

prevent abnormal genital virilization of the female foetus. Simultaneous karyotyping is done along with the genetic analysis. If the baby is normal, or if there is genetic abnormality but the foetus is a male, dexamethasone prophylaxis is stopped. This succinct review is an excellent example for the clinical utility of understanding the fundamental basics involved in these disorders. Such articles form the crowning glory of the annual reviews.

S. SIVASANKARAN

Department of Cardiology,
Sree Chitra Thirunal Institute for
Medical Sciences and Technology,
Thiruvananthapuram 695 011, India

The Ecology and Evolution of Inducible Defenses. Ralph Tollrian and C. Drew Harvell (eds). Princeton University Press, 41, William Street, Princeton, NJ 08540, USA. 1999.

The Battle of Hastings, 1066. 'The courageous leaders mutually prepared for battle, each according to his national custom. The English... passed the night without sleep, in drinking and singing, and in the morning proceeded without delay against the enemy. All on foot, armed with battle-axes, and covering themselves in front by the juncture of their shields, they formed an impenetrable body which would assuredly have secured their safety that day had not the Normans, by a feigned flight, induced them to open their ranks, which till that time, according to their custom, had been closely compacted....Then starting the Song of Roland,...the battle commenced on both sides, and was fought with great ardour,...This alternating victory, first of one side and then of the other, continued so long as Harold lived to check the retreat; but when he fell..., the flight of the English ceased not until night' (William of Malmesbury: cited in Robinson¹). From a modern-day perspective where stealth, surprise attacks, and superior weaponry are the norm, it appears strange that battles were actually fought in this pre-announced manner, giving time to the enemy camps to prepare themselves. However, historians may tell us based on available technol-

ogy and contemporary social structure, why ritualized warfare existed.

It is with the same sense of confusion, that one encounters kairomones, those 'infochemicals' produced by predators that announce their presence to prey and which induce prey to don chemical, physical, or behavioural armour. Why should predators reveal their presence to prey; why could not predators have evolved ways of either masking the signal or dampening it altogether? Through many chapters in the book edited by Tollrian and Harvell, this question bothered me; only one paper by Tollrian and Dodson (Inducible Defenses in Cladocera: Constraints, Costs and Multi-predator Environments, Chapter 10) and the concept paper by Adler and Grünbaum (Evolution of Forager Responses to Inducible Defenses, Chapter 15) alluded to this fundamental problem. It was with relief then that I later found an answer in Kusch². *Amoeba proteus* preys upon ciliates of the genus *Euplotes*. The amoebae release a signaling molecule (A-factor) or kairomone which the ciliates respond to with predator-avoidance behaviour. Why does the predator betray its presence to the prey? Kusch² has shown that the kairomone primarily serves as a self-recognition signal. Particles coated with A-factor escaped phagocytosis, indicating that it is via the A-factor that self-recognition prevents mutual consumption of amoebae many of whom are probably asexual clones. Here the fitness advantage gained by self-recognition is possibly greater than the loss incurred by defence-induction in the ciliate prey. However, not all species of ciliates recognize the A-factor. It is possible that if and when more prey species evolve recognition and subsequent avoidance behaviour, the disadvantage of the kairomone may outweigh the benefits; this would then lead to different evolutionary trajectories for the A-factor. Adler and Grünbaum outline the evolutionary snares that await the predator. The predator might try reducing the cue but the prey could be getting more sensitive or could begin to respond to new cues; the prey may latch on to a cue like a mating pheromone that the predator cannot reduce without facing disastrous circumstances, or reducing the signal may have some energetic or foraging cost for the predator.

Subsequent editions of this book, should they be attempted, would do well to incorporate new answers as in Kusch² to these old mysteries.

This book has an agreeable mixture of data review, concepts and new ideas, and spans a range of organisms with inducible defences from protozoa, rotifers, carp, larval anurans, barnacles, bryozoans to plants. The volume hinges around one fundamental question – why inducible defences? The conventional *mantra* has been that inducible defences are cost-saving compared to constitutive defences, especially if the attacks are unpredictable and of variable intensity. Agrawal and Karban (Why Induced Defenses May be Favored over Constitutive Strategies in Plants, Chapter 3) attack this conventional point of view for plants and offer six less-investigated hypotheses for the evolutionary origin and maintenance of inducible defences. Among these is the possibility that induced defences slow down the adaptation of herbivores because they do not provide consistent directional selection pressure as would constitutively defended plants. Long-lived animals have a variety-generating immune system which can keep herbivores and pathogens on the evolutionary run; the absence of an immune system in long-lived plants can then perhaps be compensated for by induced defences. It would be worth investigating the relationship between plant reproductive life-span and the constitutive-inducible defence dichotomy. With Agrawal and Karban's provocative and stimulating exposé, the path has been cleared for the investigation of new hypotheses. Yet it appears that the cost-allocation *mantra* cannot be silenced altogether because costs are notoriously hard to measure and although investigators have used various surrogates for costs of defence, the evidence has never been clear cut. Therefore, defenders of the cost-allocation paradigm can always attribute the lack of a pattern or the presence of the 'wrong' pattern to errors of measurement or the employment of the wrong currency. A pluralistic approach to the problem of cost of defences is undoubtedly necessary and, therefore, the views of Agrawal and Karban are very welcome.

Indirect defence in tri-trophic systems has always been characterized by ex-

quisite complexity. For example, *Phaseolus* plants infested by spider mites emit specific volatiles which attract predatory mites that prey upon the spider mites. Furthermore downwind uninfected neighbouring plants also attract predatory mites in a prophylactic manoeuvre. Jasmonic acid sprayed on tomato plants induces the octadecanoid pathway which may regulate production of volatiles which attract parasitoid wasps that prey upon tomato caterpillars³. In addition, these parasitoid wasp larvae had reduced performance when developing within caterpillars reared on induced plants³, indicating a direct cost to the parasitoid and an indirect cost to the plant of the defence induction. Therefore, cost-benefit analyses of such tri-trophic systems are indeed exquisitely complex and a challenge to investigators. Dicke (Evolution of Induced Indirect Defences of Plants, Chapter 4) rightly points out that indirect defences may not even be completely under the plant's control because there may be other factors that control the parasitoid or predator populations. This may then be why some plants evolve strategies to house and feed the predators as has happened in obligate ant-plant mutualisms. Agrawal⁴ has shown that ants can be considered an induced biotic defence because the constitutive level of ants that patrol the leaves increases several-fold when a herbivore chews on the leaf as a result of attraction by volatiles emitted from the damaged tissue. Ant-plants, however, do not feature in this volume.

Chemicals are not the only inducible parameter. Crucian carp when exposed to predatory pike fish increase in body outline and become deep-bodied. This body change is reversible. Brönmark, Pettersson and Nilsson (Predator-induced Defense in Crucian Carp, Chapter 11) review the foraging optima, hydrodynamic and manoeuvrability considerations that might have led to pike preference for smaller shallow-bodied carp. Yet, one wishes that there had been a review of or speculation about the possible physiological mechanisms that might result in such amazing changes in morphology. Curtis Lively (Developmental Strategies in

Spatially Variable Environments: Barnacle Shell Dimorphism and Strategic Models of Selection, Chapter 14) writes of the remarkable system of the intertidal barnacle *Chthamalus* that develops a defended shell morph in the presence of the predatory snail *Acanthina*. This morph is resistant to invasion via the operculum. However, Lively found that he could 'induce' only 45% of barnacles and concluded that the barnacle population was probably a mixture of inducibly defended and constitutively undefended individuals. He analyses the situation of two canalized developmental states, i.e. defended and undefended, and compares it to an inducible strategy that can switch to the defended morph. He explores those areas of parameter space where either one or both strategies could co-exist and whether such strategies would be evolutionarily stable.

Plasticity of behaviour in response to changing environments can be an important attribute of reproductive success. Arnholt and Werner (Density-dependent Consequences of Induced Behavior, Chapter 12) review their work with larval bullfrogs and associated dragonfly predators and describe a series of elegant experiments which essentially explore the conceptual arena of risk-sensitive foraging wherein larval bullfrogs reduce feeding activity and thereby had lowered mortality in the presence of predators. These larval anurans, like the crucian carp, also exhibit predator-induced changes in morphology. So now, Cladocera and the helmeted *Daphnia* that made text-book history should soon be overshadowed by these vertebrate examples of predator-induced changes in body form. Arnholt and Werner speculate that behavioural defences are probably preferred when predator presence is seasonal and the prey are long-lived while morphological defences are preferred when predator presence is constant. These predictions can be tested in a variety of experimental systems.

Too much attention has been paid to prey and not enough to predators – how is the predator influenced by inducible defences? Adler and Grünbaum examine the problem from the predator's per-

spective and model the predator's response to a patchy environment with defended (inducible) and undefended prey phenotypes. They also present simulations of the ESS predator signalling level via kairomones and the coupled ESS response of the prey to the signal and thus try to predict conditions for the co-evolutionary arms-race between predator and prey. Adler and Grünbaum's paper is an excellent attempt to model the evolution of the predator-prey signalling relationship.

This edited volume is a veritable gold-mine of state-of-the-art ideas on the coupled evolution between predators and prey via induced defences. It appears that inducible defences are found in varied systems and in a variety of plant and animal taxa, that inducible defences can only evolve if cues (kairomones, mechanical damage, visual signals) are reliable, and that they should evolve when the selection pressure is unpredictable and of variable intensity. This book provides a framework and a set of working hypotheses which enable us to make predictions about when and where we would expect inducible defences to evolve and then allows us to design the definitive experiments. This conceptual framework could equally be used to study constitutive defences and indeed the title of the book could very well have been 'The Ecology and Evolution of Constitutive Defences'. This is a carefully edited book with all chapters of uniformly high quality. I strongly recommend it to all who study and think about ecology, evolution and behaviour.

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RENEE M. BORGES

Centre for Ecological Sciences,
Indian Institute of Science,
Bangalore 560 012, India

Earthquakes in ancient India

R. N. Iyengar

Strong earthquakes in quick succession in the country have heightened the sensitivity of the common man towards this natural phenomenon. Effects of earthquakes can be so severe as to cause social and political upheavals apart from property damage. Thus mitigation of seismic risk in big cities is a matter of concern to engineers and administrators alike. All the current scientific approaches the world over, depend on historical records for estimating the seismic hazard in a given region. Unfortunately for the Indian subcontinent, reliable data on place and date are available for the past two hundred years only. A recent work undertaken by Iyengar *et al.*¹ has led to a reliable identification of another twenty earthquake occurrences in the medieval period (12–18th century AD). This still leaves the ancient period almost blank except for stray references. However, this does not mean that ancient Indians were not fascinated or not affected by earthquakes. The *Vedas*, *Puranas* and the epics contain many references to earthquakes and allied phenomena. But what may be of interest in the contemporary context, are the writings of persons who were acclaimed scholars of their days. There exist a large number of writings in Sanskrit on natural phenomena. Among these, at least two are available in print namely, *Brihat Samhita* (*B.S.*) of Varaha Mihira² (5–6th century AD) and *Adbhuta Sagara* (*A.S.*) of Ballala Sena³ (10–11th century AD).

Discussion on causes of earthquakes had been a perennial topic in ancient Indian literature. According to *A.S.*, the opinion of Kashyapa was that earthquakes were due to movement of sea creatures, whereas Garga opined that it was due to the sigh of elephants carrying the earth. According to Vasishtha, tremors were due to interaction of two strong winds which eventually impacted the oceans and shook the earth. Another opinion was that earthquakes occurred due to chance or unseen forces. Finally, both *B.S.* and *A.S.* give an explanation due to Parashara that once upon a time

mountains could fly and move. Thus they were frequently falling on the earth causing earthquakes continuously. At the request of the earth, the Creator ordered *Indra* (thunder) to cut the wings of the mountains so that the earth became stable. Yet, the four elements namely Wind, Fire and Water along with *Indra* cause the earth to shake. This explanation originating from the *Rig Veda* has been given in the two texts as a rudimentary theory on formation of stable continents and not in any religious sense. Ballala Sena quotes another writer Ushanas, who was categorical that the four elements shake the earth in the four quarters east, south, west and north, respectively. From the commentaries on *B.S.*, we find that Parashara was of the opinion that eclipses and planetary aberrations could also cause earthquakes. Over the centuries this idea might have been given up since *A.S.* does not list this reason.

After discussing the causes, both the books turn their attention to classification of earthquakes into four groups, depending on the time of occurrence and the reigning stellar constellation. Thus, an earthquake which occurs from north in the last quarter of the night or in the first quarter of the day under any of the stars *Asvini*, *Mrigasira*, *Punarvasu*, *Hasta*, *Chitta*, *Svati* or *Uttarapalguni* belongs to the wind group (*Vayavya*). The directions of occurrence are not explicitly mentioned in *B.S.* These were given by Ushanas as quoted in *A.S.* It is also mentioned that many scholars do not accept the classification based on the time of occurrence. Similarly, earthquakes of the *Agni* (fire), *Indra* and *Varuna* (water) group originate from south, east and west, respectively and are governed by specific star groups. Neither of the books indicate how the directions are to be fixed. It is observed that so far the effort has been only to group the earthquakes after their occurrence, according to some recognizable attributes.

About the effects of earthquakes, Varaha Mihira does not mention about

damages to buildings. However other writers are categorical that *Vayu*-type earthquakes lead to extensive destruction of houses, monasteries, temples, palaces, towers and forts. The after-effects mentioned are occurrences of windstorms within a week after such an earthquake. Similarly, the *Agni*-type earthquake induces surface fires engulfing villages and towns. Rivers and water sources dry up. *Indra*-type tremors, lead to rains and elimination of pest colonies. The *Varuna*-type earthquake kills people living along river and sea coasts. Earthquakes were also supposed to be a portent for impending death of kings, outbreak of wars and epidemics. In *B.S.* the list of regions affected, is short, whereas information given in *A.S.* from various sources including those of *B.S.* is more exhaustive. The geographical regions disturbed by earthquakes according to both the books are as follows.

Vayu-type earthquake

B.S.: Saurashtra, Kuru, Magadha, Dasarna, Matsya; *A.S.*: Yavana, Dandaka, Salva, Sauvardhana, Pulinda, Videha, Nala, Darada, Anga, Vanga, Avanti, Malva, Trigarta, Sauvira, Yaudheya, Ksudraka, Shivika, Madraka, Shaka, Kamboja, Bahlika, Gandhara, Kalinga, Sabara, Mlechha, Tangana.

Agni-type earthquake

B.S.: Ashmaka, Anga, Bahlika, Tangana, Kalinga, Vanga, Dravida, Shabara; *A.S.*: Pulinda, Yavana, Odhra, Avanti, Ikshvaku, Kuluta, Tushara, Shivika, Trigarta, Videha, Surastra, Madhyadesh, Dasarna.

Indra-type earthquake

B.S.: Kashi, Yugandhara, Paurava, Kirata, Kira, Abhisara, Hala, Madra, Arbuda, Saurashtra, Malva; *A.S.*: Kashmira, Dravida, Andhaka, China,

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Varuna-type earthquake

B.S.: Gonarda, Chedi, Kukkura, Kirata, Videha; A.S.: Kashmira, Parata, Vatsa, Abraka, Karusha, Sinhala.

It was recognized by all the authors that earthquakes may occur under any star at any time. Thus, combination-type earthquakes became possible. The places affected by such mixed-type tremors as mentioned by Parashara, are reported in A.S.

Vayu-Agni: Kuru, Salva, Matsya, Nishadha, Pundra, Andhra, Kalinga, Vindhya foothills.

Vayu-Indra: Prachya, Shaka, China, Pahlava, Yaudheya, Yavana, Magadha.

Vayu-Varuna: Avantika, Pulinda, Videha, Kashmira, Darada.

Agni-Indra: Ikshvaku, Patachara, Abhira, China, Barukacha.

Agni-Varuna: Gonarda, Anganarajya, Coastal regions.

Indra-Varuna: Kashi, Abhisara, Achyuta, Kachadvipa.

The effects of these earthquakes were supposed to be a combination of the effects of the primary types described earlier. Many of the places in the list given earlier are easily identifiable with their present-day equivalents. Several regions are outside the present-day Indian political boundary. In Figure 1, the regions are marked taking into account the ancient geography of India as described in the works of Kautilya, Varaha Mihira, Bana, Kalhana and others. A question may arise as to how widespread the knowledge was about seismic regions in ancient times, and whether Dravida was in South India. Fortunately, a book in Kannada, *Lokopakaraka*, written in 1025 AD by Chamunda Raya⁴ under the patronage of the Chalukyan king Jayasimha is available as a cross-reference. This author devotes briefly eight stanzas for describing the four types of earthquakes. For the *Vayu*-type earthquake, he indicates the affected places as Kurumagadha, Magadha, Dravida and Kuntala. In his own explanation, Chamunda Raya identifies Dravida with *Tigula Desha*



Figure 1. Possible locations of the seismic regions.

(Tamil country). For *Agni*-type earthquakes he includes in his list Anga, Vanga, Kalinga, Kerala, Bahlika and Dravida. According to this book, *Indra*-type earthquakes affect only Saurashtra and Abhisara; whereas *Varuna*-type earthquakes affect Videha, Govardhana, Nishadha and Vihara.

Interpretation of old texts concerning natural phenomena is difficult. Still, seen critically from the present-day perspective the delineation of the country into four major seismic zones of differing damage types, 1500 years ago is no mean achievement. This indicates some kind of observation and data collection. All the regions listed are presently known to be susceptible to earthquakes. But it is interesting to note that Dravida (Tamil country), Kuntala (North Karnataka), Ashmaka (Maharashtra), Andhra and Odhra (Orissa) were considered to be earthquake prone to varying degrees.

A significantly quantitative approach to earthquakes is reflected in the ancient writings. *Vayu*-type earthquake was unanimously accepted as the most destructive. Opinions differed about the

other three. Some held that *Agni*-, *Varuna*-, and *Indra*-type earthquakes in that order were decreasingly harmful. It was perhaps in this context that the ancient writings introduced the extent of ground shaking as a measure of the four types. Ballala Sena in his A.S. first cites the book *Bhargaviya* which perhaps belongs to a period earlier than B.S. According to this text, the extent of ground shaking is 200 yojanas during *Vayu*-type earthquake. The corresponding values for *Agni*-, *Indra*- and *Varuna*-type earthquakes are given as 90, 80 and 70 yojanas, respectively. It may be speculated that this order was a reflection of the descending order of socially harmful effects associated with the four types of tremors. Varaha Mihira agrees with only the first value and for the other three, his values are *Varuna*-type 180, *Indra*-type 160, and *Agni*-type 110. No information is available on how these were obtained or measured. However, these values are amenable for interpretation from a contemporary perspective. One yojana is equal to 6 miles or 9.6 km as per actual measurements carried out by Stein⁵, of distances

mentioned by Kalhana in his *Rajatarangini*. Thus, Vayu-type earthquakes could have had a radius of area of perceptibility of (100 yojana) 960 km. This may be compared with some modern values. The mean radius of perceptibility for the great earthquakes of Assam (1897) and Bihar (1934) were 1440 km and 1280 km, respectively⁶. The level of human perceptibility for ground acceleration is generally accepted as 1 cm/s². For this level of acceleration, the attenuation results currently available lead to magnitude estimates of 6–8 for the Vayu-type earthquake. It is quite well known that damage to man-made structures generally occurs from shocks of magnitude 5 and above. Thus, the regions said to be affected by Vayu-type earthquakes, shown in Figure 1, are the most likely places where damage-causing earthquakes have been felt in the ancient past.

About prediction of earthquakes, Varaha Mihira is essentially silent. In chapter 4 of *B.S.* he echoes a previous opinion that when the moon's orb appears like the yoke of a cart stretched south to north, there would be an earthquake. There was also a belief that comets were precursors for earthquakes. Parashara mentions that the comet *chala ketu* which appears once in 5000 years shakes the earth and destroys a populated country in the Madhyadesha. Similarly, he held the opinion that the comet *Dhruva Ketu* which appears at irregular intervals also portends earthquakes.

There was also a strong belief about earthquakes being an omen for further tragedy. Ballala Sena would like us to

believe earthquake citations from *Puranas* and *Mahabharatha* as historical evidence to this effect. The great epic cites earthquakes in *Udyoga Parvan*, in *Drona Parvan*, in *Salya Parvan* and three times in *Gada Parvan*. The graphic description in *Salya Parvan* is *Chachala Sabdam Kurvana Saparvatavana Mahi* (The earth moved along with mountains and forests making sound). At other places, the epic does not associate sound with the tremors. If accepted as factual, this would be the main shock accompanied by three aftershocks felt at Kurukshetra during the great war (circa 3000 BC). Apart from this speculation nothing more can be gleaned about the dates of earthquakes, from the books under reference.

The belief of linking earthquakes with the demise of important personages, appears to be derived from Buddhist traditions. Narratives⁷ about Buddha's life mention that immediately after Buddha attained Nirvana (at Kushinagara in 483 BC), the earth trembled, stars fell down and celestial music was heard. Three months prior to this final act, the traditional texts state that when Buddha was camping in a grove to the north of the village Upabhoga, there was an earthquake. Buddha himself is said to have interpreted the earthquake as the sign that he would soon pass away into Nirvana.

Earthquakes have been occurring from ancient times in India and our ancestors took considerable interest in these as with other unusual phenomena. There has been an effort over centuries, to identify places which suffered from earthquakes. Varaha Mihira's approach of describing earthquakes in terms

of the extent of ground shaking is refreshingly scientific. The information available so far though very little, is valuable. It is quite likely that there are Sanskrit manuscripts with scientific information yet to be published. It is hoped that persons responsible for preparing seismic zonation maps of the country, study the relevant literature written prior to the colonial period before drawing conclusions on the subject.

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R. N. Iyengar is in the Central Building Research Institute, Roorkee 247 667, India.