and he was squirting a stream of water from a plastic bottle onto his head as he ran. I doubt the *Globe* was trying to make a point, but in fact there might be a connection between the runner's cooling-off strategy and his victory. It had been an "exceptionally" hot day, and in a race with hundreds of nearly equally superb athletes, any one of whom could win, the margin between first and second place can be a matter of seconds. Over 26.2 miles that margin is determined by trifles, but temperature regulation is not a trifle. Athletic performance$\frac{1}{M}$indeed, all bodily activity$\frac{1}{M}$is the result of the interplay of vastly complex physiological processes, and all of them depend on temperature. All of the Boston Marathoners warmed up for maximal performance before the race started. Some ended up not at the finish line but in an ambulance, because of heat prostration, and many others trailed Fultz by minutes or hours. Against a field of supremely conditioned athletes, Fultz may have had an edge in temperature regulation.

When in the summer of 1983 I ran the final of 625.6 total loops on Bowdoin College's quarter-mile track to set an American record in the 24-hour run, I remembered the winning photo of Fultz. My "marathon" also took place on a hot day, and I dunked my head in a barrel of water alongside the track at every other lap.

We humans engage in endurance contests such as these only rarely, for the sheer fun or foolishness of it or for some symbolic trifle. For insects, however, the struggle to keep body temperature within an acceptable range is constant, and often it is a matter of life or death. Each insect is a "thermal warrior" in a contest with its predators and competitors in the context of its physical environment.

Consider the thermophilic ("heat-loving") *Cataglyphis* ants of the Sahara Desert that Rüdiger Wehner and his associates at the University of Zürich have studied. These ants, they found, are specialist foragers for heat-killed insects. The ants don't leave their subterranean colonies until it is so hot that they can be assured of finding dead and dying prey. But even these potentially lethal temperatures are not high enough$\frac{1}{M}$an evolutionary "arms race" has pushed the limits of safety. The ants wait still longer until even their own predators, heat-loving lizards, have been forced to retreat because of the heat. Only then, when temperatures are near the daily high point, which is near their own death point, does the colony march forth *en masse* to scour the searing sands for dead victims.

Masato Ono in Japan reports on another thermal warrior, the Japanese honeybee *(Apis cerana japonica).* The honeybees are heavily preyed on by the thickly armored giant hornets *(Vespa mandarina japonica).* Hovering near hive entrances, these hornets snatch bees, chew off their wings and legs, and then macerate them to a pulp to feed to their larvae. The bees' stings are useless against the hornets that have evolved heavy armor, but the bees have evolved a potent counter-strategy against the armored killer wasps. They post a large number of guards at their nest entrances, and if a hornet ventures too close, the guards rush out, clasp onto the hornet with their mandibles, and in seconds form a ball of bees around the hornet. Now the bees begin to shiver and the temperature inside the ball quickly rises to near 50°C. The hapless hornet struggles fiercely, unavoidably generating more heat of its own that is now trapped because of the bees, and it is soon dead from heat prostration.

Direct confrontations are not the only thermal battles in the insect world. Here in the New England forests, some moths have evolved thick insulation and the amazing capacity to shiver and keep warm in the cold, when their predators have migrated south or are in hibernation. And in the hot southwestern deserts, as Eric C. Toolson and associates have discovered, a sweating response allows the desert or "Apache" cicada to sing at noon on the hottest days, in the hottest part of the year, and in the hottest part of its range, while its vertebrate predators are unable to tolerate the heat and so cannot hunt it.

Temperature is extremely important to the everyday activities of almost all insects. A bumblebee, for example, that rests at a body temperature of 5°C must increase her metabolic rate 1,500 times in order to fly, but this higher metabolic rate is possible only after she first raises her thoracic temperature to near 40°C. Each insect can survive only at its own specific temperature or range of temperatures. And in each case there is meaning behind the particular requirements for body temperature.

As has been long explored by many vertebrate biologists, especially most recently by George A. Bartholomew and William

A. Colder III, a major consideration in any discussion of body temperature and metabolic rate is body mass. This is especially pertinent in insects. From our perspective as vertebrates, one of the more obvious features about insects is their small body size, although among insects that size range is about as large as the range from shrew to elephant. Other things being equal, large animal bodies cool more slowly than small ones. For example, a person-sized body with a temperature of 40°C at an ambient temperature of 10°C cools (if it has stopped producing heat) at only some small fraction of 1°C per minute. In contrast, a 100-mg bumblebee under the same situation cools at about 1°C *per second,* or a rate at least 100 times greater. The larger body would not approach the same rapid cooling rate as the bee's even at absolute zero (-273°C), the lowest temperature in the universe. Maintaining a stable body temperature, as we and many live animals do, is essential for most living beings, and some of the larger-sized insects that do so accomplish a considerably greater feat than we humans$\frac{1}{M}$in whom a high body temperature is in part an inevitable consequence of large size$\frac{1}{M}$can claim for ourselves.

In a small mass, where every point of the body is close to the exterior, the heat loss from the interior is very rapid. By the same principle, however, a smaller body also *gains* heat much faster than a large one when the heat source is external. Thus, a small insect can *heat up* several degrees per minute when perching in a sunfleck, an option that is not available to us. Size is of paramount importance to insects because almost everything in their lives depend on it. Since insects vary over 500-thousand-fold in mass, and since they can vary their metabolic rate over a thousand times depending on flight activity and temperatures, we can expect to find vastly different kinds of thermal strategies in the insect world.

I have studied insects from the standpoint of a physiologist and an ecologist, and I have marveled at their sophistication from the broader perspective of an evolutionary biologist. I have been rewarded by the thrills of discovering several novel physiological mechanisms insects use to maintain an appropriate body temperature and to enhance their endurance in flight. Indeed, one of the mechanisms of honeybees looks very much like Jack Fultz's own strategy. I count among my greatest joys the satisfaction of discovering, or seeing others discover, the ingenuity for survival that insects have evolved in the irreducible crucible of temperature. This is entertainment of the highest sort.

Insects are marvels of creation with a body plan utterly different than ours. If it were not for them and their arthropod kin (crabs, spiders, scorpions), could we even imagine that it is possible to wear one's skeleton externally, cast it off occasionally, and exchange it for a new one? Could we ever have dreamed of organisms changing completely from a worm-like form eating leaves to a brilliantly colored flying marvel, or metamorphosing from a squat, creeping, aquatic troglodyte to the world's most versatile flyer able to snatch mosquitos out of the air? Could we conceive of being born ready to respond "perfectly" to amazing details of one's environment, without having to spend a lifetime slowly acquiring the appropriate responses by learning? Contemplating these incredibly diverse gems of the natural world, one is impressed with the realization that, seen objectively, insects are perhaps the most, or one of the most, highly evolved form of life. Given the hundreds of millions of years that they have been in existence on this earth, and the very short time, often measured in weeks not decades, they need to produce a new generation, it is plain to see that insects have had the opportunity to evolve considerably more than we have. They evolved flight, building architecture, and complex social systems probably hundreds of millions of years before any other organisms on earth had done so. Their amazing diversity and their perfection of design seem to be ample evidence for their high degree of evolutionary success. If any animals have explored the diversity of ways of coping with temperature, it is surely them.

The insect world is an exemplar of Life that has evolved on a different track or at a wide tangent to our own vertebrate line. Wherever Life exists, however, it develops according to specific universal principles. All matter obeys the same physical laws, and one might learn much about mechanical devices, or vice versa, by studying nature's design in the insects. Tucked into hundreds of obscure and technical journals is a store knowledge that represents the work of explorers who have seen and described new territory. But there is still much more to see. The far reaches of the Colorado River and the Amazon, and even the topography of Mars and the moon, have been explored, but many of the peaks and canyons of the insects' physiology and ecology are hardly mapped out.

In a previous book, *The Hot-Blooded Insects,* I devoted nearly 600 pages to synthesizing and reviewing a large field of study from several perspectives. In each chapter I examined one of the many different kinds of insects$\frac{1}{M}$from giant moths to tiny fleas. I felt that if I had organized it according to general principles, then many of the fascinating details and group-specific unique features would be neglected or lost. It was also necessary to trace the confusing cross-currents in the specialist literature. That task has been done.

My attempt here is to write a short book that is necessarily sketchy and incomplete. It summarizes the main points of the previous book and incorporates a number of new developments. It was inspired by a book of only 109 pages that has had a great influence on me and that I still cherish. It was the Christmas present from my father when I was sixteen years old, and it was inscribed "Bernd Heinrich, dem Imker von seinem Vater zu Weihnachten 1956."

As the inscription indicates, my father duly acknowledged me as an "Imker" (beekeeper) even though I had only a hive or two. I did, however, spend as much time as possible on late summer days in western Maine learning the art of "lining" bees to find bee trees with my friends, the Adamses and the Potters.

Karl von Frisch's little book, titled *Bees, Their Vision, Chemical Senses, and Language,* could not have been more apropos. I even read it. Had I instead received his 566-page book on the same topic, I'm afraid that the wonder of it all might have escaped me. Certainly the book would not have been read. Indeed, I regretfully admit that my copy of the larger tome sits prominently on my bookshelf but is still unread.

It was von Frisch's *little* book that raised my eyes from the goldenrods and the pollen-laden bees flying off to old hollow hemlock trees in the woods. It was the little book that made me aware of new vistas. By way of simple and elegant experiments von Frisch described the sensory world of these creatures and their ways of communicating in a surprising symbolic language. A new world was revealed to me. It would otherwise have been locked from consciousness. The big book is a solid and valuable reference and a reminder of what stands behind the wonders that exist in the world. But nothing that I have ever read about bees has ever eclipsed the surprise and joy of learning how the author discovered what the bees sense and how they communicate with hivemates. As Donald R. Griffin stated in the introduction to the book, "The thought and the word are closely linked together; and for this reason an effort has been made to preserve in the printed page something of the pleasing directness and simplicity so apparent in the original lectures" (on which the book is based).

In later years I have been all the more mesmerized by the straightforward simplicity and purity of the little book, and in no small part I have felt its genius was due to the author's ability to leave out everything but the bare essentials. Beauty is the uncompromising economy that seeks only to illuminate truth, without obeisance to anyone, and without acknowledgment to stray thoughts or distracting concerns.

Thermoregulation perhaps no longer lends itself to uncompromising focus. On the other hand, brevity itself is a virtue to strive for, and it may be especially so in these more hurried times. I have therefore tried to concentrate on telling examples that illustrate general principles for readers who may not previously have been exposed to the field. Some aspects of insect thermoregulation may seem esoteric, but there is much of general relevance to be found by studying insects, and the study of body-temperature regulation during flight offers analogies with familiar principles of motor mechanics and vehicle maintenance. As Robert Pirsig said in *Zen and the Art of Motorcycle Maintenance*, beauty is not in what is seen but in what it means. You cannot "take apart" an insect that is smaller than your fingertip the way you can take apart a motorcycle. That has made the discovery of the marvels of design responsible for insects' extraordinarily high physical performance all the more fascinating.

In this primer I try to explain how, when, and in general what insects regulate body temperature. I also give an evolutionary perspective on the meaning of thermoregulation: why some insects (but not others) came to regulate high body temperatures. Morphology is the handmaiden of physiology, and it is essential to examine relevant insect flight-motor construction before describing specific passive and active heating and cooling mechanisms. All this is background to a discussion of the strategies of the thermal warriors themselves. To help the reader continue exploring an interest I hope this book will spark, I provide a selected list of references to the original scientific literature on the topics discussed. And to emphasize the "whole animal" approach (one that addresses physiological questions in both the ecological and evolutionary context), I have included pencil sketches of my favorite subjects.

Numerous people helped to shape this book. Michael Fisher, of Harvard University Press, encouraged me to begin writing it, and suggestions made by Doekele G. Stavenga and by two anonymous reviewers helped me revise earlier drafts. Their efforts are greatly appreciated. Erika Geiger and Suzanne Markloff were able to decipher my handwriting and patiently typed several versions.

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The Thermal Warriors

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