Sir Boris P. Uvarov

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SIR BORIS UVAROV (1889–1970): THE FATHER OF ACRIDOLOGY

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Introduction

It is now 20 years since Sir Boris Uvarov KCMG, FRS died on March 18, 1970, at the age of 82, and just over a century since he was born. For more than half a century he spearheaded *acridology,* a term he coined to cover all aspects of investigations on locusts and grasshoppers and of measures of their control.

Not only was he one of the great entomologists of the century and a world authority with an encyclopedic knowledge of locusts and grasshoppers, he also possessed a wide grasp of biological subjects and remarkable powers of organization, together with a clear vision of the necessity for international cooperation in control of migrant pests.

Uvarov, or B. P., as he was known to many, was a man of astonishing vitality, who was able to combine his academic expertise with practical ability. His skill and above all his scientific integrity enabled him to persuade and at times to argue relentlessly with those in power to produce the necessary resources for the development of acridology. His attitude towards his subject was dominated by two basic principles: First, that any rational economic control of an insect pest can only be achieved through profound knowledge of

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its biology—he was angered by those who set boundaries in studies of economic entomology, for to him all investigations on Orthoptera formed a continuum. He thus stimulated work in taxonomy, biogeography, ecology, ethology, and control measures, and he influenced physiologists by persuading them to use locusts as their experimental animals. Second, he saw clearly that the vast scale and geographical complexity of the distribution of the migrant species of locusts and grasshoppers necessitated international coordination and cooperation in any control measures applied to them. He was fond of saying that insects do not recognize any artificial, political frontiers.

In writing this article we have been fortunate to have available such outstanding sources of information as the "In Memoriam" (3a) issued by the Anti-Locust Research Centre, under the auspices of its Director, Professor P. T. Haskell CMG.; the memorials of B. P. Uvarov written by Professor Sir Vincent Wigglesworth (75) and by Professor G. I. Bei-Bienko (4); and the erudite reviews by Professors M. P. Pener (32) and D. K. McE. Kevan (24). We have freely used the information summarized by them.

Also, in an attempt to assess Uvarov's impact on the development of acridology and on its present state, we have consulted a number of eminent entomologists who knew him personally, or who have been concerned with locusts and grasshoppers. We have listed their names in "Acknowledgments" and to them we owe immense gratitude for their generous help.

Youth and Education

Boris Petrovich Uvarov was born on November 5, 1889, in Uralsk in south-eastern Russia. His father was a State Bank Manager. Both his parents were keen on outdoor activities and encouraged the love of nature in their three sons, of whom B. P. was the youngest. Among Sir Boris's earliest memories were the family's frequent outings in summer to the unspoilt countryside. The boys loaded a horse-drawn wagon with tents and other paraphernalia, among which the family cat was included. The weekends were spent camping, shooting, and fishing. From an early age Uvarov developed an interest in natural history and in entomology in particular. His interests were greatly enhanced by a gift from his father of six volumes of Brehm's *Tierleben*.

Uvarov attended a local school in Uralsk from 1895 to 1902. His interest in natural history grew, and he became a keen collector of insects, for which he was awarded several school prizes. This interest was encouraged by S. M. Zhuravlev, a teacher in the Agricultural School near Uralsk, whom B. P. remembered with affection all his life.

In 1904 Uvarov started his university studies in the School of Mining at Ekaterinoslav (now Dnepropetrovsk), but in 1906 he transferred to the Faculty of Biology of the University of St. Petersburg. He was greatly influenced

by the lectures of Shimkevitch, Wagner, and Palladin but was even more stimulated by the informal meetings of the Russian Entomological Society, where students mixed freely with the most eminent entomologists. A close circle of friends also attended meetings of the Students Biological Society, usually in the apartments of D. N. Borodin, A. A. Lyubishev, and others. There they enjoyed lively discussions on biological problems and on the results of current investigations. Students were also encouraged to visit and work on taxonomic problems in the entomology section of the Zoological Museum of the Academy of Sciences. All his life Uvarov remained indebted to the stimulating environment of his years as a student.

Two sets of circumstances influenced B. P.'s particular interest in Orthoptera, namely, the richness and diversity of the insects in his native Uralsk province, and the publication in 1905 of Jacobson & Bianka's volume on Orthoptera of the Russian empire. His own diploma paper, published in 1910 (45), was on the orthopteran fauna of the Uralsk province. This taxonomic work included many observations on habitats, i.e. it had an ecological approach to taxonomy, which was only incipient in entomology of the time. In 1910 Uvarov was awarded a first class degree and married Anna Fedorovna (née Prodanjuk).

The diploma paper was not the first of his publications. In 1909, together with D. N. Borodin, he published observations on the flora of middle Emba and an essay on Lake Chalkar, and in early 1910 papers on the lepidopteran fauna of the Trans-Ural-Kenghiz Steppe and botanical-geographical notes on Inder.

Early Life in Russia

Immediately after graduation Uvarov took up a post as entomologist at the Murgab Crown Cotton Estate in Trancaucasia, but in 1911 he joined the Department of Agriculture in St. Petersburg. From there he was sent to Stavropol province to investigate the biology and methods of control of the migratory locust, *Locusta migratoria*. At the age of 23 he became the director of the Entomological Bureau of Stavropol, where he spent three years between 1912 and 1915 developing a control strategy for *L. migratoria* and the Moroccan locust, *Dociostaurus maroccanus,* as well as for other agricultural pests. It was then that he made the classic field observations which led him to formulate his famous phase theory; at the time his conclusions were so revolutionary that he withheld their publication for a number of years (see Phase Theory).

By 1915 Uvarov was firmly established in his career, and he was asked to organize plant-protection stations in Transcaucasia. From 1916 to 1920 he held the post of director of the Bureau of Plant Protection in Tiflis, Georgia.

The bureau served a wide territory, covering present-day Georgia and Armenia.

During this period Uvarov published many papers on the Orthoptera of Caucasus and wrote reports on the activity of the bureau and a book on agricultural entomology, dealing with insects of Georgia. Simultaneously he accumulated data for an important paper on the geographical distribution of orthopteran insects in Caucasus and western Asia, later published in London (46). In this paper he emphasized the importance of arid conditions in the origin of the peculiar fauna of the desert subregion of the Palaearctic stretching from central and western Asia to north Africa. In addition to these activities, in 1919 and 1920 he became the keeper of entomology at the State Museum of Georgia and a reader in entomology in the State University of Tiflis.

In the turbulent years of 1918–1920 in the Transcaucasia, and with the rise of Georgian nationalism, Uvarov's position became difficult and he found himself without most of his paid employment. Often he had to supplement his income by selling home-made pies in the market square of Tiflis, before proceeding to the museum or to give a lecture at the university. It was fortunate that at that time young Patrick A. Buxton was among the British troops in Georgia; he provided a link with London. In 1920 Uvarov received an invitation from G. A. K. Marshall (later Sir Guy Marshall) to join the Imperial Institute (later the Commonwealth Institute) of Entomology. With his wife and their small son, B. P. left for London, which became his home for the next 50 years, until his death. He did not visit Russia again until 1968, when as an honored guest of the Academy of Sciences USSR he attended the XIIIth International Congress of Entomology, held in Moscow. There he was received with great warmth and this gave him much pleasure.

Life in England

This major part of Uvarov's life falls into three periods—the first ten years 1920–1930, the years from 1930 until his retirement in 1959, and the post-retirement period.

The first ten years are characterized by a prodigious output of publications. Of the 465 publications listed in his bibliography (75), exactly a third appeared between 1920 and 1930. Uvarov's official duties at the Imperial Bureau of Entomology (under the directorship of Sir Guy Marshall and later S. A. Neave) were to identify insects sent there from all parts of the Commonwealth. With his remarkable powers of concentration, he also found time for much taxonomic work at the British Museum of Natural History and to prepare a number of outstanding publications. Among the latter were his classic paper, formulating his theory of locust phases (48), and his book, *Locusts and Grasshoppers,* published both in English and in Russian (53, 56), in which he summarized the available data on Acridoidea. It became the bible

of Orthopterologists for several decades and found its way to the shelves of many nonspecialist entomologists. He produced simultaneously two outstanding reviews, *Insect Nutrition and Metabolism* (57) and the classic *Insects and Climate* (58), which inspired much research then and in subsequent years.

In this period of 10 years, 27 of his 156 publications appeared in the USSR. Some of the major ones, "Acrididae of the European part of USSR and Western Siberia" (51), "Acrididae of Central Asia" (52), and the keys to the orthopteran orders of insects (55) laid the foundations of Russian acridology, as has been acknowledged by eminent Russian orthopterologists [Bei-Bienko, (4) and in letters to us by Mishchenko and Stebaev].

It is impossible to overestimate Uvarov's influence in his crucial early years in Great Britain, when he continually advocated more financial support for locust research and set in train an important new line in entomology. When he was still an early immigrant, without a perfect command of English, his close friendship with Francis Hemming CMG, CBE, was particularly valuable. Hemming willingly helped him with presentation of papers. They had many fruitful discussions and worked closely together until the start of the war, when Hemming was given the post of Principal Assitant Secretary, War Cabinet Offices.

In the late 1920s serious locust plagues were widespread in Africa and southwest Asia. In 1929 the Committe on Civil Research asked the Commonwealth Institute to take part in investigations into bionomics, biogeography, and periodicity of swarming locusts. Uvarov's duties included the organization and supervision of this work. By 1930, it had been formalized into a Committee on Locust Control of the Economic Advisory Council, with Francis Hemming as its Secretary (64).

A small unit of workers on locusts, initially consisting only of B. P. and his assistant (as she then was) Zena Waloff, and later a few additional members of staff, was located in one of the towers of the British Museum, Natural History. This unit was soon recognized and (unofficially) known as the International Unit of Locust Research. Uvarov's drive and initiative to achieve coordination in research in acridology and international cooperation in control of locusts led to the famous series of International Locust Conferences held in Rome (1931), Paris (1932), London (1934), Cairo (1936), and Brussels (1938). Plans were formulated for international organizations to be set up in Africa to control the African migratory and the red locusts, but these schemes were interrupted by the outbreak of war.

When the war started, investigations on acridology came to a temporary halt, but Uvarov's advisory and organizational work greatly expanded when he became the locust control adviser to the War Cabinet. At that time, countries in the Middle East and East Africa were suffering simultaneous plagues from the desert, red, and the African migratory locusts. As protection

of strategic food supplies became vital, the organizations—the Middle East Anti-Locust Unit and the East African Anti-Locust Directorate—were created. Both organizations were inspired by Uvarov and, in an overall sense, were guided by him. It was largely through his efforts that the Middle East Supply Centre in Cairo was given the responsibility of organizing operations of locust control throughout North Africa and the Arabian peninsula and coordinating anti-locust campaigns on a paramilitary basis from Morocco to India. Although it is impossible to evaluate exactly how effective these efforts were, for the first time large scale operations clearly demonstrated the practicability of international action in combatting an insect pest which hitherto was considered to be uncontrollable. In 1945 the London Centre became established as an independent institution, known as the Anti-Locust Research Centre (ALRC) under the Colonial Office and later under the Ministry of Overseas Development. Uvarov then became the director of the Centre, a position he kept until his retirement in 1959. Wigglesworth (75) said of this time, "During the next fourteen years the Centre developed into the foremost laboratory in the world for research on locusts." Simultaneously it continued to further international cooperation in locust control and coordinated and instigated much extramural research on acridids in universities and other scientific institutions in Great Britain and abroad.

Uvarov also excelled in dissemination of information on Orthoptera and was able to create a coherence and a sense of purpose in the "World of acridology" not only of entomologists, but also in other participants in the work on locusts and grasshoppers, who were scattered over many countries and several continents.

Information, which flowed so freely from ALRC, or the Centre, was supported by a unique library, founded on Uvarov's own collection of acridological literature. It became the largest specialist library on Orthoptera in the World, containing over 30,000 publications as well as unpublished manuscripts and theses. Also, all those who worked on locusts and grasshoppers were kept up to date by the circulation of *Acridological Abstracts* and of copies of *Current Research on Orthoptera* which gave the names, addresses, and special interests of investigators on acridids.

As the work and influence of the Centre expanded, two journals were launched, the *Anti-Locust Memoirs* in 1946, which presented biogeographical and cartographical studies and the *Anti-Locust Bulletins* in 1948, which contained accounts of both laboratory and field studies. Shorter papers were also published as *Occasional Reports*. Up to Uvarov's death in 1970 eleven *Memoirs* and 48 *Bulletins* had been published.

A major task of the Centre was to ensure a regular flow of information on the current situation of the three main species of locusts, *Schistocerca gregaria, Locusta migratoria,* and *Nomadacris septemfasciata*. From the time when

the work on locusts was initiated at the Imperial Institute of Entomology, reports were received from all the British territories in tropical Africa and western Asia. These were coordinated, analyzed and the data regularly plotted on monthly maps. Over the years, these data accumulated into archives now housed in the Overseas Development Natural Resources Institute (ODNRI)—the successor of ALRC in Chatham. These archives have formed the basis of many biogeographical studies and made possible the formulation of monthly summaries and forecasts of the locust situation. Uvarov saw that special coordination of forecasting and planning of control was necessary, especially for the desert locust, whose invasion area spreads over 50 countries. He interested the Food and Agricultural Organization (FAO), which by 1953 undertook coordination of control campaigns against the desert locust. By 1958 the practice of issuing monthly situation summaries and forecasts was formally recognized by the establishment of the International Desert Locust Information Service (IDLIS, later DLIS), by agreement between the United Kingdom and the FAO; DLIS was always an integral part of ALRC, but it was partly financed by the FAO.

Among his numerous activities Uvarov played a major part as a consultant to the FAO Technical Advisory Committee, particularly as the chairman of an FAO panel of experts on the long-term policy for desert locust control. He also helped to initiate the United Nations Development Program (UNDP/FAO Desert Locust Project), in which more than 40 countries participated.

Throughout the years of his directorship, numerous governments and international organizations sought Uvarov's advice on locust and grasshopper problems, so he travelled widely to many countries in Africa, the Middle East, and southwest Asia as well as in Canada, the USA and Australia. He also enjoyed his visits to workers engaged in research or control projects in the field, unhesitatingly accepting their fairly rough camp life. Their feelings toward him were of affection and respect; many in the field referred to him as "Uncle Boris," though few did to his face.

After retiring from the directorship of the Centre in 1959, he remained there as a consultant and spent much of his time writing a new book, *Grasshoppers and Locusts,* which provided a masterly synthesis of the enormous amount of new information that had accumulated since the publication of his *Locusts and Grasshoppers* in 1928. The first volume of 481 pp. was published in 1966, and he worked on the second volume until his death in 1970. B. P.'s colleagues, Zena Waloff, R. F. Chapman, and N. D. Jago, edited the text after his death and added some supplementary material, but they did not write the additional chapters that he had planned. The second volume of 631 pp. appeared in 1977. In reviewing it, J. S. Kennedy referred to it as the "Acridologist's Vademecum."

Uvarov received many awards and public honors in his lifetime. He was

elected Fellow of the Royal Society in 1950 and received The Order of Companion of St. Michael and St. George in 1943 and Knighthood of the same order in 1961. Among his other honors were an honorary Doctorate of Science of the University in Madrid in 1935 and of Commandeur de l'Ordre Royal de Lion in 1948. He served as President of the Royal Entomological Society of London from 1959 to 1961 and received Honorary Fellowships of the entomological societies of London, of Russia, France, the Netherlands, Egypt, and India. More than 80 species and subspecies and eleven genera of Orthoptera have been named after him, among them *Uvarovium* Dirsh and *Uvaroviola* Bei-Bienko.

Taxonomy

Given his vast interests and prodigious output, it is not easy to decide in which branch of acridology, or even in the wider field of pure and applied entomology, Uvarov's contribution was the greatest. He himself regarded taxonomy as his first love, specializing in orthopteroid insects with an emphasis on the old world Acridoidea. This love for systematics began with the publication of his study of the Orthoptera of Ural in 1910 and extended for over half a century. In the later part of his life other and more pressing occupations prevented him from devoting more than a token of his time to taxonomy, but he pursued this work almost as a form of relaxation and often commented that "it is good for the soul." Over 230 of his 431 publications are on the taxonomy and general systematics of orthopteroid insects, but true to his wide interests, those of a born naturalist, most of his publications contain some data on zoogeography, biology, and ecology.

His working philosophy was to produce quick taxonomic guidance where none was previously available, rather than to undertake major revisionary studies on a limited number of groups. The quality of Uvarov's taxonomic work compares favorably with that of most of his contemporaries, not all of whom recognized, as he did, the importance of examining type material. He abhorred verbosity and his style of writing is concise; his keys are clear and unambiguous; his diagnostic figures, which he regarded as essential, were rough and simple, but adequate.

Although he himself made little use of the more modern investigations into diagnostic characters, such as those of internal genital structures, he encouraged others to do so. He had a sharp, discerning eye and was remarkably quick at identification of taxa and recognition of good diagnostic characters, but he was not one to describe new genera or species lightly and there are still some specimens in the British Museum that bear his labels "sp.n."

Although his work was not altogether faultless and occasionally he did make errors in identification, the greater part of his taxonomic work has

withstood the test of time; most of the genera (241 out of 284) and the 900 species described by him are still valid.

Uvarov's theory of locust phases stemmed partly from his taxonomic research and was first published in taxonomic context of his classic 1921 revision of *Locusta*. Among his more significant taxonomic publications were the revision of *Dociostaurus* (47), old world Cyrtacanthacridinae (49, 50), *Thisoecetrus* (61), Trinchini (62), *Sphodromerus* and its allies (63) and *Caloptenopsis* and its allies (65). Much of the rest of his taxonomic work took the form of accounts of particular collections with descriptions of new taxa in them. Most of these papers were quite short. A significant exception to this was his long-delayed account of Malcolm Burr's collection of Acrididae of Angola and Northern Rhodesia (66); this is 217 pages long. Two early papers in Russian are also important: one on the Acrididae of European Russia and Western Siberia (51) and the other on the Acrididae of Central Asia (52). His studies on the Orthopteran fauna of the Caucasus, though almost completed, were never published, but the original manuscript is deposited at the Overseas Development Natural Resources Institute, Chatham.

His last contribution to taxonomy was his final chapter in Volume I of *Grasshoppers and Locusts* (70). There he presented an up-to-date systematic suprageneric arrangement based on, but slightly modified from, researches of V. M. Dirsh. To a great extent, this arrangement seems to be generally accepted even by the more conservative systematists.

Closely related to his taxonomic research was his major involvement in curating a large section of the Orthopteran collection in the British Museum, Natural History. The size, arrangement, and the scientific reliability of this collection owes much to Uvarov's energetic curatorial work over a period of some 30 years. Uvarov was never a member of the Museum staff, but his contributions to the scientific value of the collection throughout the 1920s and 1930s were of crucial importance to its development. He added much material that he collected personally and more by exchanges with colleagues in other countries. He also encouraged potential collectors among the members of the locust control organizations and such renowned explorers as Bertram Thomas, St. John Philby, and Wilfred Thesiger.

Uvarov's impact on the taxonomy of Orthoptera will long continue, not only through his own publications, but also through many of those whom he helped, encouraged, and advised, among them such outstanding taxonomists as V. M. Dirsh, N. D. Jago, D. Keith Kevan, and L. L. Mishchenko. Moreover, he initiated full-time systematic research as part of the program of the Anti-Locust Research Centre; this had a profound influence on the progress of taxonomic acridology, particularly in Africa. It is highly gratifying that this research has been maintained by the successors of ALRC, first by the Centre for Overseas Pest Research (COPR) and now by the Overseas Development Natural Resources Institute (ODNRI).

Phase Theory

The mystery of sudden appearances and disappearances of the devastating swarms of locusts, which was a puzzle at the beginning of this century, was clarified by Uvarov's field observations in the Northern Caucasus between 1911 and 1914. From these he concluded that the two allegedly distinct species, the solitary *Locusta danica* and the swarming, migratory *Locusta migratoria,* were in fact two forms of a single species. The two forms differed in their behavior, coloration, and morphology but were able to transform from one to another and to form a continuous series of intermediates. Uvarov's conclusions were principally based on the appearance of *danica* hoppers from eggs laid by *migratoria* and were strengthened by parallel observations by Plotnikov in central Asia and by Faure on the brown locust in South Africa. However, it was not till 1921 that he proposed his momentous theory of locust phases within his taxonomic revision of the genus *Locusta* L. (= *Pachytylus* Fieb.), wherein he stated that *L. danica* and *L. migratoria* were in fact two forms of the same species in phase *solitaria* and phase *gregaria*. Further, he put forward the hypothesis that the periodical outbreaks of locust plagues were associated with phase transformation of *solitaria* to *gregaria,* which formed bands of hoppers and swarms of adults that emigrated from their breeding grounds. He also postulated that phase transformation was governed by environmental factors and that swarming could be prevented by changes in conditions of the breeding grounds by cultivation and agricultural practices.

Uvarov elaborated these concepts in *Locusts and Grasshoppers* (56) when he described phase changes in several species of acridids. By that time Faure (11) and Plotnikov (33) had confirmed their earlier observations on the effect of crowding (i.e. density) on phase change in *Locustana pardalina* and *Locusta migratoria,* and evidence of phase transformation in the desert locust, *Schistocerca gregaria,* was presented by Johnston (19) and in *S. paranensis* (now *S. piceifrons*) in Central America by Dampf (6). In addition, by examining museum material Uvarov found evidence of phase polymorphism in the red locust *Nomadacris septemfasciata* and the Moroccan locust, *Dociostaurus maroccanus.* This was later confirmed for these species and for the Madagascar race of the Migratory Locust, *Locusta migratoria capito,* the South American *Schistocerca cancellata,* and the Australian Plague locust, *Chortoicetes terminifera.* Uvarov also pointed out that the amplitudes of fluctuations in phase characters vary greatly from species to species, i.e. they may be striking or slight, but they invariably form a continuous series within a species.

Uvarov's theory of phase transformation and its relationship to locust outbreaks has provided a tremendous stimulus to investigations on all aspects of the locust problem and has led to the discovery of permanent outbreak areas of the red and migratory locusts in Africa.

The theory was developed and elaborated in a number of publications, among the most outstanding of which was the joint paper with Zolotarevsky (73) on phase nomenclature, where the terms *congregans* and *dissocians* were first introduced. In a later paper (59) he discussed the importance of effects of fluctuating rainfall and unstable environment on rapid multiplication, concentration of individuals, and phase transformation. He also suggested that hoppers forced into close association become "attuned" to their proximity and "strive" to remain in a crowd—in other words, they become habituated to one another. He expressed these views later, in a Paris colloquium (68), as well as his belief that phase transformation does not depend on increase in numbers alone, but also on sensory reactions of individuals to one another, usually in a highly unstable environment. He added that the changes in external characters were merely outward expressions of phase differences in behavior and physiology, which arose from aggregation of individuals at high densities. The title of his 1966 and 1977 volumes was deliberately changed from that of his earlier classic *Locusts and Grasshoppers* to *Grasshoppers and Locusts*, to emphasize the fact that locusts are grasshoppers which are capable of gregarious behavior.

The present day concepts of phase are well summarized by Pener (32). Typically, locust species show density dependent changes in behavior, coloration, morphology, physiology, ecological responses, and ultimately in their geographical distribution. When crowded as nymphs or adults they develop the characters of the gregarious phase, and when they are isolated, of the solitary phase. These characters may shift in either direction in ontogeny or in successive generations, and phase transformation is reversible in any developmental stage of an individual.

Phase change, however, is not the cause of locust plagues, for it follows and does not precede changes in density. Also it may occur in some populations which may not be large enough to give rise to plagues.

For gregarization to occur, the first prerequisite is a set of conditions that bring the insects into close proximity, with resulting mutual encounters that lead to habituation to being touched, which then lead to aggregation and formation of groups. This process, already recorded in the field by Kennedy (23), was studied in the laboratory by Ellis (9) and Gillett (13). Such processes seen in an outbreak of the desert locust in southern Sahara have been described in detail by Roffey & Popov (40). Yet one other important behavioral change, in addition to gregarization, that occurs with phase change is in flight behavior: solitarious adults flying by night and the gregarious individuals in swarms flying by day. This behavior, coupled with gregarious stimulation in swarms and the differences in wind and temperature conditions between day and night, explains the marked differences in the distribution of populations during outbreaks and recessions.

Many of the differences between the phases were summarized by Uvarov in

Grasshoppers and Locusts (70) and his Table on the effects of increased density on locusts is reproduced here in Table 1. To this, we add a few sentences from Pener's (32) review of endocrines and phase. Pener concluded that while hormones are involved in the regulation of locust phase polymorphism, there is no clear evidence that endocrine factors constitute a physiological prima causa in phase transformation. He emphasized that the complexity of these processes has not always been fully appreciated and that while some experimental treatments may induce considerable shifts in some phase characters, others may remain unaffected. He also considers that the widely held view that the "Juvenile hormone controls locust phase polymorphism" is an oversimplification.

Throughout his life Uvarov stressed the importance of phenotypic variation in phase polymorphism, and the role of genetic variation still remains largely unexplored. Genetic factors may be involved in phase polymorphism, as was indicated by the early experiments of Gunn & Hunter-Jones (14) as well as by those of other investigators (2, 29). It has been suggested that either genetic inheritance, or extrachromosomal inheritance through the cytoplasm of the egg, or both, may be implicated.

It is now realized that phase characters, where they occur, are species specific and show a wide variation between the species (1). At the lower end of the scale are some typical grasshoppers such as *Cyrtacanthacris tatarica* or *Kraussaria angulifera* that exhibit no density effects except for development of melanic forms in the hopper stage. Between them and the true locusts, like the desert and the migratory locusts, there are many intermediate gradations. Some pyrgomorphid species, such as *Zonocerus variegatus* and *Phymateus* spp. aggregate as hoppers, but scatter on reaching the adult stage although *Zonocerus* aggregates later, at the time of egglaying. Yet others, like *Oedaleus senegalensis* and *Aiolopus simulatrix*, on crowding may form mobile hopper bands and swarm as adults, developing melanic forms in their hopper stages. They do not, however, show any detectable morphological changes. This capacity was termed by Pasquier (30) an "aptitude," different species being more or less "gregariapte." Uvorov (70) proposed the English equivalent "gregarisable," but this term did not gain usage. The number of "gregariapte" species is probably greater than is known today. For instance, following the deforestation in Mato Grosso, Brazil, there appeared previously unrecorded swarms of *Rhammatocerus* species. Conversely, with the changes of environment associated with land usage in United States, the former plagues of the Rocky Mountain locust, *Melanoplus spretus* are now no more.

A discovery as momentous as the phase theory—surely no longer a theory, but an established fact—inevitably found numerous adherents and critics. Thus Key (25, 26) and Key & Day (27) maintain that phases must be essentially defined by morphological criteria and proposed the term

Table 1 Main effects of increased density on locusts. (> Increase; < Decrease; = No effect.) (From Uvarov 1966)

	Locusta	*Schistocerca*	*Nomadacris*	*Locustana*	*Dociostaurus*	*Chortoicetes*
Hatchlings						
Size and weight	>	>	>			
Water content	=	>	>			
Food reserves	>	>	>			
Vitality	>	>	>			
Hoppers						
Melanin	>	>	>	>		
Insectorubin	>	>	>	?		
Respiratory metabolism	>	>				
Activity	>	>				
Rate of development	>	>	>			
Instar number	=	<	<			
Adults						
Size ♂	<	<	<	>	>	>
Size ♀	<	<	<	>	>	>
Activity	>	>		>		
Maturation rate	<	>	>			
Ovariole number	<	<	<			
Eggs per pod	<	<	<	>	>	<
Pods per ♀	<	<	<			
Total eggs	<	<	<			
Viable eggs	<	<	<			

"kentromorphic phases" (kentron = stimulus). In his letter to us, dated 24.3.88 Key still defends his views. This proposal, however, did not find favor with Uvarov (70) who reiterated his view that the principal difference between phases lies in their bionomics and that changes in morphology are the result of some deep physiological differences between the phases. Uvarov considered that the term "kentromorphic" detracts from this fundamental concept. Some other criticisms concern not so much phase polymorphism per se, as its role in plague dynamics, and they are referred to in the next section.

Ecology, Zoogeography, and Applied Biogeography

Throughout his life Uvarov had a lively interest in ecology. Between 1912 and 1920 he worked in the field on the Moroccan locust and the migratory locust in northern Caucasus, and in 1931 and 1932 he paid two visits to the Middle East for the study of distribution and of further ecological characteristics of *Dociostaurus maroccanus* in Turkey, Syria, and Iraq. In later days, he much enjoyed his visits as a consultant and adviser to field investigators in East Africa and in many other parts of the world. However brief his visits, he invariably brought his sweep net and tried to find time for collecting Orthoptera and noting their habitats.

Many of his taxonomic papers contain valuable ecological data and discussions, but perhaps one of his major contributions to ecology was the publication of *Insects and Climate* (58). In this monumental work he reviewed 1150 articles in eleven languages (74). Few major changes or additions have been made to the conceptual framework provided by this work. Virtually for the first time, the many ways in which climate can affect not only Orthoptera but all types of insects in all their stages were listed and brought to light. This seminal review stimulated much interest and research.

In *Insects and Climate* Uvarov put forward his view that weather factors are the prime agents in controlling populations, and he questioned the idea that all populations are in stable equilibrium with nature. Throughout the 1950s many acrimonious disputes occurred between population ecologists as to whether natural control of populations is by density-dependent or by density-independent processes. Although Uvarov did not enter these polemics in public, his name was associated with the so-called "climatic school" wherein his true sympathies lay. These arguments are now in the past, and modern ecologists have arrived at more balanced views (see 16).

Another impact on population ecology made by Uvarov was through his phase theory of locusts, which highlighted the role of behavior in population dynamics by focusing on responses of individuals to high densities. This theory also illuminated effects of density on the qualitative changes that may occur in the individuals that make up a population.

Yet another paper that had a considerable impact on the thinking of a

number of insect ecologists concerned the aridity factor in the ecology of locusts and grasshoppers (67). Uvarov stressed the three requirements of acridids, i.e. their need for plant cover, for food and shelter, and for bare ground for oviposition. Mosaics of vegetation and bare soil thus provide areas of high carrying capacity for populations of many acridid species. On similar lines, Uvarov argued that acridids can become important pests in the zones of contact between climatic and vegetational belts, and he pointed out that many such sites arise from human activities, such as deforestation, burning, and overgrazing. The importance of changes caused by agricultural practice, especially in the tropics, on populations of insect pests were further amplified by him in his publication on the problems of insect ecology in developing countries (69) as well as in his address to the XIIIth International Congress of Entomology (71). There he discussed the significance of changes in ecological conditions, either man-made or historically longer-term ones, for the dynamics of populations of acridid species, which may be affected in opposite ways. His examples included the virtual disappearance of the Rocky Mountain locust, *Melanoplus spretus,* and conversely, the great increase in abundance in recent years of the Senegal grasshopper, *Oedaleus senegalensis.*

Among Uvarov's earlier contributions of wide zoogeographical interest was a series of papers on the origin and composition of the orthopteran fauna of the Palaearctic and of the montane Orthoptera of that region (51, 52, 54). In a later paper (60), on the composition and origin of the orthopteran fauna of the great "Eremian Desert," extending through the Sahara to western and central Asia, he developed his concept of "life-forms" in Acridoidea. The term "life-form" was introduced and explored by Raunkiaer (37) and is usually used by plant ecologists as the basis of ecological classification. In his second volume of *Grasshoppers and Locusts* (72), Uvarov has a fascinating chapter on life forms, ecofaunas, and life zones, where acridid species are grouped into Terricoles, Aquaticoles, Arboricoles, Herbicoles, and their intermediate forms, on the basis of morphological, physiological and behavioral characteristics, which evolved in response to environmental pressures.

An aspect of zoogeography in which Uvarov and his colleagues have been outstanding pioneers can be called "applied biogeography," since the results of their investigations are, up to the present day, used in planning of strategies of control.

Biogeographical studies on the desert locust, the red locust, and the African migratory locust began in 1929, when Uvarov organized the collection of information and its systematic and cartographic analysis. After formation of the ALRC, a biogeographical division was set up, headed by Zena Waloff. Its aim was to analyze and plot maps of geographical distribution, breeding sites, and migratory routes of locusts and to try to relate these to climatic, vegeta-

tional, and topographic conditions. From these analyses and from field investigations of O. B. Lean and B. N. Zolotarevsky on *Locusta,* it became apparent that the plagues of the African migratory locust and of the red locust started in relatively restricted ecological regions. These smaller regions, within the enormous total territory occupied by these species, became known as their "outbreak areas," and the vast areas occupied by them at the times of plagues as their "invasion areas."

A more complex situation was found in the desert locust, whose vast geographical distribution extends from North Africa eastwards to the Indian subcontinent. Its outbreak areas are less permanent and may arise in various locations of its area of distribution when environmental conditions, mainly climatic and vegetational, favor breeding and the subsequent multiplication in numbers, sometimes over several generations. Uvarov was the first to recognize the interdependence of the widely separated breeding areas, since they are linked by the seasonal migrations of locusts.

In view of this complexity, Uvarov established, first, an information service, with its monthly summaries of the locust situation and forecasts of future developments based on the analyses of past situations, and subsequently, of the Desert Locust Information Service (DLIS), already referred to. One of the main problems of DLIS was the insufficiency of reports from the desert locust area, which spreads over more than 50 countries and has many virtually uninhabited tracts. In building up this service every conceivable source of information was tapped: consular offices, native chiefs, missionaries, district commissioners, explorers, captains of ships at sea, to all of whom simple instructions were given (later this took the form of a small locust handbook) for collecting and reporting useful information. Simultaneously, sponsored field investigations by British entomologists attempted to locate the source areas, and similar investigations were soon taken up by entomologists from many other countries concerned with the locust problems. As the result of laboratory and field research on the desert locust, sufficient knowledge of its breeding and migration patterns accrued to allow forecasting of events, useful in the planning of control operations.

Past and Present Trends in Research and Development of Acridology

The postwar years were justly regarded by many as the golden years of research on locusts. The last 20 years of Uvarov's life saw the publication of some 7000 papers, or about one per day; they were the theme of his two volumes of *Grasshoppers and Locusts*. It is almost presumptious to enumerate the highlights among them, but some of those more familiar to us spring to mind. Among them is the classical work of Weis Fogh, and his and Jensen's work on the flight dynamics of locusts. Rainey's hypothesis on the downwind

displacement of locust swarms and their concentration in areas of convergence of air masses is fundamental to understanding and forecasting of swarm movements, as are his subsequent studies on meteorology and locust migrations (e.g. 36). The development of ultra-low-volume spraying which stemmed from the work of John Sayer of the Desert Locust Control Organization is significant, as are Z. Waloff's studies on biogeography and flight behavior of locusts, Ellis's investigations on aggregation of locust hoppers, and Norris's work on reproduction in locusts. Studies on population dynamics of the Moroccan locust by Dempster, of the migratory locust by Farrow, and of the British grasshoppers by Richards and N. Waloff, are noteworthy, as are Greathead's studies on the natural enemies of acridids, Dirsh's monumental work on acridoid taxonomy, and the publication of Johnston's *Annotated Catalogue of the African Grasshoppers* (20, 21).

After Uvarov's retirement, the stimulus of his continued presence was such that initially the Centre increased its scope of work, notably by creating its Field Research Division in 1963. After Uvarov's death the pace began to slacken when in 1971 ALRC was transformed into the Centre for Overseas Pest Research (COPR) with a greatly expanded program of investigations into other pest species, inevitably at the expense of research on acridids. In the 1980s COPR had undergone two other transformations, first into the Tropical Development and Research Institute in 1983 and then into the Overseas Development Natural Resources Institute in 1987. The declared policy of the Overseas Development Administration was that all work on acridology should be phased out by the mid-1980s. However, some outstanding research was done in this period, and in a modest way taxonomic and advisory work is still pursued.

Among the notable investigations at COPR were those of Ewer and McCaffery on the water uptake, development, and survival of acridid eggs. Taxonomic studies by Jago and his colleagues (15, 18), which included hybridization, elucidated the systematic position of the neotropic species of *Schistocerca*. Meanwhile, in the world at large, contemporary work by Key and by White in Australia on speciation in morabine grasshoppers led to important developments in the application of cytology to systematics, a method subsequently used by Hewitt in France and Baccetti in Italy. Further advances that led to the definition of several new families were made by Amedegnato (3) and Descamps (7) in the hitherto neglected orthopteroid fauna of Central and South America.

In the field, among the most important studies were those on *Zonocerus variegatus*, conducted by COPR and the University of Ibadan, under the general supervision of R. F. Chapman. These resulted in over a score of papers on different aspects of the biology, behavior, and population ecology of the grasshopper, with recommendations for its control.

After the severe drought in the Sahelian belt in Africa in 1974–1975, rains brought massive outbreaks of grasshoppers, spearheaded by *Oedaleus senegalensis*. This initiated two research and control projects: the first by COPR and OCLALAV (5, 12, 34, 35) on ecology, taxonomy, and seasonal migrations including radar observations. The second, by PRIFAS (Projet de Recherche Interdisciplinaire Francais sur les Acridiens de Sahel), resulted in many publications and in a biomodel of *O. senegalensis* (28).

A new development in control strategy was the use of remote sensing imagery in monitoring, which narrowed down the ground areas to be surveyed. Biogeographical and ecological studies during the long recession period of the desert locust (31, 35) indicated that some parts within its vast recession area, notably those associated with major relief features, show a particularly high incidence of occurrence and breeding of the locust. Monitoring for rainfall and ecological conditions suitable for the building up of populations was initially carried out by aerial surveys but is now increasingly done by satellite imagery. Such a method has been applied with considerable success in Australia for monitoring of the dynamics of *Chortoicetes terminifera* (17, 43), where the all-important phenology of the locust's foodplants is discernible from satellite imagery.

Among the most interesting developments during this period was radar entomology. The pioneering attempt to monitor locust flight in the Sahara, sponsored by ALRC in 1968, was a spectacular success. The radar showed that locusts could actively select their height of flight and maintain apparently purposeful orientation and that wing-beat frequencies, in some cases, help to identify the species (Schaefer 41). Studies in 1973, 1975, and 1978 provided further information on flight behavior and established that migrations in terms of hundreds of kilometers occurred quite regularly, not only in locusts, but also in many species of grasshoppers (38, 39, 42). Later, these studies were extended to the Australian plague locust, *C. terminifera*. Combinations of ground-based and airborne radars have also been used in investigations on migratory insect pests, other than acridids.

In Canada and the United States the problem of range grasshoppers persists, and Canada now issues regular forecast bulletins. For environmental considerations, biological control by the protozoan *Nosema locustae* baits is increasingly favoured.

In the USSR taxonomic work on acridids is continued in Leningrad by Mishchenko and Gorokhov, while studies on the ecology and zonal distribution of Acridoidea, inspired by works of Uvarov and developed by Bei-Bienko, continue under the supervision of Stebaev at the Novosibirsk Research Centre.

A number of computer models, based on several systems, have been developed during this period; among them are those by de Boer in the

Netherlands, which simulates desert locust migration as determined by wind trajectories at different heights, and by PRIFAS for *Oedaleus senegalensis*. PRIFAS needs a special mention, for it has evolved into what is now the most important center of acridological research in the Old World. It is part of the International Cooperation Center for Agricultural Research and Development (CIRAD) at Montpellier, France. PRIFAS pursues all the more topical lines of locust research, but its speciality is modelling. Having developed biomodels for the Senegalese grasshopper and the Madagascan and the African migratory locusts (8), scientists at the Center are now facing their greatest challenge in developing a model for the desert locust; this is done with participation of G. B. Popov and support from FAO.

Research and control of locusts have also been actively pursued in Australia. Among the notable recent contributions from CSIRO are Farrow's ecological studies on *Locusta migratoria migratorioides* (10). This tropical migratory locust presented no problems until the 1960s, when areas of grass, poor scrub, and woodland in the Central Highlands of Queensland were cleared for development of pasture lands. In the 1970s, these changes in land use, together with high rainfall, favored multiplication and gregarization of the locust and resulted in a severe outbreak.

Economically the most important locust in Australia is *Chortoicetes terminifera*. Past studies on this species by Key and subsequent studies by D. P. Clark in collaboration with (the then) Anti-Locust Research Centre established its patterns of migration. In more recent years, members of a federal organization, the Australian Plague Locust Commission (under the directorship of P. M. Symmons, formerly of COPR) have made further advances in the understanding of biogeography, flight behavior, and the importance of phenology of the food-plants to the dynamics of the plague locust. They have established a monthly forecasting service which contributes to the success of their control measures.

Space does not allow for enumeration of other recent advances in acridology, except for the outstanding publications of COPR, namely, Uvarov's second volume of *Grasshoppers and Locusts* in 1977, the *Desert Locust Forecasting Manual* edited by D. Pedgley in 1981 (31), and *The Locust and Grasshopper Agricultural Manual* (44) published in 1982 and initiated on Uvarov's inspiration in the mid-1960s.

Appreciation

Uvarov was not only a great entomologist, he was also a great personality, as all who came into contact with him recognized. With his far-reaching mind, his energy and enthusiasm, he was able to build up a monumental knowledge of locusts and grasshoppers and to found an institute (ALRC) which in his

time became the foremost center in the world for research on locusts and guidance to their control.

His approach to the locust problem was eminently practical; he always emphasized the necessity of international cooperation in control of acridids. In his time other research organizations also developed which in a sense were extensions of ALRC into field work (e.g. the Desert Locust Survey; International African Migratory Locust Control Organization or OICMA). Uvarov's intellectual stimulus and force of personality held the expanding world of acridology together. B. P. translated a personal vision into a concrete achievement. He was able to achieve much, because of his unquestionable scientific integrity—a phrase recurrent in memorials dedicated to him and in many letters written to us by orthopterologists.

Acridology was Uvarov's life. Although he regarded himself primarily as a taxonomist, many biologists will remember him for his phase theory of locusts. He had a great breadth of biological knowledge and a broad grasp of ecological principles. The only area of study that did not interest him was genetics, though this might have added to the understanding of the phase change and variation of the widespread species. All his life he advocated ecological methods in control of acridids, keeping the use of insecticides to a minimum. By now, his views are well supported by the numerous examples of changes in the pest status of grasshoppers and locusts (e.g. 10) that have followed on changes in land use, but it remains doubtful that manipulation of the environment is practicable in control of such wide-spread species as the desert locust.

After Uvarov died, the running down of the locust organizations gradually set in, for there was no substitute for his organizing genius. Moreover, since most of the African countries gained independence, control measures have fragmented, a process to which almost 30 years of recessions from locust plagues contributed. It is to be hoped that the recent massive outbreak of the desert locust, with the unprecedented flights of its swarms across the Atlantic on at least two occasions, will stimulate new work in acridology. It is regrettable that the successors of ALRC have given up the training of new locust personnel. Now that experienced field acridologists are needed, FAO is relying on those who have retired or are nearing retirement. New generations of acridologists will be thankful to Uvarov for his monumental volumes of *Grasshoppers and Locusts,* which will continue to be a source of information for many years to come.

In spite of the wide international recognition of his achievements and the scientific and civic honors bestowed on him, B. P. remained an unassuming and an approachable person. He was rarely satisfied, but his highly critical attitude was tempered by his dry wit and a sense of fun. He was always helpful and understanding to young people and remained receptive to new

ideas and findings to the end. He also established an easy rapport with the heterogeneous collection of locust field officers, who regarded him as a living legend.

Although in many ways he remained very Russian, he had total and unswerving loyalty to his adopted country. When asked what was it that he liked about England, he instantly replied, "the decency of the common people".

B. P. never suffered fools gladly and was a hard taskmaster, but all those who have been through his school will always remember him with gratitude, respect, and affection.

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