

Annual Review of Entomology, 2008.
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The award-winning documentary film 'An Inconvenient Truth' brought the debate over climate change and global warming into our homes; these have now become household words, and have metamorphosed into bogeymen: 'Turn-off the lights, or climate change will get you'. This atmosphere has also impacted journals and publishing houses, with many reviews and articles targeting such issues. The sense of urgency has also infected the *Annual Review of Entomology*, since in the current volume, several articles are focused around changing environmental parameters and how they may affect the biology of insects. Research is clearly needed, and can this research be focused on some key factors? Policy makers will usually immediately draw up mandates and issue directives on the sort of 'applied' research that needs to be done. However, it is often basic research that will show the way, as the review by Pablo Guerenstein and John Hildebrand on 'the roles and effects of environmental carbon dioxide in insect life' amply illustrates. This review has a seemingly innocuous title. Yet, just one example from the material cited in this review should convince the reader of the broad implications of this article. The pre-industrial world had certain background CO₂ levels, and the sensory systems of the present generations of several insect species appear to be adapted to these levels¹. Many insects use the CO₂ emanating from respiring leaves or flowers to make decisions about flower visitation, oviposition or herbivory. A pollinated flower or a damaged flower that is shutting down respiration is a target to be avoided by prospective insect pollinators². Many insects have specific CO₂ detectors which are often located in the antennae. In many cases, these detectors are temperature-compensated, such that within a certain range of CO₂ concentration and temperature, the sensitivity and accuracy of detection remains the same. However, when this range is exceeded, insects may perceive a change in temperature as a change in chemical concentration (in this case, CO₂) when the real CO₂ values are

quite different. It appears, at least for the extremely important agricultural moth pest *Helicoverpa armigera*¹, that the temperature-compensated CO₂ detection system is adapted to pre-industrial levels of CO₂. The implications of this finding for pest responses to changing climate scenarios (where both temperature and CO₂ levels are increasing at varying rates) need to be urgently investigated not only for insect pests, but also for useful insects such as pollinators or parasitoids. Similarly, the increase of ozone levels in our atmosphere from pre-industrial times is also a cause for concern from the perspective of the volatile detection systems of insects. The greater the ozone level, the greater the atmospheric degradation of volatile organic compounds that plants emit to attract insect pollinators or parasitoids of insect herbivores. A recent study has modelled the decay of volatile signals (specifically of linalool, β -myrcene and β -ocimene) with distance from the emitting plant at various ozone levels, and has proposed a significant decrease in the maximum distance to which a signal could travel and still be detected by insect antennae given their existing sensitivities³. The study found that under the present ozone levels, only insects that are within 200 m of the plants may be able to respond to these signals, while in pre-industrial times the signals would have travelled without decay for several kilometres. These findings have obvious and serious implications for the attractiveness of plants to insects at a distance and thus for the genetic mixing of natural populations by pollen flow via insects. Insect pollinators that use volatile cues to find plants may not be attracted to sources further away because of the altered atmospheric chemistry. Under such scenarios, there should also be selection pressure on plants to increase the quantum of volatiles produced in order to attract insects at greater distances. Whether this is happening, and whether plants can bear the cost of increased volatile production without compromising other life-history parameters is not known. Once again, basic research is crucial for accurate predictions. Another climate change-related paper by Scott Halstead in this volume deals with consequences of global warming for epidemiology in dengue virus-mosquito interactions. I learnt from this paper that contradictory results are observed in the relationship between

mosquito incidence and local temperatures such that a high incidence of *Aedes aegypti*-related dengue infections is being recorded during scorching summers in North India, when the abundance of mosquitoes is expected to be low. This anomaly is because the mosquitoes are breeding within the favourable microclimate of water coolers that are extensively employed at this time to bring down ambient temperatures within private and public environments. Thus while greater attention is being paid to macroclimatic change, coupled microclimatic factors can obviously not be ignored.

The most exciting paper in this volume is the one by Jeremy Niven *et al.* titled 'Diversity and evolution of the insect ventral nerve cord'. While the paper is focused on the comparative anatomy of the insect ventral nerve cord and its phylogenetic history, the subtext of the review is far more fascinating, even though the authors could not develop it, given the constraints of the review's focus. While the abstract of this review may state that there is considerable divergence as well as convergence in neuromere and ganglion fusion in the nerve cord across insect groups, it is the underlying evolutionary principles that may govern these patterns that are worthy of attention. Over the last decade, Simon Laughlin's group in Cambridge (to which Jeremy Niven belongs) has made major contributions to our understanding of the evolution of sensory systems from the viewpoint of energetic constraints. Darwin wondered about the disappearance of eyes in cavefish and erroneously attributed this to the phenomenon of disuse of organs (in the Lamarckian tradition). It is also possible to hypothesize that since cavefish do not need eyes within the dark environments they currently inhabit, there is no active selection pressure to retain the eyes, and therefore the eye trait may drift and even be lost without any serious consequences to the fish. However, Laughlin's work on the energetics of nervous tissues has shown that, for example, the mere maintenance of resting membrane potentials consumes 25% of the cost of nerve cells in terms of the actual amounts of ATP required to run the sodium/potassium and proton pumps responsible for these potentials. The energetic costs of supporting nervous tissue are so high that those cavefish who still maintained eyes despite not needing them would be at an energetic and thus selective disadvantage.

compared to cavefish in which eyes were lost. Here is an energetics-based proximate explanation for sensory system maintenance and design; this aspect has been ably reviewed in a more recent publication by the same authors⁴. Laughlin's group also addresses questions about the miniaturization of axons, i.e. how narrow or small can an axon get and still conduct impulses without being swamped by the ion-channel noise generated by thermodynamic fluctuations within the proteins that constitute the membrane ion pumps⁵? Such questions have important implications for the design of the nervous system, and as mentioned earlier, form the most interesting subtext of Niven's review on insect nerve cords. Such questions can address issues that range from epileptic electrical storms in human brains to Darwin's observations on the evolution of blind cavefish.

The economic arguments over neuronal energetics that favour blindness in cavefish follow the same principles that Darwin himself used to examine entomological data, as described in an extremely interesting paper on the reaction of entomologists to Darwin's theory of evolution, when it was first proposed (Gene Kritsky: Entomological reactions to Darwin's theory in the 19 century). This paper recounts how Darwin was an avid insect collector himself, and used the price of male versus female butterflies to determine from collectors' catalogues, whether males of a species were showier than females and thus to obtain a surrogate measure for sexual dimorphism within the species. According to Darwin's reasoning, showier males should be easier to spot and capture compared to more cryptic females. Using sound economic principles, he predicted the price of showier males to be lower than that of the less showy and harder-to-obtain females. Consequently, the price differential between males and females should reflect the degree of sexual dimorphism in the species. These and other anecdotes in this review also recount Darwin's reactions to criticism of his theory of evolution from the entomology fraternity of his time.

If maintaining neuronal tissue is costly, then learning, which depends on the presence of neuronal tissue, should also be costly. Recently, a symmetrical evolutionary trade-off was demonstrated in *Drosophila*, such that longevity appeared to be traded for learning ability.

Learning ability in long-lived flies was impaired by 40%, without any significant effect on fecundity or body mass. On the other hand, populations selected for improved learning had a 15% reduction in longevity⁶. The costs involved in such a trade-off are still not clear, and there is much to understand about learning in insects, e.g. why learning should be important even in relatively short-lived bees and wasps, and whether the capacity to learn is indefinite, or what the constraints on learning may be. Thus the review of learning in insects by Reuven Dukas (Evolutionary biology of learning) is timely and well crafted, discussing, as it also does, differences in learning between solitary and social insects. The most fascinating example of the benefits of learning described in this review is about learning in grasshoppers. It is known, for example, that in Orthoptera such as locusts, the concentration of compounds in circulating haemolymph modifies taste-receptor sensitivity, such that an animal in positive amino acid/protein balance may show reduced responsiveness to feeding on proteins⁷. With such an inbuilt mechanism, animals would not need to learn how to balance their diets. However, experiments conducted with Orthoptera such as grasshoppers, demonstrated the advantages of learning even in diet choice. In this experiment, grasshoppers in one set were given the opportunity to learn the association between cues such as colour, taste and spatial locations, and either a source of balanced diet or one providing only carbohydrates, while those in another set were not provided the opportunity to make these associations; the grasshoppers in the latter group encountered these two diets randomly. It was found that in the 'learning' group, the overall time spent feeding on the balanced diet was 99% compared to 87% spent by the 'non-learning' or random group. This difference translated into a 20% higher growth rate in the learning grasshoppers. Still, 87% was remarkably high for the random group, illustrating how accurate innate mechanisms of food quality assessment can be, and yet how, under certain situations, learning could provide a competitive edge for individuals in a population consisting of learners and non-learners⁸. The evolutionary biology of learning in insects is undoubtedly an immensely fascinating subject, as this review justifies.

Other topical subjects of general interest today include the biology of invasions, and this volume includes articles such as the biology of invasive ant species with special reference to the Argentine ant, *Linepithema humile*. It was refreshing to read a theoretical review of invasive biology from the perspective of the Allee effect (Andrew Liebhold and Patrick Tobin: Population ecology of insect invasions and their management). This is because reviews on invasive species usually focus on the ability of species to be invasive. However, in this article, the theoretical and practical aspects of curtailing invasions by bringing about Allee effects and thereby population extinction are skillfully discussed. The Allee effect is the phenomenon of decline in population growth rate when populations are small (an inverse density dependence effect). Population decline occurs because survival and reproduction are less likely when population levels are low. Among the principle causes for low reproduction at low population levels is the inability to find mates and also inbreeding effects, especially in small founder populations. Besides using reaction-diffusion models to simulate invasion fronts, this review also provides reference to success stories of possible Allee effects in containing invasions. These include the disruption of mating in invasive moth species by swamping the environment with synthetic moth pheromone, such that the male moths are unable to find virgin female moths, that are the usual source of this attractant, owing to the ubiquitous signal provided by the synthetic chemicals. In such cases, the Allee threshold can be raised, i.e. the population can crash owing to reproductive failure even at higher population levels since, even at these high levels, mates are unable to find each other.

The collection of articles in this volume spans many other equally important topics that range from sex determination in Hymenoptera, sexual selection in fireflies, to life-history strategies in parasitoids and even medical conditions arising from spider bites. Such a diversity of subjects affords the opportunity to discuss categories of articles and criteria for their possible inclusion in an annual periodical such as this one. On the one hand are the classical reviews, which collate published material and present it as a compilation of facts. Such reviews are useful because they can ensure that a

new researcher in the field will not miss any of the important literature. On the other hand are the syntheses; these are articles that go beyond literature compilation to provide a more personalized treatment of the field from the author's perspective. Another category is an opinion piece. In this category, an article may provide only a selective review of the literature to highlight particular aspects that the author may believe to be important to further research in the area. Still another category is a review that cannot quite be classified as such because it is too dispersed without a clear focus but, in fact, does reflect the state-of-the-art of a field, especially one with fledgling status. In such a case, the authors try to pull together diverse strands and suggest where future research may be directed. This volume has representative articles from all these categories, and this makes for good editorial strategy as old familiar subjects rest cheek by jowl with young upstarts. In this context, I must confess to a sense of disappointment while reading the article by Goulson *et al.* titled 'Decline and conservation of bumblebees'. This article seemed to fit into none of the categories. I would have liked, for example, to have seen a comparison between a decline in honeybees (social bees) and bumblebees (solitary bees), and for a discussion of similarities and differences in their vulnerability to current threats. This is especially important because of the vast literature and also numerous reviews (some controversial) on the pollination crisis resulting from global honeybee decline. Since *Bombus* (bumblebees) also occur in the Himalaya, and research is being conducted on the pollination crisis in Himalayan plants, I would also have liked to have seen a more global treatment of this problem. But these are small quibbles.

In summary, the *Annual Review of Entomology* has provided us once again with an exciting crop of data and ideas, combining the elements of classical whodunits (*quis, quid, ubi, quibus auxiliis, cur, quomodo, quando* [with apologies to Ngaio Marsh, *Death in a White Tie*, 1938]) with the murkiness of new intellectual frontiers to be invaded.

1. Stange, G. and Wong, C., *Nature*, 1993, **365**, 699.

2. Thom, C., Guerenstein, P. G., Mechaber, W. L. and Hildebrand, J. G., *J. Chem. Ecol.*, 2004, **30**, 1285–1288.

3. McFrederick, Q. S., Kathilankal, J. C. and Fuentes, J. D., *Atmos. Environ.*, 2008, **42**, 2336–2348.
4. Niven, J. E. and Laughlin, S. B., *J. Exp. Biol.*, 2008, **211**, 1792–1804.
5. Faisal, A. A., White, J. A. and Laughlin, S. B., *Curr. Biol.*, 2005, **15**, 1143–1149.
6. Burger, J. M. S., Kolss, M., Pont, J. and Kawecki, T. J., *Evolution*, 2008, **62**, 1294–1304.
7. Abisgold, J. D. and Simpson, S. J., *J. Exp. Biol.*, 1988, **135**, 215–229.
8. Dukas, R. and Bernays, E. A., *Proc. Natl. Acad. Sci. USA*, 2000, **97**, 2637–2640.

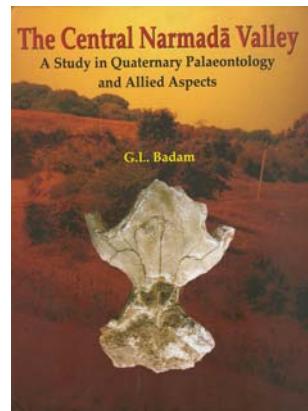
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palaeoclimate and neotectonics. The Quaternary alluvial records of the Narmada have yielded a diverse assemblage of mammalian fossils. The Central Narmada Valley became a point of attraction with the discovery of a skullcap of *Homo erectus narmadiensis* in 1984. Later, a human clavicle (collarbone) was also reported in 1997. These findings were significant from the viewpoint of the origin of early *Homo* in South Asia. The mammalian-bearing horizon is well-constrained in time, both by biostratigraphy and by radiometric dating of the associated Toba volcanic ash (~75 ka), and middle to late Pleistocene age is assigned to it. The alluvial archives of the Narmada are also well known for their middle Palaeolithic and Acheulian tools. While sections along the Narmada have yielded relics of human culture, caves in the surrounding areas are known for their records of artistic expressions of early man of Palaeolithic and later times. Bhimbetka, a UNESCO heritage site, has encouraged a number of researchers to study people–landscape interaction as depicted in its cave paintings. The Indira Gandhi National Centre for the Arts, New Delhi, has taken a major initiative in documenting the rock arts.

The records of mammalian life, including that of man, cultural tools and paintings in caves by early man make the Narmada Valley an ideal field museum to study human evolution in an integrated perspective. The Indira Gandhi Rashtriya Manav Sangrahalaya, Bhopal, initiated a project to understand Pleistocene environment and man–land relationship in the Central Narmada Valley. This book reports the findings of this project. G. L. Badam, the Principal Investigator of the project and author of the book, has spent nearly three decades in studying the palaeontological records of the Narmada. Although in this book he has primarily documented the Pleistocene mega-vertebrate fossils, the microvertebrates, Stone Age tools and rock paintings are also discussed briefly.

The Narmada is flanked by the Vindhyan in the north and the Satpuras in the south. It also cuts across the Precambrians and Gondwanas. The book starts with a brief geological description of the Narmada Valley, followed by Quaternary lithostratigraphy of selected sections. The alluvial sections and cultural tools recovered from these sections are illustrated. In recent years the stratigraphic investigations in the western part



The Central Narmada Valley – A Study in Quaternary Palaeontology and Allied Aspects. G. L. Badam. Indira Gandhi Rashtriya Manav Sangrahalaya, Post Bag No. 2, Shamla Hills, Bhopal 462 013 and D. K. Printworld (P) Ltd, 'Srikunj', F-52, Bali Nagar, Ramesh Nagar Metro Station, New Delhi 110 015. 2007. 210 pp. Price: Rs 1600.

Narmada, originating at Amarkantaka in the east and flowing across the country to meet the Arabian Sea in the west, is a sacred river of India. It exposes magnificent geological sections along its course that are potential archives of geological and cultural evolution of this part of the country. The alluvial plains of the Narmada are extensively studied for their mammalian and cultural records. In recent years, its terraces in the western part have been the subject of intensive geological studies to understand Quaternary