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Editorial for Journal of Insect Physiology Special Issue: A century of research into locust phase polyphenism

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In 1921, young entomologist Boris Uvarov, working with his friend Vasily Il'ich Plotnikov, published their discovery that two species of grasshopper – the swarming Migratory Locust, *Locusta migratoria*, and the lone-living *Locusta danica* – were actually different forms of the same species (Uvarov, 1921). Observing a swarm before the First World War, Uvarov and co-workers noted that "although the bulk of the larval swarms consisted of *migratoria*, there were many individuals which were certainly *danica*, these being different in colouration and showing a tendency to desert the swarms." Further experiments led Uvarov to conclude that the different forms "cannot be separated specifically and that they represent taxonomic units of lower grade than the species, which must be called, according to the law of priority, *L. migratoria* L. They are, however, quite distinct from each other, though connected by transitional forms." In the same publication, Uvarov also described his correspondence with the South African entomologist, Jacobus Faure, who had made field studies of the species now known as the Brown Locust, *Locustana pardalina*. Uvarov concluded that "These valuable observations of Mr. Faure's leave no doubt that *L. pardalina* has, like *L. migratoria*, two different phases, which differ in morphology and coloration, but more profoundly in the biology" (Uvarov, 1921).

In 1923, Uvarov extended his theory yet further based on *Schistocerca* specimens at the Natural History Museum, London, noting in under stated fashion that "Amongst the variations found there is one which deserves special attention, because I am convinced that it represents a solitary living phase of the species [Desert Locust, *S. gregaria*]. This form agrees perfectly well with the description of *Acridium flaviventre*, Burm. (Handb. Entom., ii, p. 631, no. 11, 1838) and I call it, accordingly, *S. gregaria* ph. *flaviventris*, Burm." (Uvarov, 1923). In the same article, Uvarov also suggested the possibility of phase polyphenism in the Red Locust, *Nomadacris septemfasciata*. Uvarov went on to lead the Anti-Locust Research Centre in London, with much of his work eventually compiled into two volumes that remain core texts in grasshopper and locust biology (Uvarov, 1966; 1977). Sir Boris Uvarov retired in 1959 and was knighted for his services to science in 1961. He died in 1970; for an obituary, see Waloff and Popov (1990).

We now understand that locust phase polyphenism is a striking example of phenotypic plasticity, the ability of an individual genotype to give rise to different phenotypes in response to different environmental conditions. During locust phase polyphenism, the environment – in this case, the local population density of other locusts – drives the expression of a suite of behavioural, morphological and physiological traits. At one extreme, locusts living at low population densities exist in the "solitarious phase". Solitarious locusts have a cryptic phenotype both behaviourally and morphologically, show relatively low levels of activity and, most importantly, actively avoid one another, thereby perpetuating their solitarious state. At the other extreme, locusts experiencing crowded conditions because of high local population densities from which they cannot escape develop "gregarious phase" characteristics, including bright warning colouration, higher levels of daytime activity, and a propensity to form cohesive groups, which again forms a positive feedback loop. Locusts can change from one behavioural phase to the other in as little as a few hours, with morphological characteristics like colour starting to follow at the next moult, but also accumulating across generations. The entire process is reversible such that local population density is a key factor driving an individual's entire life history.

We sought to commemorate the centenary of Uvarov's seminal descriptions of locust phase biology in *Locusta migratoria* and *Schistocerca gregaria*. Beyond this achievement, Uvarov was a tireless champion of the locust as the ideal model organism for studying physiology, both of insects specifically and as a model animal more generally. The widespread presence of locusts in schools and labs across the world is in no small part due to his proselytising efforts. This special Issue of the Journal of Insect Physiology brings together papers from a range of current locust research groups covering various locust species. In the spirit of Uvarov, they form an eclectic collection that spans the breadth of modern biology.

Reproductive resource allocation is a fundamental life-history trait with important fitness consequences and is one of many aspects of locust biology affected by phase change. Across two papers, Maeno, Piou and Ghaout (2021) and Maeno et al. (2022a), Maeno et al. (2022b) address the mechanisms by which gregarious phase *Schistocerca gregaria* lay fewer, larger eggs than solitarious individuals, and how embryogenesis in these larger eggs affects the size of the eventual hatchlings.

The paper by Srithiphaphirom and Robertson (2022) uses a combination of neurophysiology and neuropharmacology in *Locusta migratoria* to investigate the mechanisms underlying cold hardening, a process that enhances cold tolerance. This work exemplifies the use of locusts as a model system to address general physiological questions.

Olfaction is a key sensory modality in locusts and is central to many of their phase-specific behavioural interactions with each other. Torto, Kirwa, Kihika and Niassy (2021) compare the odour bouquets of *Schistocera gregaria* reared under captive conditions with wild-caught populations and reveal that this bouquet is much richer in the field-collected animals. Although lab-based studies have provided profound insights into locust phase physiology and behaviour, this study underlines the importance of complementing this approach with field-based studies.

These physiology-based papers are complemented by studies using a molecular approach, which was not available to Uvarov. Ragionieri *et al*. (2022) use a combination of genomics, transcriptomics and mass spectrometry to compile the most comprehensive list of desert locust neuropeptide sequences to date, which will be an invaluable resource for future molecular-based studies of physiology and behaviour. One such example is that of Foquet and Song (2021), who perform RNA interference of the neuropeptide corazonin in the Central American Locust, *Schistocerca piceifrons*, having a marked effect on dark patterning and morphology. Van Lommel *et al*. (2022) also use RNA interference to show that the nuclear receptors for the hormones ecdysone (EcR) and retinoid-X (RXR), which usually form a heterodimer, have some independent effects on male maturation in the desert locust.

We are pleased that we could include a comparative field-based study, which complements much of Uvarov's earliest work. Piou *et al*. (2022) investigate marching and thermoregulation in the South American Locust, *Schistocerca cancellata* in Argentina, and compare their findings to similar behaviours in the congeneric desert locust. This work highlights the importance of comparative studies, and presents the South American locust as a tractable species for investigating phase polyphenism in the field.

The environmental circumstances leading to marching, and how these interact with behavioural phase, are the focus of a modelling paper by Georgiou *et al*. (2022). They investigate the foraging advantages presented by increasingly heterogeneous environments, and how these advantages increase with population density. Modelling studies such as this are of vital importance in understanding the onset of collective behaviours in locusts, which are often difficult to quantify in the field given their cross-border spatial scales.

Finally, we include a personal perspective on the recent history of locust phase change research. Professor Stephen J. Simpson (2022) has made an enormous contribution to the study of locust phase change, first at the University of Oxford and subsequently at the University of Sydney. Perhaps the single greatest contribution to phase research that he and his research group has made is in developing robust metrics for the quantification of behaviour, both at the level of individual phase state and during collective marching behaviour. This in turn has led to further insights in fields as diverse as neurophysiology, endocrinology, immunology, molecular biology, and nutrition. Locust phase change has been just one strand of his diverse research career, but here Professor Simpson reminisces on his personal history in locust phase polyphenism research and the many people he has inspired and worked with.

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