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Review

Phase polyphenism and preventative locust management

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ABSTRACT

The ecology of phase polyphenism plays a major role in locust swarm formation. We describe how recent advances in the understanding of phase polyphenism can be combined with existing management approaches as part of a preventative Desert locust management strategy. We start with a brief overview of phase polyphenism with particular emphasis on the role that resource distribution patterns play in the process of locust phase change. We then review current perspective on preventative locust management, and conclude by proposing a framework for quantitatively assessing the risk that phase change will occur in local locust populations. Importantly, the data required to implement this framework can be readily collected with little additional effort or cost just by slightly modifying locust habitat survey protocols that are already in operation. Incorporating gregarization risk assessment into existing preventative management strategies stands to make a considerable contribution toward realizing sustainable goals of reductions in the pesticide, manpower and financial support necessary to combat Desert locust upsurges, outbreaks and ultimately plagues.

Contents

1. Introduction

The effective management of locusts remains the ultimate practical aim of locust research. Our goal in this paper is to provide a simple framework for assessing the risk of gregarious phase locust populations forming in a given area, a tool that can then be used to prioritize and target critical populations for early monitoring and control. Most importantly, we argue that much of the fundamental knowledge and logistical infrastructure for the implementation of such a strategy is already in place. The crucial step will be the integration of these two pools of expertise into a cohesive, biologically informed approach to preventative locust

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management. We focus primarily on the Desert locust, *Schistocerca gregaria*, because it has been the most widely studied in terms of phase polyphenism along with its underlying mechanisms and ecological consequences. In many cases there are likely to be strong parallels with respect to management of other locust species, but we acknowledge that a variety of biological, political and social factors may preclude the development of an approach that is universally applicable.

2. Phase polyphenism: an overview

Locust phase polyphenism is a remarkable form of phenotypic plasticity in which the expression of numerous physiological, morphological and behavioural traits occurs in response to changes in local population density. The process has been studied in considerable detail dating back to its initial discovery by Boris Uvarov (Uvarov, 1921), and has been the topic of many reviews and synthetic treatments, the most influential of which were by Uvarov himself (Uvarov, 1966, 1977) and more recently by Meir Paul Pener and colleagues (Pener, 1991; Pener and Yerushalmi, 1998; Pener and Simpson, 2009). Readers interested in the mechanisms of phase polyphenism, most of which are beyond the scope of this paper, are encouraged to consult the most recent of these reviews. The cause and effect relationship between the expression of phase polyphenism and locust swarm formation has been questioned in the past, most notably by Key (1950) who argued that density-dependent phase changes were a consequence rather than the primary driver of swarm formation and mass migrations. However, it is now well established that phase change plays a central role in the formation and subsequent mass migration of locust hopper bands and swarms (e.g. Buhl et al., 2006; Gray et al., 2009; Simpson and Sword, 2009; Pener and Simpson, 2009).

2.1. The central role of behavioural phase change

The role of behaviour in the process of phase change is paramount and our proposed approach to preventative locust management is based largely on recent advances in the understanding of locust behavioural ecology. Upon encountering crowded conditions, the behaviour of solitarious phase individuals shifts rapidly into the gregarious state. The behavioural tendency of gregarious individuals to aggregate, rather than avoid one another as in the solitarious state, provides a positive feedback for continued local crowding that can then lead to phenotypic changes in other, more slowly developing traits such as colouration or morphology. As a result, changes in behaviour during the process of phase transition act to couple the expression of several different and independently regulated phase traits into a single density-dependent threshold trait at the population level (Simpson and Sword, 2009). Although behavioural gregariousness alone appears to be sufficient to promote group formation and subsequent mass movement (e.g. Buhl et al., 2006; Gray et al., 2009), the expression of other density-dependent traits in gregarious populations such as warning colouration or pathogen resistance can further contribute to local population growth and crowding, leading to migratory band and swarm formation (Sword et al., 2000; Wilson et al., 2002; Simpson and Sword, 2009). If unchecked, the gregarization process will continue locally until environmental factors force a decline in population size below the threshold for gregarization, or locusts move *en masse* away from a given area, recruiting solitarious locusts as they go and merging with other migrating groups that they may encounter (Roffey and Magor, 2003; Simpson and Sword, 2009). Importantly, behavioural phase change in response to crowding occurs at a similar time-course across developmental stages ranging from first instars to adults, and even when transmitted epigenetically across generations (Pener and Simpson, 2009). Therefore, focusing on behavioural gregarization can serve as an ecological target for management that is broadly applicable across multiple life history stages.

The process of gregarization occurs in local solitarious populations well before upsurges, outbreaks and plagues. Thus, in order to be able to assess the risk of gregarization occurring in a given population, we must first be able to answer a key question: What causes solitarious phase locusts to overcome their strong predisposition to avoid other locusts, such that they come together and gregarize? The ecological answers to this question provide the rationale for developing a preventative management strategy based on our understanding of locust phase polyphenism.

3. Phase change and resource distribution

Weather and habitat structure are the two primary factors involved in promoting crowding among solitarious phase locusts. At its most basic, local population sizes increase in response to favourable conditions for survival and reproduction, most commonly associated with rainfall. As local population sizes increase, individuals are concentrated by small-scale features of the habitat such as patchily distributed host plants for feeding or microclimates for basking and shelter. Oviposition behaviour and suitable sites for egg laying provide another important ecological factor that can influence contact among either the adults themselves or their offspring (Bashir et al., 2000). It is the resulting close contact among individuals on these resources that triggers the process of behavioural gregarization (e.g. Kennedy, 1939; Bouaïchi et al., 1996; Despland and Simpson, 2000a,b). Importantly, weather and habitat structure can interact in different ways at different scales, the results of which can either positively or negatively influence the likelihood of local crowding and gregarization (Despland et al., 2004). Below, we consider these effects on gregarization first at the fine scale relevant to individual insects within a habitat (i.e. the scale at which individual gregarization occurs) and then scale up to landscape and regional consequences.

3.1. Local habitat structure

It has long been observed that local crowding on discrete resources in the habitat such as host plants, basking or shelter sites appears to cause initially solitarious phase locusts to come into contact with one another and trigger the shift to the gregarious phase (Kennedy, 1939; Chapman, 1955; Ellis, 1963; Roffey and Popov, 1968). Direct empirical tests of these observations were facilitated by the development of a behavioural assay that allowed for the phase state of an individual locust to be quantified in response to various experimental treatments under controlled laboratory conditions (Roessingh et al., 1993). Through the use of this assay, a detailed picture emerged of the time-course, mechanisms and stimuli involved in phase change within the life of an individual locust, as well as the epigenetic inheritance of phase characteristics across generations [see Simpson et al. (1999) and Pener and Simpson (2009) for reviews]. Of particular relevance to the preventative management of locusts is that this assay system has been used in both the laboratory and field to directly test hypotheses about the ecological factors involved in locust gregarization (Bouaïchi et al., 1996; Despland et al., 2000; Despland and Simpson, 2000a,b) and to parameterize individual-based simulation models for exploring population-level consequences of habitat structure (Collett et al., 1998). These studies confirmed that the mutual stimulation arising from aggregation of individuals on discrete resource patches does, in fact, result in the gregarization of initially solitarious phase individuals (Bouaïchi et al., 1996; Despland and Simpson, 2000a). Such experiments also