peptides that regulate female behavior and physiology. The interaction between JH and 20-hydroxyecdysone during postembryonic development regulates the development and differentiation of the glands. Juvenile hormone alone may also control the synthesis of those specific proteins that are transferred to the female. The accumulation of some secretory peptides in the glands that are enhanced by JH may be either enhanced or inhibited by the simultaneous presence of 20-hydroxyecdysone. In the German cockroach, *Blattella germanica,* the activity of the corpora allata, which is the source of JH, declines during the formation and transfer of the spermatophore and may thus initiate a new cycle of male accessory gland maturation.

See Also the Following Articles

Accessory Glands • Ecdysteroids • Juvenile Hormone • Spermatophore

Further Reading

Chapman, R. F. (1998). "The Insects: Structure and Function" 4th ed. Cambridge University Press, Cambridge, UK.

Dumser, J. B. (1980). The regulation of spermatogenesis in insects. *Annu. Rev. Entomol.* **25,** 341–369.

Friedländer, M. (1997). Control of eupyrene–apyrene sperm dimorphism in Lepidoptera. *J. Insect Physiol.* **43,** 1085–1092.

Gillott, C., and Gaines, S. (1992). Endocrine regulation of male accessory gland development and activity. *Can. Entomol.* **124,** 871–886.

Klowden, M. J. (2002). "Physiological Systems in Insects." Academic Press, San Diego.

Research Tools, Insects as

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In addition to serving as classic experimental laboratory animals (e.g., *Drosophila* flies in genetics, *Periplaneta* cockroaches in neurophysiology, *Manduca* moths and *Schistocerca* grasshoppers in physiology), insects have been essential to the formulation and testing of many general theorems in ecology and evolutionary biology. Scientists seek to develop general synthetic theories in biology, just as in physics and chemistry,that provide answers to questions of how and why things are as they are. Perhaps more importantly, these generalities make predictions that allow us to test what we think we know. The use of data to constantly reevaluate our theories divides empirical science from personal belief systems and popular metaphysics. The latter two are concerned with understanding the fundamental nature of all reality and often are based on abstract elements. In contrast, hypotheses in mainstream science are typically explanations of the processes that exist in nature and are tested against empirical observations.

To develop these testable hypotheses in science a constellation of data from model systems is needed, especially in biology. Insects are used as many of these model systems. In part this is because they are so abundant and species rich that, in terms of diversity, they make up the bulk of terrestrial species and, in many habitats, the greatest number of individuals. Because of this dominance, comprehensive biological hypotheses must account for insects if the hypotheses are to be generally accepted. Insects provide the numerous observations that are essential for developing and supporting broadly applicable hypotheses explaining the diversity and distribution of life on earth.

Insects are a magnificent source of observations. The sheer number of units for study at all levels—species, populations, and individuals—provide the repeated patterns of variation that provoke questions and provide data for hypothesis testing. Also, insects usually have a relatively short life cycle, often more than one generation per year. This allows scientists to make multiple observations of all life stages of a species in a relatively short time period. Insect species can be widespread, but typically they are localized, making it easy to accumulate distributional data for at least the more conspicuous taxa. Certainly there is an important human factor as to why insects are so important in the study of biology. Insects delight us with their forms and behaviors and seem to embody all that fascinates humans about the natural world—beauty, diversity, mystery, and perhaps most of all discovery. Once a biologist, or any naturalist, is exposed to the wonders of insects they are usually hooked for life.

Biology has benefitted greatly from both reductionist and integrative research. The reductionist program attempts to minimize the number variables in the study system and identify causal mechanisms. Stunning success has been achieved using *Drosophila* as a laboratory animal to investigate developmental and genetic systems and to discover basic mechanisms from which inferences about general principles in biology are made. An integrative or synthetic approach is also essential in biology. Insects have been crucial model organisms, providing some of the most important advances in synthetic theory.

THEORETICAL WORK IN THE 19TH CENTURY

Evolution, or the theory of natural selection, is the most influential of all biological theories, and the two men who codified the basic mechanisms of descent with modification were dedicated observers and collectors of insects. Charles Darwin and Alfred Wallace shared what Wallace referred to as a "child-like" passion for beetles; Wallace even suggested this may have been a common thread that helped to lead both of them to arrive independently at similar conclusions about the evolutionary origin of species. Both present colorful stories of collecting insects. Wallace wrote wonderful passages on "one good day's work" collecting in Borneo, recalling species by species those collected and those that escaped one day, to be pursued the next. Darwin recalls with great passion his beetle collecting and the unfading thrill of discovering rare or new species. Wallace earned much of his livelihood collecting and providing specimens to museums and private collectors. He sold thousands of specimens at about 2 cents each to fund his tropical expeditions. For both Darwin and Wallace, attention to details necessary for separating species, subspecies, and varieties of insects was fundamental to developing their ideas. The diversity of forms and sheer reproductive output of insects provided examples that cultivated in their minds the theory of natural selection.

Wallace traveled with another entomologist and great naturalist, Henry Bates. In 1842 Wallace and Bates went to the Amazon to explore and to collect insects. These explorations and Bates' collections (Wallace's were unfortunately lost in a ship fire) became incredibly valuable in terms of insights into natural history and evolution. For 11 years, Bates collected insects, primarily butterflies and beetles, that were and remain a source of awe and study material for students of insects and users of European museum collections. Bates readily accepted Darwin's and Wallace's ideas of natural selection as the mechanism of evolution and went on to develop his theory of mimicry. Known as Batesian mimicry, this concept stemmed from his experience with tropical butterflies. This theory is widely applied throughout biology as an explanation for the similar and convergent appearance of some organisms.

THEORETICAL WORK IN THE 20TH CENTURY

Willi Hennig is best known for developing a coherent theory for phylogenetic systematics, a field of research that investigates and presents relationships among taxa. Hennig's theoretical works form the core of modern cladistic methods (use of shared derived characteristics to elucidate sister group relationships of taxa). Hennig was also the foremost authority on flies (Diptera) and produced many publications, including his series of publications on maggots (dipterous larvae), which became the standard work on the subject. Throughout his classic work *Phylogenetic Systematics* he relied on insect examples. Today our ideas about how to develop hypotheses of relationships for animals in an evolutionary scheme and how to classify them are largely based on theories and methods developed with insects as models.

Biogeography is a major field of biology that strives to understand the spatial relationships of organisms and looks at both historical and contemporary questions regarding biodiversity. Darwin, Wallace, and Hennig were all prominent contributors to this field, each drawing on ample observations from the insect world. Wallace was particularly influential in developing ideas that are still important in biogeographical studies. Biogeographical regions of the earth presented by Wallace, which were modified from Philip Sclater's previously published scheme, are still a standard part of describing the geographic distribution of animals. Most prominent is Wallace's observation of a distinct change in fauna between Bali and Lombok in the East Indies, known as Wallace's line. Wallace drew heavily on his knowledge of insect life histories, dispersal abilities, and distribution of some conspicuous insects (beetles and butterflies) to develop his biogeographical ideas.

A significant change from thinking about biogeography only in terms of evolutionary and historical scenarios to looking at ecological dynamics began in the 1960s. Robert MacArthur and E. O. Wilson published the equilibrium theory of island biogeography, a model based on land area and distance from source populations that explained how newly available islands could become populated with plants and animals, ultimately coming to a point of equilibrium in terms of species number. This became one of the most influential works in the field. Noted biologist and entomologist Ed Wilson is an ant systematist and he used these insects to support the development of this theory.

Wilson's contributions to biology are many, but some of the best known and most controversial are the ideas presented in sociobiology. In general this field seeks explanations of social behavior in animals based on common biological and evolutionary concepts. Largely this synthesis is based on his knowledge of ants, animals that are truly social. Many other insect groups, including beetles, butterflies, termites, dragonflies, and bees, just to name a few, are exemplar taxa used to illustrate concepts of sociobiology. Sociobiology is broad and interdisciplinary; insects are a vital part of the hypotheses that span many fields of inquiry.

LOOKING FORWARD IN THE 21ST CENTURY

Whether through reductionist approaches or the development of synthetic theories of biology, it is clear that the study of and passion for insects is an incredibly important part of our understanding of the world we live in and realizing our place in the natural system. Just as insects have proven to be essential in developing theories using the integrative approach, they will continue to be prominent in studies at all levels of organization from the molecular to the ecosystem.

See Also the Following Articles

Biodiversity • Drosophila melanogaster • Mimicry

Further Reading

Bates, H. W. (1862). Contributions to an insect fauna of the Amazon valley: Lepidoptera: Heliconidae. *Trans. Linn. Soc. London* **23,** 495–566.

Darwin, C. (1859). "The Origin of Species by Means of Natural Selection: Or, the Preservation of Favoured Races in the Struggle for Life." Murray, London.

Darwin, C., and Wallace, A. R. (1858). On the tendency of varieties to depart indefinitely from the original type; and on the perpetuation of varieties and species by natural means of selection. *J. Proc. Linn. Soc. Zool.* **3(9),** 53–62.

Dethier, V. G. (1962). "To Know a Fly." Holden–Day, San Francisco.

Hennig, W. (1966). "Phylogenetic Systematics." University of Illinois Press, Urbana. [Translated by D. Dwight Davis and Rainer Zangerl]

MacArthur, R. H., and Wilson, E. O. (1967). "The Theory of Island Biogeography." Monographs in Population Biology, No.1. Princeton University Press, Princeton, NJ.

Rogers, B. T., and Kaufman, T. C. (1997). Structure of the insect head in ontogeny and phylogeny: A view from *Drosophila. In* "International Review of Cytology" (K. W. Jeon, ed.). Academic Press, San Diego.

Sclater, P. L. (1858). On the general geographical distribution of the members of the class Aves. *J. Linn. Soc. Zool.* **2,** 130–145.

Statzner, B., Hildrew, A. G., and Resh, V. H. (2001). Species traits and environmental constraints: Entomological research and the history of Ecological Theory. *Annu. Rev. Entomol.* **46,** 291–316.

Wallace, A. R. (1855). Concerning collecting dated 8 April 1855, Si Munjon Coal Works, Borneo. *Zoologist* **13,** 4803–4807. [Letter]

Wallace, A. R. (1876). "The Geographical Distribution of Animals, with a Study of the Relations of Living and Extinct Faunas as Elucidating the Past Changes of the Earth's Surface." Macmillan & Co., London.

Wilson, E. O. (1975). "Sociobiology: The New Synthesis." Harvard University Press, Cambridge, MA.

Respiratory System

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The primary goals of the insect respiratory system are to deliver oxygen from the air to the tissues and to transport carbon dioxide from the tissues to air. Gases are transported through the tracheal system by both diffusion and convection, with the relative importance of these two mechanisms varying across and within species. Aquatic and endoparasitic insects exchange gases by a variety of mechanisms; most have tracheae and tracheoles within thin-walled appendages that function as gills. Within individual insects, the structure of the tracheal system can be altered dramatically during ontogeny and in response to rearing conditions, such as low oxygen. With a given tracheal structure, the ability of the tracheal system to transport gases can be modulated dramatically by varying spiracular opening, ventilation, and the fluid level in the tracheoles. Control of flexibility in tracheal gas exchange capacity depends strongly on neuroendocrine control of muscles that drive convection or control spiracular opening.

DEVELOPMENT

In most insects, the tracheal system first appears in the embryo. In general, the size of the tracheal system increases with age in order to support the increased gas-exchange needs of the larger insect. However, major changes in tracheal structure, including changes in spiracle number and tracheal system organization, can occur at each molt and during the pupal period for endopterygote insects. During the molts, the cuticular lining of the trachea is drawn out of the spiracle with the old integument.

Changes in tracheal system structure are not limited to molting periods, because the tracheoles can change structure within an instar. In the event of injury or oxygen deprivation, local tracheoles grow and increase in branching. If no undamaged tracheoles are nearby, damaged tissues produce cytoplasmic threads that extend toward and attach to healthy tracheoles. These threads then contract, dragging the tracheole and its respective trachea to the region of oxygen-deficient tissue.

Both tracheoles and trachea are fluid-filled in newly hatched insects, and fluid fills the space between the old and the new trachea at each molt. Usually, this fluid is replaced with gas shortly after hatching or molting. In some cases, the spiracles must be open to the air for gas-filling of the tracheae to occur, suggesting that gas-filling occurs as fluid is actively absorbed by the tracheal and tracheole epithelia, with air entering through the spiracle to replace the absorbed fluid. However, in aquatic insects that lack spiracles, the tracheae also become gas-filled, indicating that this gas can be generated by the tissues or hemolymph.

MECHANISMS OF GAS EXCHANGE

Insect gas exchange occurs in a series of steps. Oxygen molecules first enter the insect via the spiracle, then proceed down the branching tracheae to the tracheoles. The terminal tips of the tracheoles are sometimes fluid-filled, so at this point gas transport may occur in a liquid medium rather than air. Oxygen then must move across the tracheolar walls, through the hemolymph, across the plasma membranes of the cells, and finally through the cytoplasm to the mitochondria. Carbon dioxide generally follows a reverse path.

Diffusion

Diffusion is the passive movement of molecules down their concentration gradient, driven by random molecular motions. Because oxygen is transported to the tissues as a gas and the diffusion rate of oxygen is much more rapid in air than in water, the insect tracheal system is capable of high rates of gas exchange by diffusion. Consumption of oxygen by the tissues lowers internal oxygen levels, creating a concentration gradient from air to tissues that drives oxygen through the tracheae. The converse occurs for carbon dioxide. The final steps of oxygen delivery, from the tracheoles to the mitochondria, may occur by diffusion in all insects, because diffusion operates rapidly over micrometer distances. In the initial steps of oxygen delivery (across the spiracles, through the tracheae), the importance of diffusion is more variable. Simple diffusive gas exchange through the tracheae and spiracles likely occurs in some pupae, as washout rates of inert gases are similar to those predicted from their diffusion coefficients. Additionally, in a variety of insects, no ventilatory movements have been discerned, which may mean that these insects exchange gases by diffusion through their tracheae and spiracles.

Convection

Convection is the bulk movement of a fluid (gas or liquid) driven by pressure. Differential air pressures can drive gas movement through the tracheae and spiracles at much higher rates and over longer distances than diffusion. In many insects, well-coordinated actions of muscles and spiracles produce regulated convective air flow through the tracheae and spiracles.