Locusts and Grasshoppers: Behavior, Ecology, and Biogeography

Guest Editors: Alexandre Latchininsky, Gregory Sword, Michael Sergeev, Maria Marta Cigliano, and Michel Lecoq

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Editorial Board

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Editorial

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Alexandre Latchininsky,[1] Gregory Sword,[2, 3] Michael Sergeev,[4, 5] Maria Marta Cigliano,[6] and Michel Lecoq[7]

[1] *Department of Renewable Resources, University of Wyoming, 1000 E. University Avenue, Laramie, WY 82071, USA*

[2] *School of Biological Sciences, University of Sydney, Sydney, NSW 2006, Australia*

[3] *Department of Entomology, Faculty of Ecology and Evolutionary Biology, Heep Building, Texas A&M University, College Station, TX 77842-2475, USA*

[4] *Department of General Biology and Ecology, Novosibirsk State University, 2 Pirogova Street, Novosibirsk 630090, Russia*

[5] *Laboratory of Insect Ecology, Institute of Systematics and Ecology of Animals, Siberian Branch, Russian Academy of Sciences, 11 Frunze Street, Novosibirsk 630091, Russia*

[6] *Division Entomologia, Museo de La Plata, Universidad Nacional de la Plata, Paseo del Bosque S/N,1900 La Plata, Argentina*

[7] *CIRAD Bioagresseurs, TA A-106/D, Campus International de Baillarguet, 34398 Montpellier cedex 5, France*

Correspondence should be addressed to Alexandre Latchininsky, latchini@uwyo.edu

Locusts and grasshoppers (L&G) (Orthoptera: Caelifera, Acridoidea) are an essential component of both, healthy, and disturbed grassland ecosystems. These insects are abundant in natural and anthropogenic habitats (rangelands, wetlands, agricultural fields, lawns, etc.). They stimulate plant growth, participate in nutrient cycling, and play important role in food chains [1–5]. Some grasshoppers are proposed as ecological indicators of ecosystem qualities and efficacy of ecological networks [6]. On the other hand, when their populations grow to catastrophic dimensions, L&G are among the most devastating enemies of agriculturists. Outbreaks of locusts such as *Schistocerca gregaria* (Forskål, 1775), *Nomadacris septemfasciata* (Serville, 1838), *Locusta migratoria* Linnaeus, 1758, *Calliptamus italicus* (Linnaeus, 1758), *Dociostaurus maroccanus* (Thunberg, 1815), *Chortoicetes terminifera* (Walker, 1870), and many abundant grasshopper species continue to occur on all continents except Antarctica and affect the livelihoods of one in every ten people on Earth. Such L&G outbreaks are now better controlled and their frequency and size have been reduced with the application of preventative strategies [7, 8]. However, invasions still persist. During the outbreak of the Desert locust *S. gregaria* in Africa in 2003–2005, over eight million people suffered from severe 80 to 100% crop losses [9]. To combat the locust swarms, 13 million hectares in 22 countries on three continents were treated with broad-spectrum neurotoxins. Such transcontinental operation, including the food aid for affected population, cost over half a billion US dollars to the world community [10].

Losses to L&G are not limited to crop and rangeland destruction. Besides the economic damage and its subsequent negative social impact, L&G outbreaks may seriously alter ecological processes across landscapes (e.g., carbon and water cycles). The rapid loss of vegetation cover may result in soil erosion and increased runoff. L&G can also destroy food sources for many animals and thus affect biodiversity; such effects may be particularly pronounced in isolated insular ecosystems [11]. Large-scale L&G control programs can also affect biodiversity, including that of nontarget grasshoppers [12]. Despite decades of intensive research, the mechanisms underlying L&G population dynamics (and for locusts: phase transformation) are not fully elucidated. Only recently, significant advances were made in our understanding of L&G behavior and ecology, particularly individual and group movement, nutritional requirements, and biochemical mechanisms underlying the transformation between solitarious and gregarious locust phases [13–15]; see also review in [16].

Besides the notorious pests, this group of insects includes many understated rare species which require protection [17–19]. To complicate the picture, following landscape changes induced by human agricultural activities, some economic pests may become exceedingly rare [20]. On the other hand, many orthopteran species benefit from human-induced landscape changes and increase their abundance [18, 21]. Disturbed and new habitats can be important for spreading and living of some native and alien grasshopper forms [18, 21, 22]. At the same time, many of rare grasshopper species are threatened by anthropogenic influences, such as overgrazing and ploughing [18]. However, in various areas, such as temperate Eurasia or in Tropical Madagascar, several centers of orthopteran diversity and endemism overlap with areas of frequent L&G outbreaks [23–25]. This means that problems of plant protection and conservation biology should be solved on the complex basis of a holistic approach. However, it is hardly ever the case; pests and rare species are usually studied separately, and their possible relationships are not explored.

Although the general patterns of grasshopper distribution are described for different regions [26–28], the main factors and processes determining grasshopper diversity patterns at different scales are still under discussion. Importance of temperatures and precipitation is evident, but the distribution of many species, populations, and assemblages could not be explained by macroclimatic factors only [29]. This means that the role of other factors and processes should be investigated more thoroughly. At a regional level, it is possible to establish the general pattern of regional biodiversity and explain how the spatial distribution of populations permits species with various origins and different ecological preferences to coexist [30].

An example of this approach is the opening article for this special issue of Psyche, in which M. G. Sergeev reviews distribution patterns of over 130 species of grasshoppers and their kin in the boreal zone. Grasshoppers and their relatives occupy there almost exclusively open habitats, such as meadows, mountain steppes and tundras, clearings, openings, bogs, and stony flood plains. The boreal orthopteroid assemblages exhibit low species diversity and abundance. Based on the biogeographic analysis, the author concludes that relationships between the faunas of the Eurasian and North American parts of the boreal zone are relatively weak.

Local grasshopper distribution patterns have been discussed since the beginning of the 20th century. Possible relationships between grasshopper diversity, plant species composition, and habitat structure have been discussed for many decades. The paper of D. H. Branson (second in this special issue) provides an example of such studies. The author found these relationships too complicated for simple explanations. The type, level, strength, and complexity of these relationships may be determined not only by local but also by regional patterns. Consequently, to evaluate general trends in grasshopper diversity one should study all main regions and ecosystems in the same manner. This idea may serve as a basis for an ambitious regional study.

The third paper of the special issue is devoted to a complex terminological issue. Acridologists have used a variety of terms to describe groups of grasshoppers, including assemblage, community, guild, and population. This terminological diversity has raised the question of whether one of these descriptors is the correct one. The author, J. A. Lockwood, argues that a term is correct if it accurately reflects the conceptual framework of the investigator and effectively communicates this perspective to others. He describes the contexts in which the most common terms are appropriate.

In the next paper, O. Olfert et al. investigate the impact of climate changes on distribution and relative abundance of a pest grasshopper of major economic importance in North America, *Melanoplus sanguinipes*. Various scenarios of climatic changes were used to parameterize a bioclimatic model of this species. Compared to predicted range and distribution under current climate conditions, model results indicated that *M. sanguinipes* would have increased range and relative abundance in more northern regions of North America. Conversely, model output predicted that the range of this crop pest could contract in regions where climate conditions became limiting. However, some caution has been expressed by authors. The impact of biotic factors such as natural enemies should also be considered, and bioclimatic modeling of grasshopper populations will surely benefit in the future from a multitrophic approach (host plants-grasshoppers-natural enemies).

The fifth paper of this special issue by H. Song reviews the current state-of-the-art regarding locust phase polyphenism in species other than the two model locusts. Although the mechanisms of locust phase transformation are relatively well understood for the Desert locust and the Migratory locust, they remain largely obscure in nonmodel locust species. The author found similar density-dependent phenotypic plasticity among closely related species. He emphasized the importance of comparative analyses in understanding the evolution of locust phase and proposed a phylogeny-based research framework for future analyses.

In the next paper M. Lecoq et al. present a typology quantifying density-dependent color change in the Red locust nymphs. This information can contribute to improving the reliability of the data collected by the National Locust Centers when surveying this major pest. The authors, in Madagascar, sampled hoppers from several populations of different density and measured the color of different body parts as categorical variables. They found that color change is positively correlated with population density. This study is an important contribution to our knowledge of locust coloration in the field, for which there is currently a weaker understanding than that for laboratory populations.

The seventh paper of this special issue by S. O. Ely et al. discusses the diel behavioral activity patterns of solitarious Desert locust adults. The authors found that the insects were more attracted to volatiles from potted *Heliotropium ovalifolium* in scotophase than in photophase. The attraction towards the host plant odors, in both photophase and scotophase, concurs with previous observations on locust oviposition preferences near these plants.

In the eighth paper, R. B. Srygley and S. T. Jaronski report experiments with *Beauveria bassiana* (Fungi: Ascomycota), an entomopathogenic fungus that serves as a biological control agent of Mormon crickets *Anabrus simplex* Haldeman (Orthoptera: Tettigoniidae) and other grasshopper pests. They demonstrated an immune response of infected Mormon crickets and concluded that circulating phenoloxidase may be an important enzymatic defense against *Beauveria* infection, and that it is associated with attempted clearing of *Beauveria* blastospores and hyphae from Mormon cricket hemolymph.

Alexandre Latchininsky
Gregory Sword
Michael Sergeev
Maria Marta Cigliano
Michel Lecoq

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Review Article

Distribution Patterns of Grasshoppers and Their Kin in the Boreal Zone

Michael G. Sergeev[1, 2]

[1] *Department of General Biology and Ecology, Novosibirsk State University, 2 Pirogova Street, Novosibirsk 630090, Russia*
[2] *Laboratory of Insect Ecology, Institute of Systematics and Ecology of Animals, Siberian Branch, Russian Academy of Sciences, 11 Frunze Street, Novosibirsk 630091, Russia*

Correspondence should be addressed to Michael G. Sergeev, mgs@fen.nsu.ru

The distribution patterns of Orthoptera are described for the boreal zone. The boreal fauna of Eurasia includes more than 81 species. Many of them are widely distributed. The monotypic genus *Paracyphoderris* Storozhenko and at least 13 species are endemics or subendemics. About 50 species are known from boreal North America. Four endemic species are distributed very locally. Relationships between the faunas of the Eurasian and North American parts of the boreal zone are relatively weak. The boreal assemblages are usually characterized by the low levels of species diversity and abundance. Grasshoppers and their relatives occupy almost exclusively open habitats, such as different types of meadows, mountain steppes and tundras, clearings, openings, bogs, and stony flood plains. The local endemics and subendemics are found only in some habitats of the eastern part of Eurasia and the north-western part of North America. Retrospective and prospective of the boreal fauna of Orthoptera are also discussed.

1. Introduction

The boreal zone is the huge area in the Northern Hemisphere where the coniferous forests form the main type of vegetation [1], average temperatures are relatively low (mean temperatures of the warmest month vary from 6.5°C to 19°C, the same for the coldest month, from −6°C to −49°C), and annual precipitation varies from relatively high near Atlantic and Pacific oceans (more than 1600 mm per year) to very low in the inner parts of the continents (less than 200 mm) [2]. From the ecogeographic point of view, in Eurasia, this life zone almost corresponds with the so-called taiga area [1, 2]. In North America, it occupies the significant part of the so-called Spruce-Caribou Biome [3] and almost corresponds to the united boreal life zone *sensu* Merriam [4]. From the zoogeographic point of view, in Eurasia, the boreal zone almost coincides with the Eurosiberian Region (or Subregion) (without the Subarctic and Arctic areas) erected mainly on the basis of the species distribution analysis [5–8]. In North America, it more or less coincides with the so-called Canadian Region [5].

The climatic conditions and dominated coniferous forest habitats are not comfortable for most grasshoppers and their relatives. The general level of their diversity is relatively low [7, 9–12]. Ecological peculiarities and adaptations of most species associated with the boreal zone are almost unknown [9, 11]. There are no species inhabiting coniferous trees and shrubs. Almost all forms prefer openings with herbaceous vegetation and meadows. Several species (mainly from the tribe Melanoplini and some widely distributed katydids) usually settle shrubs along forest edges [9, 13, 14]. A few forms prefer herbaceous microhabitats under a coniferous forest canopy. Among them are *Podismopsis silvestris* Storozh. [15] and, in some parts of its range, *Prumna primnoa* (F.d.W.) (our unpublished data). Many species are univoltine with overwintering eggs, but in North America several forms are semivoltine: they pass the first cold season as eggs and the second as hoppers [16]. Their development is limited by a relatively short warm season. This results in more or less simultaneous development of almost all species [13]. Besides that, many local grasshoppers prefer to lay egg pods on leaves, in leaf axils, grass stems, rotten woods, leaf litter, and in the upper soil layer [11, 13, 14, 17].

Uvarov [13] emphasized that the boreal area can be regarded as devoid of grasshoppers. However, there are different types of meadows, openings, and bogs that can be settled by some species. Beside that, mountains are well developed in different parts of the boreal zone, especially in the eastern part of Eurasia and in the western part of North America. A complicated relief of the mountain systems provides a level of landscape diversity comfortable for many grasshoppers and their kin. There are many dry and warm habitats with steppe-like vegetation, especially along southern slopes of ridges, and alpine and subalpine meadows, often with shrubs, above the timberline. As a result, the boreal zone is populated by both endemic taxa and extremely abundant species which can form outbreaks during droughts. The main aim of this paper is to establish general patterns of Orthoptera distribution in the boreal zone.

2. Methods and Materials

Both qualitative and quantitative data were used. The analysis of geographic distribution was based on published and unpublished species range maps. Species data points for Eurasian Orthoptera were plotted onto base maps, usually on a scale of $1:25,000,000$. My own collections, the collections of different museums, and published data were used [6, 7]. Besides, several maps published by Albrecht [18] for Fennoscandia were adopted. I also analyzed the published species range maps of North American Orthoptera [10, 11, 16, 19, 20].

The analysis of ecological distribution was based on quantitative samples collected in natural and seminatural habitats. Samples captured during a fixed period of time were made in every habitat investigated [6, 21]. Using this method, insects were caught with a standard net over a period of 10–30 minutes. Results for every habitat were recalculated for an hour. This method allowed us to obtain repeatable and comparable results for different regions and years. These samples were collected in some parts of the Eurasian boreal zone by the expeditions of the Department of General Biology and Ecology (Novosibirsk State University) and the Laboratory of Insect Ecology (Institute of Systematics and Ecology of Animals) from 1972 to 2003. Several published papers [14, 15, 22–28] describing orthopteran assemblages in different parts of the boreal zone were also used.

3. Geographic Distribution

The general distribution of grasshoppers and their kin in the Holarctic Region reflects the southern thermophilic character of these insects and their common association with open habitats, such as different grasslands, openings, bogs, and so forth [7, 11–13]. Grasshoppers are not typical of the tundra life zone [16, 29, 30] although a few species occur in the southern tundra and forest tundra. The only species penetrating in the northern tundra of North America is *Aeropedellus arcticus* Heb. [19]. The most common grasshopper of the tundra as a whole is *Melanoplus frigidus*

(Boh.). The fauna of the boreal life zone includes about 130 species of Orthoptera. Many of them are distributed only in its southern part. Hundreds of species are found southwards, in the nemoral (broad-leaf) forest, steppe, and prairie life zones [7].

Bey-Bienko [9] analyzed the general distribution patterns of Orthoptera in the boreal zone of the former USSR. He noted occurrence of 31 species in its western part and 44 in the eastern one (51 species in total). Prevalence of species preferring grass layers of local ecosystems was also emphasized. Bey-Bienko described some differences between orthopteran distribution patterns in the western (where dark coniferous forests dominate) and eastern (mainly with light coniferous forests) taiga. In the western part, grasshoppers usually settle openings and bogs. In the eastern part, local species settle both the same set of habitats as in the western taiga and more or less dry plots (steppes, dry meadows), but often on the higher level of abundance. They also can survive winters with very low temperatures.

The fauna of the boreal part of Eurasia includes more than 81 species of Orthoptera, about 3/4 of them are the members of the family Acrididae. Many species are widely distributed in the boreal zone of Eurasia, usually from Atlantic Ocean to the Pacific one (Figures 1 and 2). Among them are *Podisma pedestris* (L.), *Melanoplus frigidus*, *Aeropus sibiricus* (L.), *Aeropedellus variegatus* (F.d.W.), *Stethophyma grossum* (L.), *Bryodema tuberculatum* (F.), *Chrysochraon dispar* (Germ.), *Omocestus haemorrhoidalis* (Charp.), *O. viridulus* (L.), *Chorthippus montanus* (Charp.), *Ch. albomarginatus* (Deg.), *Metrioptera brachyptera* (L.), *Decticus verrucivorus* (L.), *Tetrix subulata* (L.), and *T. fuliginosa* (Zett.). Besides, there are many species which populate either the western (European) part of the zone (*Chorthippus pullus* (Phil.), *Oedipoda caerulescens* (L.), *Sphingonotus caerulans* (L.), *Tetrix undulata* (Sow.), and *Pholidoptera griseoaptera* (Deg.)), or the southern Siberian Mts. (*Montana tomini* (Pyln.), *Stenobothrus eurasius* Zub., and *Bryodema holdereri* Kr.), or its eastern part (*Zubovskya koeppeni* (Zub.), *Chorthippus fallax* (Zub.), *Sphagniana ussuriana* (Uv.), and *Tetrix japonica* (I. Bol.)) (Figures 1–3). They often occur in the northern parts of the taiga and, in some cases, penetrate in the tundra, especially either in the European or Beringian ones. The sparse local populations of the Migratory locust (*Locusta migratoria* L.) are also found in the European taiga area [18]. Almost all widely distributed species are associated with either the subboreal areas (especially with the forest-steppes, steppes and semideserts in the inner territories of Eurasia) or the deciduous forest life zone of Europe or the Far East. In the boreal zone, they often settle very dry habitats, for example, openings in pine forests on sandy soils. Some widely distributed grasshoppers (e.g., *Aeropus sibiricus*, *Melanoplus frigidus*, and *Podisma pedestris*) have isolated populations in the mountains of south temperate Eurasia (from Pyrenees to Central Asia) (Figure 2) [31, 32].

The genus *Paracyphoderris* Storozhenko (with one species—*P. erebeus* Storozhenko) (Figure 1) and at least 13 species are endemics or subendemics of the boreal zone of Eurasia. All of them are distributed only in its eastern part. Some endemic species have relatively broad ranges
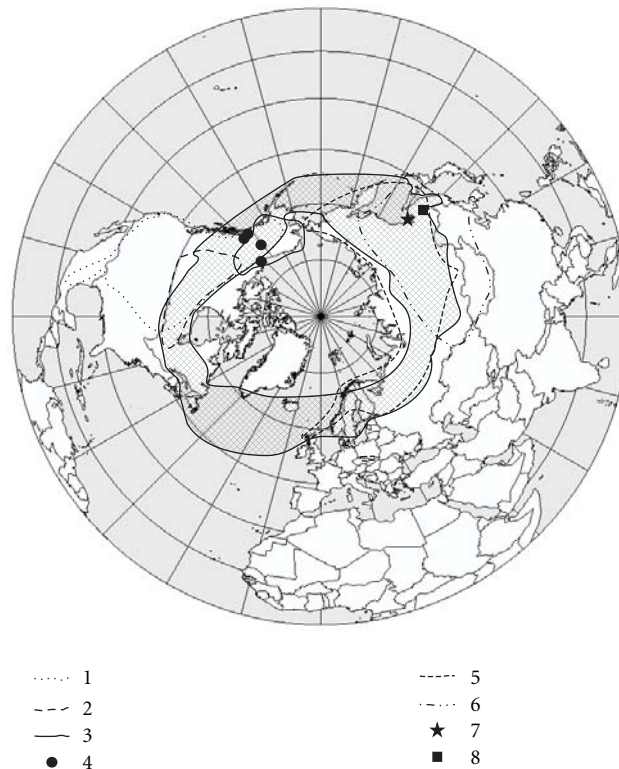
Figure 1: Distribution of *Arphia conspersa* (1), *Sphagniana sphagnorum* (2), *Aeropodellus arcticus* (3), *Xanthippus brooksi* (4), *Tetrix fuliginosa* (5), *Chorthippus fallax* (6), *Ch. shantariensis* (7), and *Paracyphoderris erebeus* (8) relative to the boreal zone (cross-hatching) (see text and references for details). The boundaries of the boreal zone based on [1, 2, 5] with some minor changes and simplification. The basic map is "Northern Hemisphere of Earth (Lambert Azimuthal projection)" by Sean Baker from http://commons.wikimedia.org/wiki/file:Northern_Hemi- sphere_LamAz.png, under the CC-by-2.0 license.

(usually from the Enisej River basin to Pacific ocean): *Prumna polaris* Mir., *Zubovskya koeppeni*, *Podismopsis jacuta* Mir., and *P. gelida* Mir. (Figures 2 and 3). Their local populations can be usually found in the mountains of South Siberia and Mongolia and in the southern tundra of northeastern Siberia. The others are distributed locally (*Prumna specialis* (Mistsh.), *P. arctica* (Zhang et Jin), *P. montana* (Storozhenko), *Chrysochraon amurensis* Mistsh., *Podismopsis silvestris*, *P. insularis* Mistsh., *Chorthippus shantariensis* Mistsh., and *Paracyphoderris erebeus*) (Figures 1–3). Among them are both insular (*Podismopsis silvestris*—Sakhalin, *P. insularis* and *Chorthippus shantariensis*—Shantar Islands) and montane endemics (*Prumna specialis*, *P. montana*—Sihote-Alin, and *P. arctica*—Greater Khingan). It is interesting that the majority of endemics are from two acridid tribes: Melanoplini (Figure 2) and Chrysochraontini (Figure 3). Besides, in the southern part of the Russian Far East, there are two montane endemics, namely, *Hypsopedes kurentzovi* B.-Bienko and *Prumna kurentzovi* (Mistsh.), which have populations outside the boundaries of the boreal zone, but above the timberline. All endemics have relatively short or no wings. Hence, their possibility to migrate is very limited.

Thus, in the boreal zone of Eurasia, the main area of diversity and endemism of Orthoptera is in the eastern

(Pacific) part. Its endemics are mainly close relatives of forms associated with the Manchurian Subregion [7].

The general patterns of Orthoptera distribution in North America were described by Vickery [10] and Kevan [33]. Both authors noted that there are several widely distributed species, mainly from Acrididae and Tetrigidae. Vickery [10] emphasized that only a few species are found in the tundra of this continent. More than 50 species are known from the boreal zone of North America [10, 11, 19, 20, 34]. About 57% are members of the family Acrididae. There are at least 5 species of crickets (both Gryllinae and Nemobiinae). Another specific feature is presence of several species of the genus *Melanoplus* Stål.

Many species are widely distributed in the boreal zone of North America, usually from Pacific Ocean to the Atlantic one. Among them are *Stethophyma gracile* (Scudd.), *S. lineatum* (Scudd.), *Chloealtis conspersa* (Harris), *Ch. abdominalis* (Thomas), *Chorthippus curtipennis* (Harris), *Pardalophora apiculata* (Harris), *Camnula pellucida* (Scudd.), *Trimerotropis verruculata* (Kirby), *Melanoplus borealis* (Fieb.), *M. fasciatus* (F. Walk.), *M. sangunipes* (Fabr.), and *Tetrix subulata* (L.) (Figures 2 and 3). They often occur in the northern parts of the taiga and, in some cases, penetrate in the tundra. *Aeropedellus articus* is almost
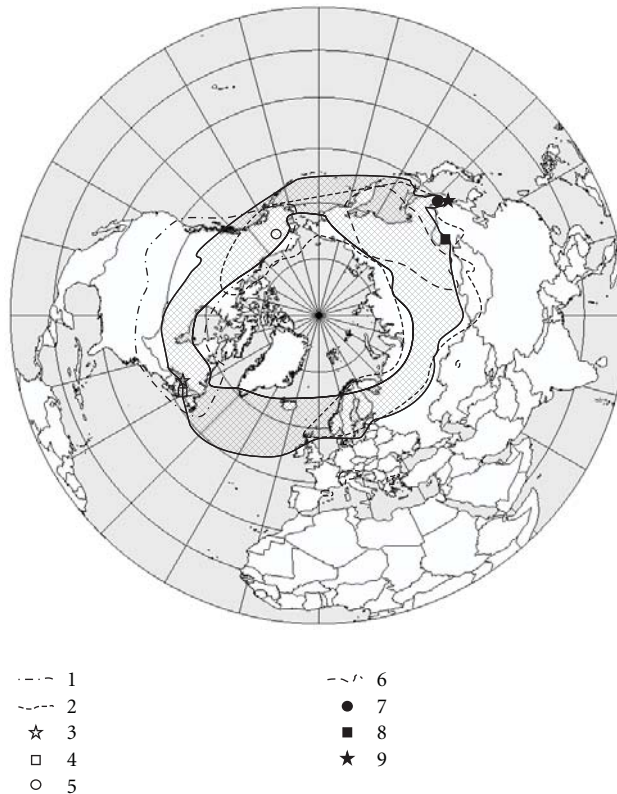
Figure 2: Distribution of the Melanoplini grasshoppers: *Melanoplus borealis* (1), *M. firgidus* (2), *M. gaspesiensis* (3), *M. madeleineae* (4), *M. gordonae* (5), *Prumna polaris* (6), *P. specialis* and *P. montana* (7), *P. arctica* (8), and *P. kurentzovi* (9) relative to the boreal zone.

unique grasshoppers penetrating in the northern tundra of north-western North America (Figure 1). Almost all widely distributed species are associated either with the subboreal areas, especially with the prairies and forest-prairies in the inner territories of North America, or with the mixed and deciduous forest areas of the Atlantic coast (Figures 2 and 3). Besides, there are several species which occupy the western part of the zone (*Arphia conspersa* Scudd. and *Encoptolophus costalis* Scudd.) (Figure 1).

Two North American species may be characterized as subendemics of the boreal zone with relatively broad ranges. *Aeropedellus arcticus* is distributed in the north-western part of the continent (Figure 1). This grasshopper prefers different tundra habitats [16]. The second species is the katydid *Sphagniana sphagnorum* (F. Walk.) which occurs in the central part of the boreal life zone. The main part of the range of *Xanthippus brooksi* Vickery (Figure 1) is in the western part of the boreal zone, but the local population is found near the delta of the Mackenzie River, outside this zone [10, 16]. Four endemic species are distributed very locally. *Melanoplus gordonae* Vickery is found in the vicinities of Fairbanks (Alaska) (Figure 2). *Bruneria yukonensis* Vickery is distributed in the southern part of Yukon [16, 28]. *Melanoplus gaspesiensis* Vickery and *M. madeleineae* Vickery and Kevan are limited by the small territories on the Atlantic coast (Figure 2). The latter occupies the Magdalen Islands. Both species are close to *M. borealis* [35]. Unlike the endemics of boreal Eurasia, the North American have

either short or well developed wings (*Xanthippus brooksi* and *Melanoplus gordonae*).

Thus, in the boreal zone of North America, the two very weak regions of Orthoptera endemism are in the western and eastern parts. Their relatives are quite different from the zoogeographic and taxonomic points of view and occur in boreal and subboreal Eurasia (*Sphagniana sphagnorum* and *Aeropedellus arcticus*), in the Great Plains and the Rocky Mountains (*Xanthippus brooksi* and *Bruneria yukonensis*), and in the temperate areas of North America (*Melanoplus gordonae*). Compared to the fauna of the boreal Eurasia, the local fauna of Orthoptera looks like impoverished. The main reasons of this distinction can be significant difference both in the areas occupied by the boreal zone in North America and Eurasia (correspondingly about 5.4×10^6 and 8.4×10^6 km^2, based on soil distribution patterns [36]) and in the Pleistocene history of the regions. For instance, during the last glacial maximum, the northern half of North America was covered by the ice sheet (except some areas in Beringia) [37]. On the contrary, in Eurasia, the Asian part was almost free from plain ice sheets, but relatively small ice sheets developed in mountains and in the north-western part. These reasons do not exclude one another.

Relationships between the orthopteran faunas of the Eurasian and North American parts of the boreal zone are relatively weak, but they are more significant than for the whole Palaearctic and the whole Nearctic Regions. There are only two common species: *Tetrix subulata* and

Melanoplus frigidus (except invasive forms, such as *Roeseliana roeselii* (Hagen.)). Moreover, *Melanoplus frigidus* occurs only in the north-western part of North America. Several North American species have close relatives in Eurasia: *Chorthippus curtipennis* is the member of the *Chorthippus parallelus* group, and *Aeropedellus arcticus* is similar to *Ae. variegatus*. Besides, there are some common genera. However, these genera can be divided into two groups: the first includes genera distributed mainly in the Holarctic area (*Stethophyma* Fisch., *Sphagniana* Zeun., and *Melanoplus* Stål), and the second one includes genera (*Conocephalus*, *Gryllus*, *Tetrix*) widely distributed in both the temperate and tropical regions. Relationships between genera (e.g., *Bruneria—Stenobothrus*, *Chloealtis* Harris—*Chrysochraon* Fisch., *Ageneotettix* McNeil—*Dociostaurus* Fieb.) are not so evident and should be discussed after taxonomic revisions of these groups.

4. Ecological Distribution

The general pattern of ecological distribution of boreal Orthoptera is relatively simple: they prefer different types of meadows, steppes, edges, openings, river valleys, and bogs. However, the quantitative data concerning ecological distribution and assemblages of these insects in the boreal zone are extremely limited. There are several publications for different parts of Eurasia and only one paper for North America.

Bey-Bienko [22] was the first orthopterist who described assemblages of Orthoptera in the boreal zone, in the eastern part of West Siberian Plain. He noted the low levels of diversity (4–9 species) in all habitats and relatively high levels of abundance of *Chorthippus albomarginatus*, *Glyptobothrus biguttulus* (L.), and *Aeropus sibiricus* at the dry openings of the local pine forests on sandy soils. The main species over the flood plain meadows were *Tetrix subulata*, *Stethophyma grossum*, and *Chorthippus montanus*. Bey-Bienko also emphasized evident localization of all orthopteran populations.

Chernyakhovskiy [14, 25] described main parameters for the assemblages of Orthoptera in the middle taiga of European Russia (Pechoro-Ilychskiy State Reserve). The level of species diversity is also low (2–11 species). The maximal numbers of species are found in meadows and clearings. The minimal diversity is in the lower flood plains and bogs. *Omocestus viridulus* and *Chorthippus apricarius* (L.) dominate in meadow habitats, whereas *Stethophyma grossum* is the most abundant form in bogs.

In the southern taiga of West Siberian Plain, the orthopteran assemblages investigated include from 3 to 11 species. The general abundance is relatively low. The maximal numbers of registered species and specimens (up to 676 per hour) are found on the meadow terraces. *Metrioptera brachyptera* (L.), *Chorthippus apricarius* (L.), and *Glyptobothrus biguttulus* are the common dominants on the plain and terraces. *Stethophyma grossum* is abundant in the assemblage of the wet flood plain meadows. The similar pattern is described by Chernyakhovskiy [24] for the vicinities of Tomsk.

In the middle taiga of Central Siberia, the level of species diversity is similar [23]. The local assemblages usually include several species of grasshoppers. *Chorthippus apricarius* is common in the plain meadow habitats. *Tetrix tenuicornis* (Sahlb.) dominates in the bog ecosystems. The maximal number of species (10) is registered on the stony flood-plains. *Glyptobothrus brunneus* (Thnb.) [? – M.S.], *Chrysochraon dispar*, *Aeropus sibiricus*, and *Podisma pedestris* are abundant here.

The specific, near-polar steppes of north-eastern Yakutia are mainly inhabited by the widely distributed steppe grasshopper [27]. The similar situation is in the dry parts of central Yakutia, in which *Chorthippus albomarginatus*, *Aeropus sibiricus*, *Glyptobothrus maritimus*, and *Omocestus haemorrhoidalis* are the most common species over all meadow and steppe-like habitats. The local openings are characterized by dominance of *Podisma pedestris* and *Melanoplus frigidus*. This part of the boreal zone is very specific due to short, but hot and often dry summer season. After several years with droughts, the general abundance of grasshoppers may increase significantly. As s result, they can damage almost all vegetation [38].

In the middle taiga of south Yakutia, the orthopteran assemblages are relatively diverse and include many species (from 11 to 27) [26]. This pattern may be determined by the rather complicated mosaic of mountain slopes, river valleys, and plateaus. Beside that, this area is near the northern boundary of the Manchurian Subregion of the Palaearctic. As a result, some species associated with the broad-leaf forest life zone penetrate northwards. *Podismopsis gelida* and *Aeropedellus variegatus* are the common species in the mountain tundra. Dry slopes are mainly inhabited by *Melanoplus frigidus* and *Gomphocerus rufus* (L.). *Tetrix fuliginosa*, *Melanoplus frigidus*, *Chrysochraon dispar*, and *Podismopsis poppiusi* dominate in the different assemblages in the bog and meadow habitats.

In the boreal part of Sakhalin, Storozhenko [15] found orthopteran assemblages similar to the continental ones. The species number varies from 1 to 9. The local populations are sparse. The endemic *Podismopsis silvestris* is the only species inhabiting plots of the spruce forests with green mosses. This grasshopper is found only here. Another endemic distributed in the Pacific part of the boreal zone, namely *Aeropus kudia* (Caud.), settles all more or less open habitats. *Prumna primnoa* and *Zubovskya koeppeni* are dominants on openings. *Chorthippus intermedius* (B.-Bien.) are the most abundant form in different meadow habitats. *Glyptobothrus maritimus* (Mistsh.) dominates on the lower flood plains.

Berman et al. [28] described ecological distribution and assemblages of grasshoppers in the habitats of the southern part of Yukon. The levels of species diversity and abundance are very low. The first varies from 2 to 8 and the later from 18 to 61 specimens per hour. *Bruneria yukonensis* and *Melanoplus kennicottii* Scudd. dominate in different variants of the sagebrush steppes. *M. kennicotti*, *M. borealis*, *M. fasciatus* (F. Walk.), and *Cloealtis abdominalis* are the most abundant grasshoppers in the different mountain tundra. The local endemics, namely *Bruneria yukonensis* and *Xanthippus brooksi,* are found in
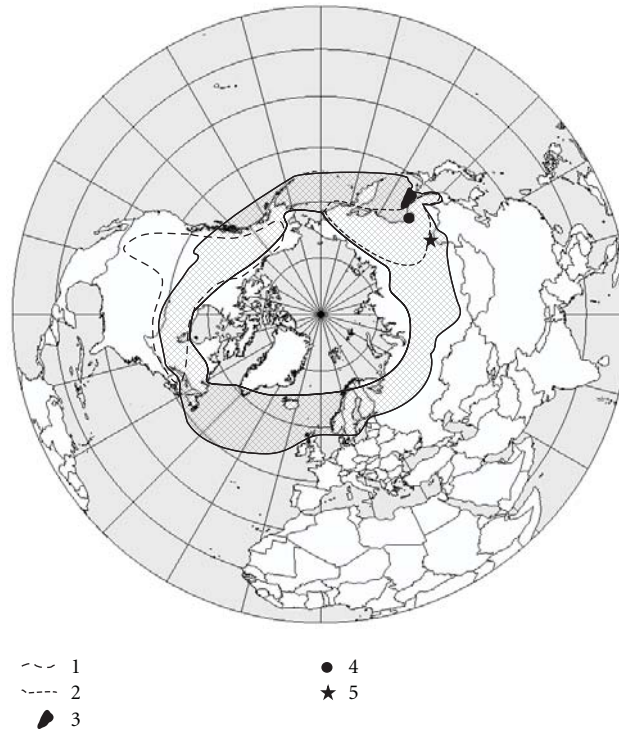
FIGURE 3: Distribution of the Chrysochraontini grasshoppers: *Chloealtis conspersa* (1), *Podismopsis gelida* (2), *P. silvestris* (3), *P. insularis* (4), and *Chrysochraon amurensis* (5) relative to the boreal zone.

the steppe habitats. The abundance of the first one is relatively high.

Thus, compared to the orthopteran assemblages of the southward territories [39, 40], the assemblages described from the boreal zone are usually characterized by the low levels of species diversity and abundance. In this area, grasshoppers and their relatives occupy almost exclusively open habitats, such as different types of meadows, mountain steppes and tundras, clearings, openings, bogs, and stony flood plains. In the main part of the zone, orthopteran assemblages are composed from widely distributed species usually inhabiting the broad variety of life zones and ecosystems. The boreal endemics and subendemics are found only in some habitats of the eastern part of Eurasia and the northwestern part of North America. However, they are often abundant and may dominate in local assemblages. In Eurasia, the local endemics occupy different open habitats, from the mountain tundras to openings. The only *Podismopsis silvestris* is found in the spruce forest [15]. In North America, the local endemics investigated are associated with the mountains steppes [28].

5. The Boreal Orthoptera: Retrospective and Prospective

As one knows, reconstruction of the past of many taxa faces numerous problems. The most important of them is the shortage of their fossils. This results in development of different hypotheses explaining biogeographic and ecological history of such groups. In the absence of adequate fossil data, an applicable approach may be based on a complex analysis of the limiting factors, adaptations to particular living conditions, and the optimum conditions, which may be evaluated based on the species range shape and the population distribution within the range [6, 41, 42]. A phylogeographic approach also allows us to reconstruct some important events and processes of the past [43–47]. However, these studies should develop on the basis of integration of historical geographic and genetic data [47].

The history of the boreal Orthoptera was discussed in a number of papers. Uvarov [48] noted that the orthopteran fauna of the northern Palaearctic area, especially in Europe, was seriously suffered during last glaciations. He also emphasized the role of "an enormous invasion of strange fauna swept over Europe from the East" (p. 1519). This group is associated with the eastern territory of temperate Asia. Uvarov suggested to call the group "the Angara fauna" and included in it the group Chorthippi (i.e., *Chorthippus* Fieb. and its relatives), the genera *Podisma* Berth., *Melanoplus* Stål, *Stethophyma* Fisch., *Bryodema* Fieb., *Aeropus* Gistl, *Podismopsis* Zub., and so forth. He also mentioned some relationships between the Angara fauna and the faunas of the southern parts of East Asia. Later Bey-Bienko [9] developed some Uvarov's idea concerning the Angara fauna of Orthoptera. He suggested to separate the so-called Siberian forest meadow group of Orthoptera associated with eastern part of Siberia. It includes at least *Podismopsis poppiusi*, *Chorthippus fallax,* and *Ch. intermedius* (B.-Bien.).

Lindroth [49] discussed different aspects of zoogeographic connections between Europe and North America

and emphasized their relative weakness. He noted that more or less evident relationships may be for arctic and subarctic forms and some taxa at "a lower evolutionary stage." Lindroth also showed the extremely significant role of species invasions due to human activity from Eurasia to North America and *vice versa*. Lindroth [49] also discussed different hypotheses of earlier transatlantic land-connections. He noted that the continental drift took place too early to trace their biological consequences for the North Atlantic area.

Vickery [35] described some possible stages and ways of origination of the North American fauna of Orthoptera. He noted that the distribution of many Orthoptera taxa reflects very old, at least the Tertiary, connections between continents. However, other species, for example, *Tetrix subulata* and *Melanoplus frigidus,* could cross the Bering land bridge during the Quaternary period. He suggested that such grasshoppers might survive glaciations (especially the last one) in Beringia where some refugia with relatively mild and dry climate existed. Two endemics of the eastern part of the North American boreal zone look like to evolve (or survive) in small areas which were unglaciated.

Sergeev [6, 41] noted that the autochthonous component in the boreal zone of Eurasia is weak and associated with its eastern territories, which were unglaciated during the Quaternary period. Usually the autochthonous forms are close relatives of taxa connected with regions of East Asia where the broad-leaf forests, both temperate and subtropical, dominate. The widely distributed species usually inhabiting different meadows and steppes could spread over the boreal zone during glaciations when open habitats (tundras, tundra-steppes, and cold steppes) occupied huge territories in North Asia. Several species mainly associated with the nemoral zone of the Far East could distribute during interglacials and the climatic optimum of the Holocene [6, 9, 41]. Beside that, one should note that some data for beetles show that spreading rates of terrestrial insects during glacial-interglacials changes might be enough for their wide distribution [50]. This means that the main events determining the modern character of the boreal fauna could take place during the Quaternary period.

Thus, in the boreal zone, grasshoppers and their kin represent groups of different origins.

(1) The main part of genera is evidently associated with the southward areas of each continent. Their species can be usually interpreted as more or less recent invaders in the boreal zone, especially in North America. This group also includes the genera widely distributed in both the New and Old World (*Conocephalus* Thnb., *Gryllus* L., *Tetrix* Latr.).

(2) Another group of the genera is associated with the Holarctic Region. These Orthoptera are often cold resistant. They could distribute over the boreal zone from the end of the Neogene. However, the molecular phylogenetic analysis [51] showed that the dispersion time of some taxa from Eurasia to North America (e.g., the ancestors of the North American *Stethophyma*) could be considerably earlier than the estimations published [35]. The interchanges between Eurasia and North America could take place many times across the Bering land bridge. Several related genera (e.g., *Bruneria* McNeil—*Stenobothrus* Fisch.) demonstrate

relatively old connections (probably, associated with first glaciations), on the contrary, two species distributed in North America and Eurasia (*Tetrix subulata, Melanoplus frigidus*) could cross this bridge during the last glaciations.

The boreal endemics of Eurasia and North America look like quite different. The first group consists from the species associated with territories not covered by ice sheets during the Quaternary period. Although they are ecologically diverse and prefer various types of habitats (from mountain tundras to openings and meadows), the nemoral origin of almost all of them is evident. The differentiation of possible ancestral forms could be resulted from separation of different types of the forest landscapes (especially the boreal ones) in the end of the Neogene. However, the evolution of the several species of the genus *Prumna* Motsch. might be determined by the significant level of isolation of local populations and by limited dispersal opportunities.

The local endemic of North America can be divided into two pairs. Origin of both can be explained by the refugium distribution during the last glaciations. One pair includes species associated with the north-western part of the continent. The evolution of both forms could take place in the Beringian refugia [35]. This hypothesis is supported by data concerning fossil beetles [52]. Two species of the genus *Melanoplus* were evidently evolved during the last glaciations when the areas of their origination remained off ice sheets [35].

Hence the distribution patterns of the boreal Orthoptera show that one can estimate the number of stages and sequence of their evolution and interchanges, but do not allow us to determine the exact periods of these processes and the directions of interchanges between two continents. For instance, the main migration direction of *Melanoplus frigidus* is still debatable [35, 44]. However, last comparative studies of molecular phylogeny of melanopline grasshoppers showed that the main direction dispersal could be from South America to Eurasia [45].

One of the principal results of retrospective views on faunas and populations is the opportunity to forecast their possible changes in the future. If the trend of global warming will hold, the boreal zone will shift northwards and its area will reduce [53, 54]; however, the precipitation will decrease [54]. This should result in the Orthoptera distribution pattern. Grasshoppers occupying the boreal zone will shift the northern boundaries of their ranges northwards, up to Arctic Ocean. Local endemics may be eliminated due to high rates of changes. This is especially important for the high montane forms occurred above timberline, because their native landscapes will disappear. Abundance and diversity of other boreal grasshoppers with isolated populations in mountains and on plain openings and meadows will potentially decrease down to their full elimination [55]. On the contrary, some widely distributed species associated with the steppe and forest steppe life zones will be able to spread northwards along different anthropogenic habitats, such as clearings, roadsides, agricultural fields, and pastures [41]. Besides, their abundance may increase and some of them may become potential pests.

Acknowledgments

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Research Article

Relationships between Plant Diversity and Grasshopper Diversity and Abundance in the Little Missouri National Grassland

David H. Branson

USDA-Agricultural Research Service, Northern Plains Agricultural Research Laboratory, Sidney, MT 59270, USA

Correspondence should be addressed to David H. Branson, dave.branson@ars.usda.gov

A continuing challenge in orthopteran ecology is to understand what determines grasshopper species diversity at a given site. In this study, the objective was to determine if variation in grasshopper abundance and diversity between 23 sites in western North Dakota (USA) could be explained by variation in plant species richness and diversity. In this system with relatively low plant diversity, grasshopper species richness and abundance were not significantly associated with plant species richness in either year. Although a number of significant associations between plant diversity and grasshopper diversity were found through regression analyses, results differed greatly between years indicating that plant species richness and diversity did not lead to strong effects on grasshopper diversity metrics. Plant species richness appears to be too coarse grained to lead to accurate predictions of grasshopper species richness in this system dominated by generalist grasshopper species.

1. Introduction

Grassland insect diversity is often linked to plant species composition and habitat structure [1–4]. Several general hypotheses have been proposed to explain relationships between plant and herbivore species richness [5, 6], with insect herbivore diversity often thought to generally increase with increased plant species richness due to increased resource diversity [3, 5]. Although habitat associations with grasshoppers have been studied since the early 1900s [7], it remains a continuing challenge in grasshopper ecology to understand patterns of species diversity [4, 8]. Numerous factors could influence grasshopper species diversity including resource availability, habitat structure, escape space, and predators [4, 9, 10]. Furthermore, management practices such as livestock grazing and fire impact plant species composition and subsequently affect grasshopper species composition [4, 11]. Many studies have examined relationships between grasshopper community composition and vegetation patterns in grassland ecosystems worldwide (e.g., [2, 4, 8, 12–14]). Plant diversity often positively affects grasshopper species diversity, but relationships are not consistent. Additionally, grasshopper feeding patterns can have important impacts on local plant abundance and community structure [15–17]. In most grassland ecosystems the nature of relationships between plant species richness and grasshopper abundance and diversity remains unclear [3, 4].

Grasshoppers are often the dominant native herbivore in grassland ecosystems worldwide, with widespread economically damaging grasshopper outbreaks occurring frequently in western North America [11, 15]. Despite the economic importance of grasshoppers in the area of this study, the northern Great Plains [18, 19], relationships between plant diversity and grasshopper diversity and abundance are not clearly defined. In contrast to the majority of herbivorous insects, most grasshopper species tend to be generalist feeders that consume a variety of unrelated plant species [20, 21]. As a result, relationships between plant species richness and grasshopper species richness could be weaker in grass dominated ecosystems with numerous grass or mixed feeding generalist grasshoppers. The objective of this study was to determine if variation in grasshopper abundance and diversity between 23 sites in western North Dakota (US) could be explained by variation in plant species richness and diversity.

TABLE 1: Characteristics of each site in western North Dakota.

Site	Elevation (m)	Coordinates	Plant species		Grasshopper species	
			2001	2002	2001	2002
Charbonneau	689	47°46′33N 103°49′30 W	11	6	19	19
Cheney	603	47°44′29N 104°01′35 W	5	8	*	16
Devitt	600	47°38′37N 104°01′53 W	12	7	18	14
East	710	47°36′35 N 103°56′09 W	8	7	13	18
Plant	609	47°38′05 N 104°01′08 W	8	5	17	16
Jacobson5A	690	47°48′04 N 103°48′31 W	6	5	19	24
Klandl	667	47°38′27 N 103°57′24 W	5	6	19	27
IndergardN	675	47°35′14 N 103°49′39 W	8	7	15	13
IndergardS	730	47°34′43 N 103°50′46 W	7	6	23	22
Rau	757	47°42′08 N 103°57′15 W	11	9	14	20
Saltwell	751	47°36′32 N 103°56′05 W	5	8	15	24
SD101	700	47°33′23 N 104°00′21 W	8	5	17	18
101 Creek	654	47°33′44 N 104°00′30 W	9	8	11	18
SM02	686	47°39′28 N 103°51′18 W	5	4	19	20
SM05B	740	47°37′42 N 103°45′45 W	10	7	20	21
SM05NB	747	47°37′03 N 103°45′58 W	10	8	21	20
SM07B	655	47°36′54 N 103°48′54 W	8	9	13	19
SM11	708	47°43′37 N 103°52′24 W	8	9	21	20
SM12	719	47°43′55 N 103°50′46 W	7	5	13	19
SM13	704	47°43′11 N 103°49′05 W	7	9	17	18
Shadwell	717	47°26′03 N 104°02′30 W	8	5	18	19
Whited	703	47°28′36 N 104°04′21 W	8	7	15	16
Windmill	658	47°39′07 N 104°00′11 W	3	4	15	20

2. Materials and Methods

The study was conducted on the Little Missouri National Grasslands in western North Dakota (USA), managed as part of the United States Forest Service Dakota Prairie Grasslands. The area of the study is characterized by wide summits and networks of gullies [22]. The historic plant community is a mixed grass prairie dominated by grasses including western wheatgrass (*Pascopyrum smithii*), blue gramma (*Bouteloua gracilis*), needle and thread (*Hesperostipa comata*), and green needlegrass (*Nassella viridula*). The region is semiarid and receives approximately 355 mm to 400 mm of precipitation annually; most of which occurs during the growing season. Mean daily temperatures range from $-17.2°C$ in winter to $29.4°C$ in summer. Precipitation measured at a nearby weather station during the growing season of 2001 was slightly above, while precipitation during 2002 was slightly below the long-term average.

During the spring and early summer of 2001, 23 sites were established in the Little Missouri National Grassland. The sites were located within 35 km of each other, ranged in elevation from 600 to 751 m, and were randomly chosen to include a range of grassland habitat types (Table 1). Nearly all sites were dominated by native vegetation. At each site, a 10 m by 10 m subplot was established for sampling vegetation species composition and grasshopper densities. Grasshopper population densities were determined by counting the number of grasshoppers that flushed from within 20, 0.1 m^2

aluminum wire rings, following the methods of Onsager and Henry [23]. Rings were arranged in a grid of four rows, with 5 rings per row, and held in place by landscape staples. Sites were sampled for grasshopper population densities and species composition four times in 2001 and six times in 2002, between the last week of June and the first week of September. Sampling took place when air temperature was greater than 23°C. A sweep net sample was taken, using an insect aerial net with a four foot handle, in the vegetation surrounding the 10 m by 10 m sampling plot to establish grasshopper community composition. Vegetation structure was dominated by grasses and forbs, with few shrubs. An equal number of 150 sweeps were taken while walking slowly that rubbed on the soil surface and that passed through the vegetation canopy while walking rapidly [24]. Sweep net samples were frozen, and grasshoppers were later identified to species in the laboratory. To adjust for differences in sweep net sample sizes between sites, individual species densities were estimated by combining the percentage composition in sweep samples with grasshopper densities from ring counts.

Vegetation species composition was examined in early July 2001 and 2002. Each side of the sampling site served as a 10 m transect with a fifth transect in the middle of the plot, with 500 sampling points per site. Along each transect, every one meter a standard 10-pin frame was used to determine vegetation composition based on the total number of contacts by a pin. A contact was considered as the pin point coming into contact with the basal area of a

plant, bare ground, or litter. Across both years of sampling, western wheatgrass was a dominant or codominant grass at 14 sites, blue grama at 13 sites, junegrass at eight sites, threadleaf sedge at three sites, needle and thread at two sites, crested wheatgrass (*Agropyron cristatum*) at two sites, green needlegrass at one site, and Kentucky bluegrass (*Poa pratensis*) at one site. For each site, total plant species richness, proportional coverage of live vegetation, and plant diversity were calculated.

Relationships between insect species diversity and plant diversity could differ seasonally but were not assessed in this study. As grasshopper sample sizes were low in some sweep net samples from sites with low population densities, all sweep samples were pooled prior to analysis to reduce error [24], increase the probability that rare grasshopper species would be incorporated [5], and better account for varying grasshopper phenologies [2]. Grasshopper abundance data was also averaged across sample periods within a year to reduce the influence of random sampling variation when few individuals are detected in density subsamples [25]. Data was transformed as needed. The majority of grasshopper species present at the sites overwinter as eggs and hatch in late spring or early summer; however four nymph-overwintering grasshopper species that hatch in late summer and become adults in the spring were caught in sweep samples. Only egg-overwintering grasshopper species were included in the analysis, as plant-grasshopper relationships would be expected to differ due to the divergent phenologies of these two groups. Patterns of grasshopper species diversity were examined using numerical species richness, Shannon index of species diversity, and Simpson evenness index [26]. Regression analyses were conducted to examine habitat variables responsible for grasshopper abundance and diversity. Systat 12 (Systat Software Inc.) was used for all analyses.

3. Results and Discussion

Cumulative plant species richness was relatively low, with a total of 31 species detected across all sites. Mean plant species richness was 7.24, with a maximum species richness of 12 species at a site (Table 1). Forb species richness ranged from zero to six species, while grass species richness ranged from two to seven. Vegetation was dominated by grass and sedge species, as is typical in this northern mixed grass prairie [22, 27, 28]. An average of ~88% of live vegetation hits were grasses and sedges. Abundant grasses and sedges were blue grama (*Buteloua gracilis*), western wheatgrass (*Agropyron smithii*), junegrass (*Koeleria macrantha*), and threadleaf sedge (*Carex filifolia*). The most abundant forb was the relatively ephemeral exotic common dandelion (*Taraxacum officinale*), which is frequently present in native dominated grasslands throughout the United States. Fringed sage (*Artemisia frigida*), scarlet globemallow (*Sphaeralcea coccinea*), and phlox (*Phlox* spp.) were other relatively common forbs.

Egg-overwintering grasshopper species richness ranged from 11 to 27 across sampling sites in a given year, with a mean species richness of 18 (Table 1). A total of

Table 2: Egg-overwintering grasshopper species caught in sweep samples in 2001 and 2002.

Species	2001	2002
Ageneotettix deorum	1,553	2,374
Melanoplus sanguinipes	1,162	1,631
Phoetaliotes nebrascensis	863	1,084
Opeia obscura	575	668
Encoptolophus costalis	490	590
Philbostroma quadrimaculatum	487	720
Melanoplus gladstoni	411	314
Melanoplus femurrubrum	343	490
Melanoplus infantilis	273	387
Orphulella speciosa	206	277
Trachyrhachys kiowa	165	281
Amphitornus coloradus	140	185
Melanoplus dawsoni	128	350
Aulocara femoratum	126	176
Hypochlora alba	115	152
Melanoplus packardii	111	185
Melanoplus keeleri	109	205
Aeropedellus clavatus	92	197
Spharagemon equale	36	64
Arphia pseudonietana	33	68
Aulocara ellioti	31	64
Melanoplus confusus	24	39
Mermiria bivittata	16	19
Hadrotettix trifasciatus	16	24
Melanoplus bivittatus	14	51
Hesperotettix viridis	12	17
Melanoplus differentialis	10	0
Dissosteira carolina	8	2
Metator pardalinus	7	36
Dactylotum bicolor	1	1
Total caught	9,236	13,590

34 egg-overwintering grasshopper species were collected (Table 2). Mean grasshopper species richness per site was slightly higher than Kemp [29] and Joern [4], while total species richness was within the range observed in other similar studies in the western US (e.g., [4, 29–31]). Average grasshopper density across sites was 7.4 per m^2, with a low of 1.9 and a maximum of 20.8 per m^2 at a given site. Relative to long-term grasshopper densities in the area, the densities were not exceptionally high. Just prior to this study, grasshopper densities were documented at 40 and 130 per square meter [18, 19]. However, grasshopper densities were much lower during a five-year period immediately following this study [17].

Common grasshopper species are presented in Table 2. Plant diversity did not affect grasshopper abundance (Table 3), similar to the findings of Joern [10] in tallgrass prairie. There was no effect of plant species richness on grasshopper species richness in either year (Figure 1, Table 3). Although several significant associations were

TABLE 3: Results from regression analyses of plant species richness, live cover percentage, Shannon diversity, and Simpson evenness on grasshopper abundance and diversity. Regression equations are provided for results with a P value less than .1.

Independent (plant)	Dependent (grasshopper)	Statistical data
A. 2001		
Species richness	Species richness	$R^2 = 0.002, P = .84$
	Shannon diversity	$Y = 1.70 + 0.055X; R^2 = 0.17, P = \mathbf{.057}$
	Simpson evenness	$Y = 0.215 + 0.024X, R^2 = 0.19, P = \mathbf{.045}$
	Abundance	$Y = 8.6 - 0.32X; R^2 = 0.02, P = .5$
Shannon diversity	Species richness	$R^2 < 0.001, P = .99$
	Shannon diversity	$R^2 = 0.1, P = .16$
	Simpson evenness	$R^2 = 0.06, P = .26$
	Abundance	$R^2 = 0.03, P = .43$
Live cover	Species richness	$Y = 8.23 + 0.292X; R^2 = 0.4; P = \mathbf{.001}$
	Shannon diversity	$R^2 = 0.1, P = .15$
	Simpson evenness	$R^2 = 0.016, P = .6$
	Abundance	$Y = -3.37 + 0.329X; R^2 = 0.2, P = \mathbf{.036}$
Evenness	Species richness	$R^2 = 0.003, P = .8$
	Shannon diversity	$R^2 = 0.11, P = .12$
	Simpson evenness	$R^2 = 0.05, P = .33$
	Abundance	$R^2 = 0.024, P = .5$
B. 2002		
Species richness	Species richness	$R^2 = 0.01, P = .6$
	Shannon diversity	$R^2 = 0.08, P = .2$
	Simpson evenness	$R^2 = 0.09, P = .15$
	Abundance	$R^2 = 0.06, P = .25$
Shannon diversity	Species richness	$Y = 24.01 - 3.882X, R^2 = 0.19, P = \mathbf{.04}$
	Shannon diversity	$R^2 = 0.05, P = .32$
	Simpson evenness	$Y = 0.168 + 157X, R^2 = 0.21, P = \mathbf{.03}$
	Abundance	$Y = 15.0 - 6.96X, R^2 = 0.24, P = \mathbf{.015}$
Live cover	Species richness	$R^2 = 0.02, P = .53$
	Shannon diversity	$Y = 1.8 + 0.014X, R^2 = 0.2, P = \mathbf{.03}$
	Simpson evenness	$Y = 0.158 + 0.008X, R^2 = 0.212, P = \mathbf{.027}$
	Abundance	$R^2 = 0.003, P = .8$
Evenness	Species richness	$Y = 15.4 - 9.6X, R^2 = 0.25, P = \mathbf{.016}$
	Shannon diversity	$R^2 = 0.035, P = .39$
	Simpson Evenness	$Y = 0.151 + 0.348X, R^2 = 0.22, P = \mathbf{.025}$
	Abundance	$Y = 15.7 - 15.36X, R^2 = 0.26, P = \mathbf{.014}$

found through the regression analyses, results differed greatly between years (Figure 1, Table 3). Grasshopper community Shannon diversity and Simpson evenness were positively associated with plant species richness in 2001, indicating that sites with increased plant diversity had a more evenly distributed grasshopper community assemblage. By contrast, grasshopper species richness, evenness, and abundance were all positively associated with Shannon diversity of plants in 2002. Grasshopper species richness and abundance were positively associated with the percentage of live plant cover in 2001, while diversity and evenness of the grasshopper community were positively associated with live cover in 2002. Grasshopper species richness, evenness, and abundance were

all positively associated with plant species evenness in 2002. As significant relationships differed almost entirely between years, it appears unlikely that either plant species richness or diversity was a strong causative factor responsible for observed significant statistical results. However, a consistent result in both years was that grasshopper species richness was not positively associated with plant species richness (Figure 1). Although specialist grasshopper richness would be expected to increase with plant species richness, this is a highly grass dominated system with many generalist feeding grasshoppers [32].

Strong conclusions regarding the nature of the relationship between plant species diversity and grasshopper species
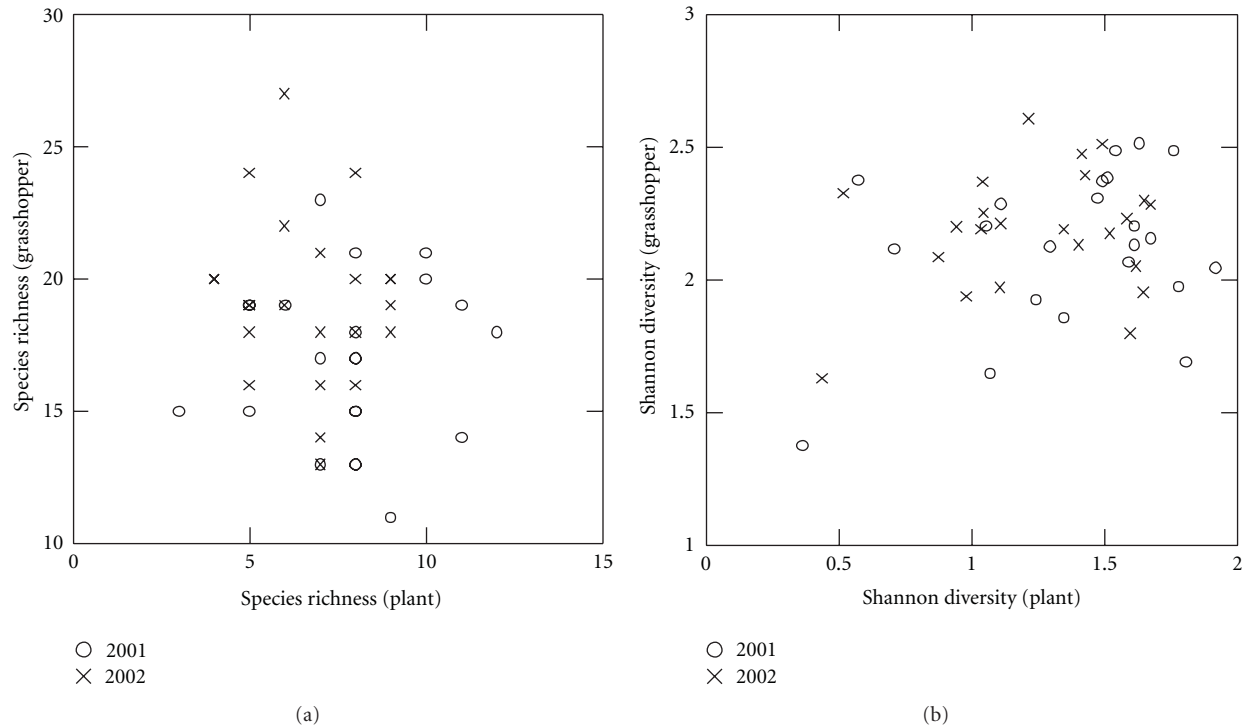
FIGURE 1: Relationship in 2001 and 2002 between (a) species richness of grasshoppers and plants and (b) Shannon diversity of grasshoppers and plants.

diversity in North America remain difficult. In a study across an elevational gradient in Montana, Wachter et al. [13] found no significant relationships between plant cover or species richness and grasshopper species richness, diversity, and abundance. By contrast, Fielding and Brusven [14] found a positive correlation between plant and grasshopper species richness in semiarid rangeland. In a more productive tallgrass prairie system, Evans [12] and Joern [4] also found grasshopper species richness was positively related with plant species richness. Plant species richness was similar in the study by Joern [4] and higher in the study by Fielding and Brusven [14]. In this study, as well as in Joern [4] and Fielding and Brusven [14] where positive relationships were found between grasshopper and plant species richness, the ratio of grasshopper species to plant species was typically greater than 1.0. In a desert environment in the southwestern US with low grasshopper species diversity but several specialist species, Otte [9] found a positive relationship between grasshopper and plant species diversity when the ratio of grasshopper species to plant species was always less than 0.43. As a result, the lack of a relationship between plant and grasshopper species richness does not appear a result of grasshopper or plant species richness varying by orders of magnitude from other studies. As pointed out by Fielding and Brusven [14], "grasshopper species richness is probably not a simple function of plant species richness."

Grasshopper populations are highly cyclical in this area and respond to weather conditions [18, 19, 27]. Drought has been shown to reduce grasshopper species diversity at nearby sites in eastern Montana [33], while a late summer rainfall

event led to a three-fold increase in grasshopper densities in the following year [19]. Precipitation patterns during 2001 and 2002 were not extreme outliers relative to long-term averages. Given the variation in correlations between years, longer-term sampling would be required to determine if consistent patterns emerge and if patterns vary with precipitation or densities. Grasshoppers were relatively abundant during the period of the study and density dependent factors could have influenced grasshopper or plant species composition. Both intraspecific and intraspecific exploitative competition can play an important role in grasshopper population dynamics and plant composition [19, 34, 35]. In addition, preferential grasshopper herbivory has been shown to influence plant species diversity in study area when abundant [17]. Although grasshopper herbivory could have removed all visible plant material prior to plant sampling, vegetation sampling occurred relatively early in the summer.

Many of the hypotheses proposed to explain positive relationships between plant and herbivorous insect diversity are based on the fact that many insects are relatively specialized [5]. However, many grasshopper species are generalists [17, 32]. As a result, inconsistent and weak relationships could be reflective of the ability of generalist grasshoppers to feed on numerous plant species or could be an artifact of difficulties in sampling rare species [5]. Haddad et al. [5] conducted an 11-year experiment manipulating plant diversity and examining effects on arthropod herbivores and predators and found herbivore arthropod species richness was strongly positively related to plant species richness only when examining cumulative species richness across the

11 year time period. This illustrates the potential importance of longer term sampling when examining relationships between plant and grasshopper species richness.

The results from this study also support Kemp et al. [36], who argued that plant species richness is too coarse grained a measure to lead to accurate predictions of grasshopper species richness. Although plant community associations are likely to be a better predictor of grasshopper species richness than plant species richness in a variety of ecosystems [36, 37], a potential constraint is that ordination techniques may result in system specific conclusions regarding relationships between plant communities and grasshopper species.

Acknowledgments

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Research Article

The Ontology of Biological Groups: Do Grasshoppers Form Assemblages, Communities, Guilds, Populations, or Something Else?

Jeffrey A. Lockwood

Department of Philosophy, University of Wyoming, Department 3392, 1000 E. University Avenue, Laramie, WY 82071, USA

Correspondence should be addressed to Jeffrey A. Lockwood, lockwood@uwyo.edu

Acridologists have used a variety of terms to describe groups of grasshoppers, including assemblage, community, guild, and population. This terminological diversity has raised the question of whether one of these descriptors is the correct one. I take the position that these terms pick out different features of the natural world such that there is no unconditionally or uniquely correct term. By adopting the framework of constrained perspectivism—a form of philosophical pragmatism—it is argued that a term is correct if it accurately reflects the conceptual framework of the investigator and effectively communicates this perspective to others. Such an approach gives rise to terminological pluralism that avoids the problems of relativism (the subjectivist's view that any term can be used) and absolutism (the objectivist's view that there is a single correct term). I describe the contexts in which the most common terms are appropriate.

1. Introduction: The Problem

Acridologists have used various terms to describe the groups of grasshoppers that are the focus of their work. The terms most often used are assemblage, community, guild, and population. Using the Google Scholar [1] to analyze how frequently scientists have used these terms revealed that of 1,459 hits: "grasshopper assemblage" appeared 65 times (4%), "grasshopper community" 413 times (28%), "grasshopper guild" 1 time (<1%), and "grasshopper population" 980 times (67%).

One might respond to the assortment of terms by asserting that such variety does not imply a problem or confusion. In fact, this view was expressed by three reviewers of this paper. These scientists tacitly agreed that the ecological terms were well defined (we will see that this is demonstrably not the case in the discussion of "population" and to some extent with "community" and "guild") or at least there was no confusion among acridologists. But their explications revealed a conceptual morass with various contradictions.

The first reviewer maintained that "the only issue is the occasional sloppy individual who calls a grasshopper assemblage a community." For this scientist, there is a single, correct term for groups of grasshoppers, which is "assemblage" (for the moment, let us set aside the fact that the supposedly sloppy use of "community" occurs far more often than the putatively correct term of "assemblage"—and "population" is more commonly used than either of these). By this account, all right-thinking acridologists know that groups of grasshoppers are called "assemblages," so the case is closed.

In an ironic twist, the second reviewer contended that all the terms have "tight and accepted usages," such that there is simply no confusion among acridologists. For this scientist, there are four standard terms that are variously and correctly used to describe groups of grasshoppers. But both reviewers cannot be correct. Either the first acridologist is in error (not all groups are "assemblages") or the second reviewer is mistaken (terms other than "assemblage" are conceptual errors).

The situation becomes no clearer with the assertion of the third reviewer that, "the choice of terms by researchers seems relatively uninformative/unimportant as some researchers may rather arbitrarily choose a term." In other words, this scientist agreed with the first in that some researchers were sloppy, but s/he seemed quite uncommitted to the notion that all groups are properly called "assemblages." And this reviewer also contradicted the second in suggesting that the chosen term is uninformative. The resolution, according to the third reviewer, is that the word choice is unimportant: "what matters is the context of how those words are used in a journal article." This represents a wholly inefficient approach to terminology—rather like referring to locusts in a title or abstract, only to have the reader discover that the paper is about grasshoppers—and it presumes that scientists take the time to read entire articles. Oftentimes and justifiably, researchers use titles to find the literature on a particular kind of grouping (e.g., community), and if others use an arbitrary term (e.g., assemblage or population) as a label, then important work will be overlooked and irrelevant publications will be sought.

At this point, all we can safely assert is that at least some acridologists—including apparently three highly qualified and experienced practitioners—are collectively confused by the terminology applied to groups of grasshoppers. Based on my experience, many graduate students and junior scientists working in this field are also somewhat bewildered by which term should be used to describe a group of grasshoppers in a habitat. So, it would appear that the editors of this special issue of *Psyche* were on to something in identifying one of the topics of interest as "Grasshopper species in a habitat: a community or an assemblage?"

One solution is to simply presume that the correct term is that which is used by the majority of scientists. If so, then a group of grasshoppers should be called a population (not "community" or "assemblage", as proposed by the editors). However, this seems entirely too quick of a solution to the terminological problem. It is certainly possible that most workers are misusing or misunderstanding a term. Moreover, we cannot summarily conclude that all of the scientists describing grasshopper groups are necessarily referring to one and the same thing. To clearly frame the problem—along with possible solutions and their shortcomings—it is helpful to consider four possibilities.

1.1. The Terms for Grasshopper Groups Are Synonyms. The various terms might be synonyms, much as one might refer to "short-horned grasshoppers" in one paper and to "acridids" in another, or to "nymphs" in one place and "hoppers" in another. If so, the inconsistencies are not substantive at all. However, the problem with the different expressions for groups of grasshoppers seems more than a matter of alternative words for the same entity. Ecologists form different impressions from the various terms used by acridologists; a "population" picks out something in nature that is not the same thing as a "community" [2]. Hence, the possibility of substantive errors and misunderstandings is real.

1.2. The Terms for Grasshopper Groups Are Subjective Constructs. The various terms may simply reflect human artifice. The manner in which grasshoppers are grouped could be an entirely subjective matter, such that there is no basis to argue for one formulation over another. A nominalist (i.e., one who holds that beyond the reality of individual entities, all higher groupings are human inventions) might contend that while individual grasshoppers actually exist, any amalgamation of these individuals represents a cultural construct—a sort of potentially useful fiction [3]. As such, one could be a realist about single grasshoppers but an antirealist about groups of grasshoppers [4]. Taken to an extreme, one could just as defensibly combine grasshoppers based on the potential they have as fish bait, the third letter of their scientific name, or the color of their tibia as one might group them in terms of competitive interactions, behavioral tendencies, or taxonomic relations. But such a strong nominalist view strikes us as rather implausible. Certain groupings of grasshoppers seem to reflect nonarbitrary qualities of the organisms (e.g., those that eat only grasses) much more so others (e.g., those that happen to be airborne at a given moment).

1.3. The Terms for Grasshopper Groups Are Objective Truths. There could be an objective fact of the matter as to which term uniquely picks out a real thing in the world [5]. A realist might argue that groups of grasshoppers are actual, mind-independent entities and that these possess some unifying property that makes it correct to call them communities but not populations, for example. Perhaps groups of grasshoppers are like deer herds, wherein the individuals have interactions or relationships which form a distinct entity. However, a strong realist position seems difficult to defend. It is not unambiguously evident what relationship among the grasshoppers makes the collective into an actual, objectively existing whole. At least there does not appear to be a single candidate for such a relationship, as the interactions might be understood in various terms (e.g., mutualism with regard to predator swamping or competition in terms of food acquisition). And this leads us to the fourth and most viable possibility.

1.4. The Terms for Grasshopper Groups Are Interactional Perspectives. The terms used to describe groups of grasshoppers could reflect neither purely subjective nor objective criteria. There may be multiple, biologically compelling ways of identifying groups although it will also be the case that some approaches are absurd. For the pluralist [6, 7], there is more than one way of being right (contrary to the objective absolutist), but it is still possible to be wrong (contrary to the committed subjectivist). As such, the groupings of grasshoppers are interactional [8], being "made"—rather than subjectively created or objectively discovered—through the interests of the scientist interacting with the rich (but not unlimited) possibilities of the real world. That is to say, reality can be divided in many ways, but not just any way. Thus, the researcher has a particular perspective with respect to

a line of inquiry and thereby picks out one of the biologically plausible ways to group grasshoppers.

Such an approach to understanding some biological groups has been advanced—at least implicitly—by ecologists. In his analysis of the concept of communities, Underwood [9] described the subjectivist and objectivist views. The former position is that "communities are simply a human invention...used to describe the collection of organisms that are found in the same place at the same time," and the latter view is that communities are "valid and necessary object[s] of study" which are held together through biological interactions. Underwood [9] observed that these two perspectives have been alternately in favor and that "the reality is probably somewhere in between" although he does not specify an intermediate view. However, his contention that no definition will satisfy all—or even most—ecologists, opens the door to the possibility of a pluralistic approach.

2. Analogous Cases and Their Implications for Grasshopper Groups

2.1. Perspectival Approaches to Individual Entities. Is an axe a weapon or a tool? The group of implements to which an axe belongs does not seem to be objectively (or at least singularly) determinable. The right assignment of the axe depends on how it is used. In the hands of Lizzie Borden (who according to legend and the children's ditty "took an axe and gave her mother forty whacks"), the thing should be considered a weapon, but in the hands of Paul Bunyan (the mythic lumberjack), it is a tool. Nor is the correct term for the axe merely a philosophical puzzle—the consequences of being wrong could be serious. The problem of how to perceive an axe persists even when the instrument is not in the hands of others. That is, my own intentions or interests are critical to what category of things the axe belongs to when I reach for the instrument.

The "axe problem" reveals an important aspect of how we categorize objects. The subjective perspective of the individual engaging the objective entity is critical to our understanding. Scientific perspectivism [10] is the view that the ontology (what is real) and metaphysics (the properties of real things/processes) are both constrained by the facts (e.g., the axe is a heavy, sharp object so it is nonsensical to use it as a pillow) and open to an array of possible interests (e.g., weapon, tool, doorstop, etc.). The pluralism that arises from this understanding underwrites a philosophy of ecology that is called constrained perspectivism [11].

Starting with the categorization of an axe creates an accessible starting point, but groups of entities (e.g., grasshoppers) are not necessarily single things. We might contend that an axe is not a single item but is composed of a handle and a head, but these parts seem to be so intimately related in terms of the function of the whole that treating an axe as a particular item is appropriate. In fact, that is the matter we are trying to resolve: are groups of grasshoppers real things (ontology) and what sorts of things are they (metaphysics)?

2.2. Perspectival Approaches to Collective Entities. Imagine that a person walks into a room containing old furniture. The individual wants to describe what he sees and wonders about the correct term to use for the group of chairs, tables, lamps, and whatnot. The challenge is whether there is a single, right way to convey to others what he has observed—is there an objective descriptor? It seems not, as the most accurate term will depend on his interests and those of the persons with whom he will be communicating. If the man is a furniture dealer, he may tell his assistant that he has come across an "inventory of antiques." However, if he is a historian and recognizes that the furniture is a matched set from a single room of Louis XIV, the grouping might be termed a "17th century salon." But if the fellow is an artist, he might see the placement and spacing of the furniture as aesthetically pleasing and refer to the items as a "balanced arrangement of three-dimension forms." And finally, if the man is a millionaire, he might perceive the furniture as a "collection of status-enhancing objects." The point here is that there appears to be no uniquely right term for the assembled items. The interests of the observer and those with whom he is speaking are inextricably woven into choosing the right description.

This is not to say that there is no way to be wrong about a term for the furniture. In fact, there are at least two mistakes to be made. First, the man could simply use a term that does not pertain to groupings of furniture. For example, the millionaire could tell his interior decorator that he found a "squadron of furniture" or the antique dealer could tell his assistant to prepare the shop for a "herd of chairs and tables". Neither description is meaningful or appropriate for items of furniture—there is a category error in using such terms.

Second, the man could use a term that is uninformative or even misleading to the listener. If the artist tells his impoverished bohemian friend that he should go to see the "collection of status-enhancing objects," the other fellow would likely be confused—or at least not understand why he ought to be interested. Or if the historian submits a paper to the *Journal of French History* reporting that he came across a "balanced arrangement of three-dimensional forms," then he has failed to tell his colleagues what is important about his observation.

2.3. Perspectival Approaches to Scientific Referents. Before we consider the importance of terminology for groups of grasshoppers, it is useful to briefly consider two analogous cases in science and why the use of alternative terms mattered.

In physics, there has been considerable debate as to the nature of light [12, 13]. Following Newton, most scientists accepted some version of the "corpuscular hypothesis" in which light was taken to be composed of particles. In the 18th century, Leonhard Euler advocated a wave theory of light (Newton also contended that "aetheric waves" played a role, although this was largely ignored). Both the particle and wave advocates were able to construct sound arguments and compelling experiments in defense of their views. Thomas Young's famous double-slit experiment set the stage for our

contemporary understanding that light is both wave and particle—and how one perceives its nature depends on the choice of instrument or, in effect, one's interests. It matters a great deal in physics whether something is a wave or a particle, but at least with respect to light there is no objective fact of the matter.

In ecology, one's interests are critical to the interpretation of an organism's role in a habitat. Consider the case of *Echium plantagineum* in Australia [14]. For those with an interest in producing high-grade honey or ruminant livestock feed in drought stricken regions, the plant is a beneficial component of the ecosystem and warrants the common name "Salvation Jane". But for those who have an interest in restoring native habitats or producing quality forage on disturbed pastures, the plant deserves the moniker "Patterson's Curse". Whether this plant is a beneficial or pest species matters a great deal—and the right classification or term depends on one's interests.

So, is there a correct term for a group of grasshoppers? The American pragmatist William James [15] argued that:

> the human mind is essentially partial. It can be efficient at all only by picking out what to attend to, and ignoring everything else,—by narrowing its point of view. Otherwise, what little strength it has is dispersed, and it loses its way altogether. Man always wants his curiosity gratified for a particular purpose.

This position would suggest that the acridologist must choose a perspective, that there is some particular interest being served by an investigation. Terminology is thus pragmatic (reflective of interests), perspectival (based on where one stands conceptually), and pluralistic (dependent on more than a single, correct, or objective viewpoint). So there is a right term to use for a given situation—whatever most accurately conveys the intentions of the researcher and communicates this point of view to fellow scientists.

3. The Right Term for a Group of Grasshoppers: Conceptual Context

If the pragmatic philosophy of constrained perspectivism with its pluralist solution is to be adopted by acridologists, there are three concepts to keep in mind as we consider the various terms that might be used to describe groups of grasshoppers.

3.1. Role of Objectivity. The acridologist faced with multiple terms for groups of grasshoppers might worry that the pluralist approach is a slippery slope. Can objectivity check the slide toward radical subjectivism? I will have more to say about this later, but for the present it is sufficient to maintain that objectivity can limit pluralism in two ways.

First, constrained perspectivists take it to be the case that there is a mind-independent world "out there", and reality constrains the ways in which we can productively frame our understanding [11]. In short, the world "pushes back" when we form beliefs that lead to actions which do not accord with external reality. If we think of a group of grasshoppers as a

terrorist cell and launch a full-scale military attack to destroy them, the world pushes back through the economic costs, political repercussions, environmental damage, and social condemnation of our foolishness.

Second, objectivity is an important "regulative ideal"—an unattainable goal which we can rationally adopt so as to orient our pursuits (not unlike global peace or economic justice). But our understanding is invariably domain-specific. As Reiners and Lockwood [11] maintained, "We can rise above individual bias, but we cannot ascend to a God's eye view such that truth is no longer relative to a particular conceptual system." So, we must be keenly aware of our chosen perspective and then aspire to unbiased understanding within this framework. One might even say that we should try to be as objective as possible about and within our subjective context.

3.2. Nature of Groups. In some biological settings, groups are readily observable. The group of cells comprising an organism is quite evident, and even some ecological groups are discernible (e.g., a herd of deer, a school of fish, a swarm of locusts). However, most groups of grasshoppers that are studied by ecologists are not visible. This is not a challenge particular to acridology. Indeed, Reiners and Lockwood [11] made the case that:

> [M]any ecological entities are not perceived (i.e., seen by our eyes or instruments), but conceived...ecology is particularly prone to ontological and metaphysical problems such that we are concerned with how to carve up the world into entities and processes that are often unobservable (has anyone actually seen species, speciation, communities, metabolism, ecosystems, or equilibrium?).

For the most part there are not directly observable properties of a group of grasshoppers that provide a kind of objective taxonomy. That said, we may be able to infer qualities of the collective via sampling (e.g., density and species composition). Furthermore, various instruments and measurements have been developed to discern the effects of the group (e.g., forage loss and nitrogen levels).

3.3. Practical Relevance. In the context of pragmatism, James [15] maintained that "There can *be* no difference anywhere that does not *make* a difference elsewhere." That is to say, a distinction between "population" and "community", for example, is vacuous if there is no actual consequence of calling a group by one or the other of these names. Perhaps this is why there seem to be few arguments about whether acridologists should refer to "nymphs" or "hoppers"; the distinction makes no difference in terms of our beliefs and actions. As will be evident in the following section, the terms which we apply to groups of grasshoppers may well make a difference with regard to orienting the research agenda of science, communicating our findings, and perhaps even developing sound government policies and taking effective management actions. These potential consequences should not be surprising in light of other cases in which how

scientists have chosen terms and perspectives mattered (see *Perspectival approaches to scientific referents*).

3.4. Principled Relevance. Assuming that the reader is not entirely on board with the framework of pragmatism that is captured by constrained perspectivism [11], there is a principled reason why the choice of terms in science matters. That is, science is thought by many to be our closest approximation to the way the world actually is. Indeed, scientists generally favor the realist's view that we are justified in taking the referents of science to correspond with objective reality. If so, then the matter of what ecologists call groups of organisms is not an artificial controversy. Rather than making a philosophical mountain out of a scientific molehill, being clear and accurate in our language is vital to the practice of science. We would not countenance saying that 3.4 grasshoppers/m^2 was 4 grasshoppers/m^2 nor would we allow a colleague to refer to a katydid as a locust, so we should not be complacent about referring to a population as a community if, as I argue, we believe that these are essentially different entities.

4. The Right Term for a Group of Grasshoppers: Plausible Options

The predominant terms used to describe groups of grasshoppers are assemblage, population, community, and guild. Other terms for ecological groupings, such as association, inventory, and biocoenosis, can be subsumed under these more conventional descriptors.

4.1. Grasshopper Assemblage. An assemblage has the connotation of being a haphazard or accidental grouping of objects. This sense is reflected in the definitions used by ecologists. Allaby [2] provided the most fully elaborated account of the term:

> a collection of plants and/or animals characteristically associated with a particular environment that can be used as an indicator of that environment (e.g., in geobotanical exploration). The term has a neutral connotation. Its use does not imply any specific relationship between the component organisms, whereas terms such as "community" imply interactions.

The idea that an assemblage is whatever organisms happen to be present was echoed in Lewis' [16] more concise definition: "A collection of co-occurring populations." Although Underwood [9] did not explicitly define an assemblage, he used the term to describe collections of organisms that do not appear to form integrated units but simply reflect a shared physiological tolerance for a particular environment. Such a notion is clearly consonant with those of Allaby [2] and Lewis [16]. Lincoln et al. [17] provided a definition within the context of paleontology: "a group of fossils occurring together in the same stratigraphic level (an assemblage zone)." Even this definition is consistent with the "same place, same time" notion used by ecologists. Other authors of ecological and environmental references omit "assemblage"

entirely [18–20], so one might presume that the term is somewhat limited in its use. However, Google Scholar [1] produced 1,100 hits for "bird assemblage" and 12,600 hits for "fish assemblage", so the term is evidently common with regard to some organisms. Botanists use the term "association" for stable plant communities [17, 19] which are taken to have greater ecological coherence than assemblages of animals.

If acridologists accept that a "grasshopper assemblage" is just whatever species happen to coexist in some habitat, then the term seems peculiar in light of scientific investigations. The neutrality of "assemblage" suggests that the scientist had no particular theoretical interest in the group of insects with respect to ecology or evolution. This would lead one to wonder why the individual bothered to amass data about a set of objects without some hypothesis having structured the research. Perhaps the most plausible response to this pertains to those works that are not hypothesis driven but represent descriptive natural histories. Pfadt's *Western Grasshoppers* [21] is a fine example of this kind of conceptual neutrality. In addition to purely descriptive scientific works, there may be nonscientific reasons for knowing about the grasshoppers at a particular time and place. However, these other reasons are not neutral with respect to other human interests.

Pest managers may not be acting within any conceptual ecological framework in making decisions about grasshoppers. Along with a decision support system (e.g., [22]), simply knowing what species are present and at what densities may be all that is required for economically sound action. As such, a scientist who is emulating the perspective of a pest manager might well be justified in referring to a "grasshopper assemblage"; all of the individuals present (and thereby constituting a potential object of suppression) are being perceived as a group without regard to further ecological inquiry.

As with pest managers, environmental managers of public lands, private reserves, and other habitats that support grasshoppers may be acting from the basis of agency standards, legislative mandates, or advisory board policies. Likewise, conservation objectives are grounded in a set of values external to ecological theory although they may be informed by scientific concepts. Just as the pest manager's interest is economic, the environmental manager's concern may be social, legal, or moral.

In the context of environmental management, "assemblage" would seem to be appropriate although there is also some use of "inventory" (this term generated 119 hits in Google but none in Google Scholar). This latter term seems to conceptually align with the metaphorical perspective of biodiversity conservation insofar as managers attend to the protection of a biological stockpile or warehouse. "Grasshopper inventory" was used by Walter et al. [23] in the context of conservation biology, and the term appears on the websites of the Konza Prairie Educational Program [24] and the Medford Oregon office of the Bureau of Land Management [25]. However, conservation biologists seem to more often refer to grasshopper assemblages; for example, "Responses of grasshopper assemblages to long-term grazing management in a semi-arid African savanna" [26] and

"Effects of fire disturbance on grasshopper (Orthoptera: Acrididae) assemblages of the Comanche National Grasslands, Colorado" [27].

4.2. Grasshopper Population. The most common term for a group of grasshoppers is "population". In this regard, two questions are pertinent: is it legitimate to refer to a group of multiple species as a population, and what is the ecological interest/perspective that differentiates a population from an assemblage?

Various references are inconsistent with regard to whether the definition of population applies to more than one species. Lewis [16] favored the single species notion of a population as "A collective group of individuals of the same species (or other taxa in which individuals exchange genetic information) occupying a particular space." Likewise, Allaby [2] defined a population as "a group of organisms all of the same species, which occupies a particular area," but he goes on to note that this term can also be used in a statistical context for "any group of like individuals" (which presumably could include more than one species). The dual possibility of single and multiple species was echoed by Lincoln et al. [17].

Explicit allowance that "population" can refer to a group composed of one or more species is found in Allaby's earlier reference in which he maintained that a population can be individuals within a species ("e.g., the human population of a particular country") or a larger taxonomic group ("e.g., the bird population of a particular area") [19]. This broader approach was endorsed by Martin and Hine [20], who defined a population as both, "A group of individuals of the same species within a community" and "The total number of individuals of a given species or other class of organisms in a defined area, e.g. the population of rodents in Britain." So, it appears that acridologists are not misusing "population" when referring to a group comprised of more than a single species.

The ecological perspective that is reflected in referring to a group as a population is evident in the definitions. Allaby [19] states that this term obtains when a group is "considered without regard to interrelationships among (the individuals)," and "when describing phenomena that affect the group as a whole (e.g., changes in numbers)." Hence, it is the dynamics of the group, its spatial distribution, or temporal changes, that motivate the investigation of a population. Indeed, many references include entries pertaining to these qualities, such as "population biology", "population density", "population dynamics", "population ecology", and "population growth" [17–20, 28]. Thus, an acridologist seems to be justified in calling a group of grasshoppers a population if the purpose of the investigation is to understand the factors which explain the spatial patterns or (particularly) temporal dynamics of the organisms. As such, it seems quite appropriate to use this term in contexts such as: "A perspective of grasshopper population distribution in Saskatchewan and interrelationship with weather" [29] and "A simulation model for testing the dynamics of a grasshopper population" [30].

4.3. Grasshopper Community. Aside from "population", the most common term for a group in acridology is "grasshopper community". And once again, two questions are pertinent: is it legitimate to refer to a group comprised of only a single family as a community, and what is the ecological interest that differentiates a community from an assemblage or population?

Although few terms in ecology generate full agreement with regard to definitions, there appears to be considerable consensus as to what makes a group of organisms a community. In all of the references considered for this paper, the authors made clear that a community is comprised of different species [2, 16–20, 28]. However, there appears to be no indication that these species must include members of different higher taxa (i.e., multiple families, orders, classes, phyla, or kingdoms). Only Martin and Hine [20] refer to communities as including plants and animals, but they also note that "Larger communities can be divided into smaller communities," which could presumably include a single taxonomic family. In fact, Google Scholar [1] searches for "bird community" and "fish community" both generated more than 10,000 hits. As such the term "grasshopper community" seems entirely appropriate with regard to its scope of taxonomic inclusion. This leaves the question of what qualities make a group of grasshoppers a community.

There is also considerable agreement that for a group of organisms to constitute a community there must be interactions (e.g., trophic, mutualistic, and competitive relationships) among the individuals that provide structure [2, 17, 20]. Even definitions that do not make the relational aspect explicit are suggestive of such a criterion. Both Parker's [18] "distinctive combination of species" and Allaby's [19] "naturally occurring group of organisms that occupy a common environment" would seem to imply, if not require, that a relational factor unites the collective.

The matter of there being valid grasshopper communities would seem to be settled except for the confusion that arises with an allied term. Underwood [9] opens the door with his description of early marine ecologists who had to dredge or otherwise grab samples in a haphazard fashion because they were unable to see into the habitat. The term used to describe the group of collected organisms was "biocoenosis". This was evidently a nonnatural collection of species taken from a particular location at a given time. As such, one might suppose that this would have been an assemblage. However, the ecologists described these groups in terms of being equilibrial communities, so the interactions among the organisms served as the conceptual context. The result of this hybridization of assemblage and community was terminological confusion. While Parker [18], Lewis [16], and Lincoln et al. [17] equated "biocoenosis" with "community", Allaby [19] explicitly defined a coenosis as "A random assemblage of organisms that have common ecological requirements, as distinct from a Community." To make matters worse, Lincoln et al. [17] noted that biocoenosis is often used as an alternative term for "ecosystem", and Allaby [2] equated it with "biome". With regard to acridology, Google Scholar [1] revealed no citations with the term

TABLE 1: Terminology used for groups of grasshoppers and the perspectives in which these descriptors are most appropriate.

Term	Context
Assemblage	When there is primarily a nonecological interest in the economic or other values of the group, such as in pest management or conservation
Inventory	When there is primarily a nonecological interest in the group as a component of biodiversity, most often for the purposes of conservation
Population	When there is primarily an ecological interest in the spatiotemporal dynamics of the group and the factors that account for these quantitative changes
Community	When there is primarily an ecological interest in the interactions within the group (e.g., mutualism and competition) and how these structure membership
Biocoenosis	Perhaps equivalent to "community," but the ambiguity in use is such that the term is probably not a clear expression of a particular perspective
Guild	When there is primarily an ecological interest in the role that the group plays in its use of a common resource, usually in a similar fashion

"grasshopper biocoenosis," although there was one reference to "grasshopper coenosis".

Given the ambiguity and rarity of (bio)coenosis to describe groups of grasshoppers and the most common view that the term is equivalent to "community", it seems reasonable to suggest that the latter term be used. The appropriate context for the use of "grasshopper community" is when the scientist is interested in the ecological relationships among the individuals (e.g., competition for food or trophic interactions) and how these bind the collective into a coherent group. It should be noted that "grasshopper community" may include nongrasshopper species as communities are often named for the dominant, but not sole, taxon [17]. Examples of studies in which interactions are the perspective taken by the researcher include "Arid grassland grasshopper community structure: comparisons with neutral models" [31] and "The role of vertebrate and invertebrate predators in a grasshopper community" [32].

4.4. Grasshopper Guild. The term "guild" is not often used to describe a group of grasshoppers. However, it is worth considering what sorts of features this concept picks out and the contexts in which it would be appropriately used (versus assemblage, population, or community).

Although "guild" is not defined in several of the sources used in this analysis [18, 20, 28], those that include the term agree on its meaning: a group of (perhaps closely related) species which use an ecological resource, usually in a common fashion [16, 17, 19]. Like a community, a guild includes multiple species. But the distinguishing feature of the group is more specific than in the case of a community, where any relationship could provide a conceptual unification. Because of their reliance on a common resource, members of a guild have a similar role in the community [17].

It is the scientist's interest in this ecological function (and the fact that such a function actually exists) that makes it appropriate to refer to the "forbivore guild of grasshoppers" or the "scavenger guild of grasshoppers". An apropos use of

the term is exemplified by Owen-Smith and Dankerts [33]:

> Grasshoppers in the Pyrgomorphidae, as well as certain of the Pamphagidae, Catantopinae and Tettigoniidae, feed primarily on forbs and small shrubs. Evidently nibbling by the grasshopper guild is more evenly spaced over the herbaceous layer than is grazing by ungulates.

"Guild" is presumably uncommon in the acridological literature because of the relatively narrow specificity of the research interest. The diverse feeding habits of grasshoppers means that they are collectively subsumed under herbivory (detritivorous and necrophagous behaviors notwithstanding), and to refer to the "herbivore guild" (or even the "insect herbivore guild") would entail many taxa other than Acrididae or Orthoptera. However, there would appear to be some cases in which grasshoppers can be reasonably understood to comprise a guild.

4.5. Terminological Perspectivism. The terms used for groups of grasshoppers should (and often do) reflect the interests of the scientist, such that others can reasonably infer the ecological or other perspective of a particular study. There may well be more terms for groups than I have analyzed here, and should these alternatives more effectively communicate the nature of an investigation they ought to be used. However, the descriptors in Table 1 represent the most common terms used by acridologists and ecologists and cover many, perhaps most, of the ways that we perceive grasshoppers in the field.

5. Summary: The Pragmatist's View of the Right Term for a Group of Grasshoppers

No investigation of a group of grasshoppers is motivated by all of the interests pertinent to acridology. For example, if one is attempting to understand the interactions among individuals within a given year, then it is not plausible to be also investigating the environmental factors associated with

the numerical dynamics of the group over the course of a century. But neither is it defensible to contend that one or the other of these perspectives is better or somehow more reflective of actual groups of insects in the world. We might think of the ways of perceiving a group of grasshoppers as being ecological lenses. The features visible through the "community lens" are not evident via the "population lens". Giere [10] recognized the importance of understanding scientific inquiries as partial truths when he argued the following:

> [T]his multiple rootedness need not lead to "anything goes" perspectival relativism, or an antinaturalist worship of common sense, experience, or language. It yields a kind of multi-perspectival realism anchored in the heterogeneity of "piecewise" complementary approaches common in biology and the study of complex systems.

At this point, one might reasonably wonder about the nature of truth for the advocates of constrained perspectivism. Is terminology merely a matter of linguistic convention or can we assert that a term is correct? The philosophy of pragmatism entails what has been called radical empiricism [34], an approach consonant with scientific inquiry. We know what is true via our testing of ideas through their application in the world. The pragmatists eschewed debates about ontology and metaphysics that were not based on biophysical evidence. Arguing about reality and its properties was a fruitless endeavor unless there were actual consequences of being right (or wrong). This view gave rise to Richard Rorty's analysis that truth is the compliment we pay to ideas that work [11]. What then does it mean for an idea to "work"?

According to the pragmatists, an idea worked if it served as the basis for an action resulting in an outcome that satisfied genuine (not superficial or merely expedient) needs and desires. In short, an idea was true if it led to behaviors that fulfilled our interests as human beings. It is this concept that allows one to assert that a particular term for a group of grasshoppers is the right one.

The test of whether "grasshopper population" or "grasshopper community" is a true description of a group of these insects is rather straightforward. Does adopting a particular perspective and using the associated term allow us to act in the world in ways that accord with our interests (both with regard to understanding the organisms and being understood by our colleagues)? The term "grasshopper population" is the right choice if this conceptual framework facilitates our investigation of a feature of the group (e.g., the rate of change in the density of the insects by the application of an appropriate model) and conveys to others the nature of our inquiry (e.g., our investigation concerns spatiotemporal dynamics rather than interactions structuring the group or other possible interests).

In this pragmatic context, I would propose that one of the reasons why pest management of rangeland grasshoppers is often conducted with nominal regard to beneficial and innocuous acridid species is the conceptual lumping that follows from referring to "grasshopper population

outbreaks". In effect, treatment programs target all of the grasshopper species which are amalgamated into a single group of pestiferous insects. And such homogenization can have highly deleterious consequences, such as the inadvertent suppression of high densities of beneficial species [35]. One has to wonder whether such mistakes might be avoided if we focused on ecological relations and referred to treatments of "grasshopper communities". Such a terminological shift might entail our paying significantly greater attention to the more ecologically complex functions of these insects. In this context, treating a "grasshopper assemblage" might be politically expedient but fail to convey the environmental concerns that attend pest management interventions.

As scientists, we want to pick out "natural kinds" in the world—those groups that represent objective, mind-independent collections of individuals [36, 37]. And there is reason to believe, for example, that "all of the grasshoppers that eat forbs" in a given habitat reflects an actual ecological group of individuals much more so than "all grasshoppers that were named by Samuel Hubbard Scudder". In the end, however, the pragmatist recognizes that we do not have direct access to the way the world really is; we cannot know if our perspective uniquely or wholly corresponds with objective reality. What we can know is whether reality exists in such a way that our acting as if a group was real leads to actions that yield results consistent with human needs and wants. The right term for a group of grasshoppers is one that picks out and communicates one of a large number of "useful kinds" [11]—and it is my hope that this paper has made some practical contribution to our understanding of the natural world and one another.

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Research Article

Application of General Circulation Models to Assess the Potential Impact of Climate Change on Potential Distribution and Relative Abundance of *Melanoplus sanguinipes* (Fabricius) (Orthoptera: Acrididae) in North America

O. Olfert,[1] R. M. Weiss,[1] and D. Kriticos[2]

[1] *Agriculture and Agri-Food Canada, Saskatoon Research Centre, 107 Science Place, Saskatoon, SK, Canada S7N 0X2*
[2] *CSIRO Entomology, GPO Box 1700, Canberra, ACT 2601, Australia*

Correspondence should be addressed to O. Olfert, owen.olfert@agr.gc.ca

Climate is the dominant factor determining the distribution and abundance of most insect species. In recent years, the issue of climatic changes caused by human activities and the effects on agriculture has raised concern. General circulation model scenarios were applied to a bioclimatic model of *Melanoplus sanguinipes* to assess the potential impact of global warming on its distribution and relative abundance. Native to North America and widely distributed, *M. sanguinipes* is one of the grasshopper species of the continent most responsible for economic damage to grain, oilseed, pulse, and forage crops. Compared to predicted range and distribution under current climate conditions, model results indicated that *M. sanguinipes* would have increased range and relative abundance under the three general circulation model scenarios in more northern regions of North America. Conversely, model output predicted that the range of this crop pest could contract in regions where climate conditions became limiting.

1. Introduction

Climate is the dominant factor determining the distribution and abundance of most insect species [1]. The issue of climatic changes caused by human activities and the effects on agriculture has raised concern in recent years. The overall global temperature has increased 0.7°C over the last 100 years, with the 1990's being the warmest decade on record [2]. Climate change scenarios using low greenhouse gas emissions suggest that temperatures will increase by 1–3°C over the next 100 years and temperatures have been predicted to increase by 3.5–7.5°C for scenarios with high gas emission [3]. However, Walther et al. [4] suggest that species respond to regional changes that are highly heterogeneous and not to approximated global averages. Many species have already responded to regional conditions that have occurred during the 20th century. In a study of 694 animal and plant species, Root et al. [5] investigated the change in timing of events over the past 50 years and reported that changes in timing of spring events (breeding, blooming) occurred 5.1 days earlier per decade. Warming conditions may impact grasshopper populations by extending the growing season, altering the timing of emergence from overwintering sites, increasing growth and development rates, shorting generation times, increasing the numbers of eggs laid, and changing their geographic distribution [6, 7].

Analogue scenarios which make use of existing climate data are useful to identify geographic regions that may be susceptible to establishment of insects, when comparing the results of climate change scenarios to those regions where the species in question is already established [8]. However, the magnitude of predicted temperature change associated with climate change is not within the historical experience of modern agriculture. Hence, it is unlikely that we can use historical data as analogues to predict the impact of climate change on pest species. As a result, simulation models have been used to assess impact and related system vulnerability due to climate change.

TABLE 1: CLIMEX parameter values used to predict potential distribution and relative abundance of *Melanoplus sanguinipes* in North America.

CLIMEX growth parameters		
Temperature		
DV0	Limiting low average weekly temperature	$10.0°C$
DV1	Lower optimal average weekly minimum temperature	$16.0°C$
DV2	Upper optimal average weekly maximum temperature	$28.0°C$
DV3	Limiting high average weekly maximum temperature	$32.0°C$
Moisture		
SM0	Limiting low soil moisture	0.02
SM1	Lower optimal soil moisture	0.05
SM2	Upper optimal soil moisture	0.30
SM3	Limiting high soil moisture	0.70
Diapause		
DPD0	Diapause induction day length	11 h
DPT0	Diapause induction temperature (average weekly minimum)	$11.0°C$
DPD1	Diapause termination temperature (average weekly minimum)	$3.0°C$
DPD	Diapause development days	120
DPSW	Summer or winter diapause	0
CLIMEX Stress Parameters:		
Cold stress		
TTCS	Cold stress threshold (average weekly minimum temperature)	$-18.0°C$
THCS	Rate of cold stress accumulation	-0.0004
Heat stress		
TTHS	Heat stress threshold (mean weekly maximum temperature)	$35.0°C$
THHS	Rate of heat stress accumulation	0.008
Dry stress		
SMDS	Dry stress threshold (mean weekly minimum soil moisture)	0.020
HDS	Rate of dry stress accumulation	-0.003
Wet stress		
SMWS	Wet stress threshold (mean weekly maximum soil moisture)	0.7
HWS	Rate of wet stress accumulation	0.001

Bioclimate simulation models have been used successfully to predict the distribution and extent of insect establishment in new environments [9–12]. Bioclimatic modeling software, such as CLIMEX, enables the development of models that describe the potential distribution and relative abundance of a species based on climate [1, 13]. CLIMEX derives an Ecoclimatic Index (EI) which describes the suitability of specific locations for species survival and reproduction. Model parameters include temperature (TI), diapause (DI), light (LI), moisture (MI), heat stress (HS), cold stress (CS), wet stress (WS), and dry stress (DS). The EI values are obtained by combining a Growth Index (GI) with stress indices (dry, wet, cold, and hot) that describe conditions that are unfavourable for growth.

Native to North America and widely distributed, *Melanoplus sanguinipes* (Fabricius) (Orthoptera: Acrididae) is responsible for more economic damage to grain, oilseed, pulse, and forage crops than any other grasshopper species [14–16]. A bioclimate model was developed to predict the potential distribution and relative abundance of *M. sanguinipes*, within Canada [17]. Ecological sensitivity analyses were then conducted using incremental scenarios for all combinations of temperature (0, +1, +2, +3, +4, +5, +6, and +7°C of climate normal temperature for each grid) and of precipitation (−60%, −40%, −20%, −10%, 0%, 10%, 20%, 40%, 60% of climate normal precipitation for each grid). Compared to predicted range and distribution under current climate conditions, model results indicated that *M. sanguinipes* would have increased range and relative abundance for temperature increases between 1°C and 7°C. The model predicted that the range of this crop pest could be extended to regions that are not currently used for agricultural production in North America. Mika et al. [18] stated that at an ecosystem level, climatic variables will vary both spatially and temporally. Therefore, they suggested that the widely accepted and more commonly used general circulation models (GCMs) should be used in conjunction with bioclimate models, rather than incremental scenarios. Further, they encouraged the application of multiple GCMs due to the variability of climate projections between models.

The objective of this study was to use the bioclimate model for *M. sanguinipes* [17] to assess the impact of three

TABLE 2: Baseline(CRU) and general circulation model (NCAR273 CCSM, MIROC-H, CSIRO MARK 3.0) scenarios and resulting Ecoclimatic Inex (EI), temperature (TI), moisture (MI), diapause (DI), growth index (GI), cold stress (CS), heat stress (HS), number of weeks GI was positive (Weeks GI Positive), and core distribution, for *Melanoplus sanguinipes* at six locations.

Location	Scenario	EI	TI	MI	DI	GI	CS	HS	Weeks GI positive	Core distribution
Fairbanks, AK	NCAR273 CCSM	20.1	22.3	83.2	38.5	20.7	2.9	0	18.2	97
	CSIRO MARK 3.0	18.3	22.9	83.2	40.1	20.9	12.7	0	18	87.1
	MIROC-H	18.2	21.5	87.3	37.7	20	8.6	0	17.1	91.3
	CRU	5.4	12	88.6	33.1	11.1	54.2	0	13.9	45.7
Peace River, AB	NCAR273 CCSM	23.8	34.2	71.9	42.1	23.8	0	0	20.7	97.3
	CSIRO MARK 3.0	29.2	33.2	77.9	43.4	29.4	0.1	0	22.4	98.8
	MIROC-H	25	30.2	79.5	41.3	25	0	0	21.2	98.6
	CRU	14.7	21.8	80.2	36.9	16.5	9.6	0	19	87.9
Saskatoon, SK	NCAR273 CCSM	34.9	37.8	92.3	45.6	34.9	0	0	23.8	100
	CSIRO MARK 3.0	36.3	37.5	94.3	46.5	36.3	0	0	24.2	100
	MIROC-H	35.2	36.6	91.7	44.6	35.2	0	0	23.3	100
	CRU	26.7	30.7	96.1	41.8	28.8	8.2	0	21.8	91.8
Gillette, WY	NCAR273 CCSM	24.4	29.9	96.9	48.8	24.4	0	0	19.7	100
	CSIRO MARK 3.0	24.1	30.1	98.2	50.2	24.9	0	3.9	18.3	96.1
	MIROC-H	24.9	30.4	95.8	47.1	24.9	0	0	20	100
	CRU	31.7	35.2	98.5	44	31.7	0	0	23	100
Lincoln, NE	NCAR273 CCSM	10.8	31.6	64	55.8	11.3	0	2.6	14.4	95.9
	CSIRO MARK 3.0	12.2	28.6	91.7	57.2	18.8	0	40.8	16.7	65.7
	MIROC-H	15.9	30.3	77.6	54.5	16.3	0	1.9	18.8	98.1
	CRU	21.3	39	70.3	52.5	21.3	0	0	24.3	100
Lubbock, TX	NCAR273 CCSM	14.1	37.4	96.2	43.7	18.1	0	50.1	13.8	58.3
	CSIRO MARK 3.0	5.2	34.8	98.6	44.2	15.5	0	167.7	11.5	21
	MIROC-H	9.5	33.9	97.5	47.3	17.9	0	95	13.4	40.2
	CRU	30.6	39.3	98.7	57.1	31.1	0	1.6	22.1	98.4

general circulation models on population distribution and relative abundance across North America.

2. Methods

The bioclimatic model for *M. sanguinipes,* developed using CLIMEX 2.0 [19], has been previously described [17]. CLIMEX is a dynamic model that integrates the weekly responses of a population to climate using a series of annual indices. It uses an annual Growth Index to describe the potential for population growth as a function of soil moisture and temperature during favourable conditions, and Stress Indices (cold, wet, hot, and dry) to determine the effect of abiotic stress on survival in unfavourable conditions. The weekly Growth Index is a function of temperature (TI), diapause (DI), and moisture (MI). The growth and stress indices are calculated weekly and then combined into an overall annual index of climatic suitability, the Ecoclimatic Index (EI), that ranges from 0 for locations at which the species is not able to persist to 100 for locations that are optimal for the species [17]. Model parameter values are listed in Table 1. Initial parameter values were obtained from published papers. Model parameters were then adjusted to ensure

that EI $\geq$ 30 in geographical regions historically affected by *M. sanguinipes,* indicating that climatic conditions were favorable for development of densities associated with crop loss. Historical grasshopper population data were used for model validation. Annual surveys of abundance of adult grasshoppers have been conducted in Saskatchewan since 1931 [20]. Relative abundance was validated by comparison with adult grasshopper survey data from Saskatchewan over the period of 1970 to 2004 [17]. The model was tested by comparing the occurrence of observed life history events against those predicted by the model.

Climate change projections were obtained from the Intergovernmental Panel on Climate Change [21] as monthly means for three GCMs, based on current climate, 30 yr average (1961–1990) dataset (A1B emission scenario) (CRU— Climate Research Unit, East Anglia, UK). The three GCMs selected were CSIRO Mark 3.0 (CSIRO, Australia), NCAR273 CCSM (National Centre for Atmospheric Research, USA), and MIROC-H (Centre for Climate Research, Japan). All three had relatively small horizontal grid spacing and the requisite climatic variables at a temporal resolution appropriate for CLIMEX. The data were pattern-scaled to develop individual change scenarios relative to the base
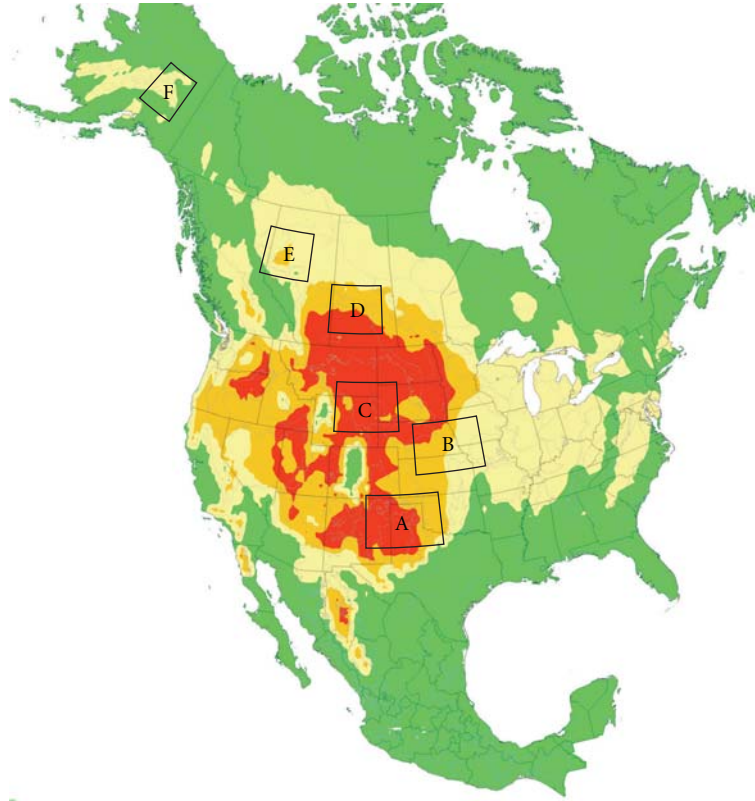
Figure 1: Predicted distribution and abundance (EI) of *Melanoplus sanguinipes* for current climate (CRU) at six regions: (A) Lubbock, TX; (B) Lincoln, NE; (C) Gillette, WY; (D) Saskatoon, SK; (E) Peace River, AB; (F) Fairbanks, AK. Green = "Unfavourable" (EI = 0–5); Tan = "Suitable" (EI = 5–20); Orange = "Favourable" (EI = 20–30); Red = "Very Favourable" (EI ≥ 30).

climatology [22]. The three models cover a range of climate sensitivity, defined as the amount of global warming for a doubling of the atmospheric CO_2 concentration compared with 1990 levels [23]. The respective sensitivities are: CSIRO Mark 3.0 (2.11°C), NCAR-CCSM (2.47°C), and MIROC-H (4.13°C).

The resulting database was queried to analyze data at a regional scale. A geographic rectangle, 4° latitude by 7° longitude, was used to delineate a regional template. The defined region was approximately the size and shape of Colorado (270,000 km^2) and, for each of the datasets, consists of 112 grid cells. Specific regions, based on latitude and longitude coordinates, were defined and output (averaged across the region) was generated for detailed analysis. The datasets permitted comparison of variables, both spatially and temporally (weekly intervals). Analyses were based on values centered on six locations including Lubbock, Texas (33.6°N, 101.9°W), Gillette, Wyoming (44.3°N, 105.5°W), Lincoln, Nebraska (40.9°N, 96.7°W), Saskatoon, Saskatchewan (52.1°N, 106.6°W), Peace River, Alberta (56.2°N, 117.3°W), and Fairbanks, Alaska (64.8°N, 147.7°W).

Contour maps were generated by importing EI values into geographic information system software, ArcView 8.1 [24]. Final EI values were displayed in the four categories defined above: "Unfavourable," "Suitable;" "Favourable;" and "Very Favourable."

3. Results and Discussion

Comparisons were made to determine if differences in baseline climate data would result in differences in output. The New et al. [25] climate data represents a splined 0.5° world grid dataset. The EI output the baseline CRU data agreed with that produced using the New et al. [25] climate data set in Olfert and Weiss [17]. Initially, there appeared to be some differences in model output between the two approaches for Peace River and Saskatoon (Table 2). Olfert and Weiss [17] reported that the EI values for Peace River and Saskatoon were 24 and 30, respectively. This study showed that EI values for Peace River and Saskatoon were 14.7 and 26.7 (Table 2). These differences occurred because the original paper reported values for single grid cells. However, the current analysis was based on averages across large regions that are composed of 112 grid cells. When single grid cells for Peace River and Saskatoon were examined in the current study, it was found that EI values were indeed 24 and 30.

Results, based on the CRU data for current climate, indicated that *M. sanguinipes* would have highest EI values across
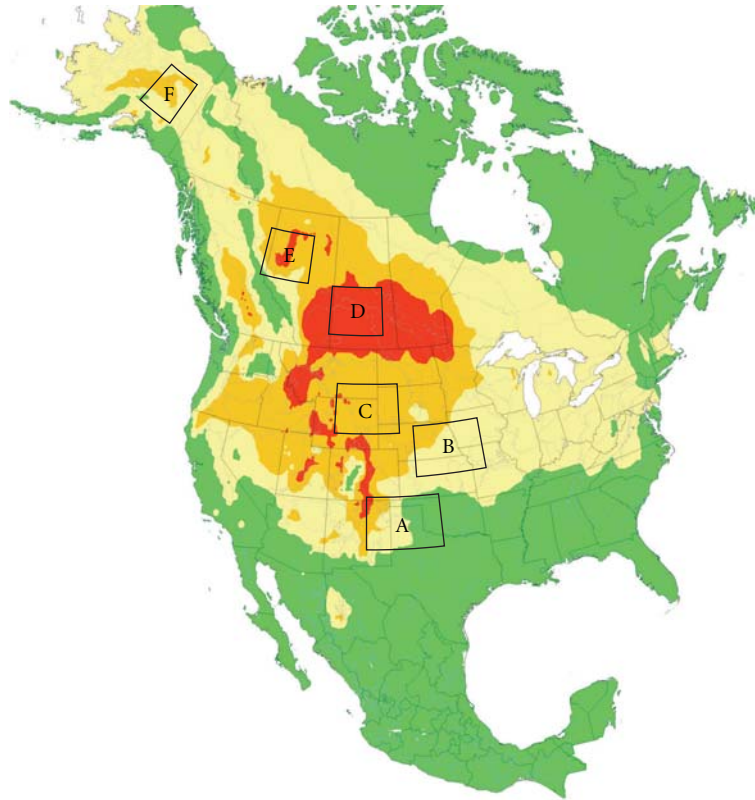
FIGURE 2: Predicted distribution and abundance (EI) of *Melanoplus sanguinipes* for 2080 (CSIRO MARK 3.0) at six regions: (A) Lubbock, TX; (B) Lincoln, NE; (C) Gillette, WY; (D) Saskatoon, SK; (E) Peace River, AB; (F) Fairbanks, AK. Green = "Unfavourable" (EI = 0–5); Tan = "Suitable" (EI = 5–20); Orange = "Favourable" (EI = 20–30); Red = "Very Favourable" (EI ≥ 30).

most of the Great Plains of North America, extending from northern Texas to southern Saskatchewan (Figure 1). These results agreed with the distribution of *M. sanguinipes* as described by Riegert [20] and Pfadt [26]. Compared to these results, each of the three GCMs resulted in large differences for most model parameters, particularly EI (Figures 2–4; Table 2). Across North America, the overall mean EI values were 4.9 (CRU), 7.5 (CSIRO MARK 3.0), 7.9 (MIROC-H), and 7.3 (NCAR273 CCSM). Olfert and Weiss [17] grouped ecoclimatic indices into four categories: "Unfavourable" (EI = 0–5), "Suitable" (EI = 5–20), "Favourable" (EI = 20–30), and "Very Favourable" (EI ≥ 30). Unfavourable described regions where *M. sanguinipes* would be very rare or may not occur; "Suitable" defined areas were grasshoppers would occur, usually in low densities; "Favourable" defined areas were densities could be high enough to result in crop loss; "Very Favourable" defined areas where grasshoppers regularly occur in high enough densities that result in crop loss. Based on this study, the extent of the area predicted to be "Very Favourable" were 11.2% (CRU), 16.2% (CSIRO MARK 3.0), 16.2% (MIROC-H), and 18.1% (NCAR273 CCSM) of North America.

Species are more vulnerable to variations in temperature and precipitation when located near the outer limits of their geographic range than when located in the core area of the range. Sutherst et al. [19] defined a core area as a region with high EI values and little or no stress. Populations near the outer limits of the core area spend a greater amount of time in climates that are marginally suitable (exposed to climatic stress), while populations near the core experience a greater amount of time in favourable conditions (minimal exposure to climatic stress). In this study, EI values tended to increase in a northwestern direction and decrease for southern locations when the three GCMs were applied to the bioclimate model for *M. sanguinipes*. The percent of area (on a regional basis) with EI ≥ 20 varied across North America. For example, under current climate conditions (CRU), the model predicted that 0% of the Fairbanks region had EI ≥ 20 (Table 3). This value increased to as much as 57% of the area under conditions predicted by NCAR273 CCSM. As a result, the increase in the biological suitability of Fairbanks, AK, due to climate change was predicted to be similar to that of Lincoln, NE, under current climate conditions (CRU). In turn, the model predicted that the area surrounding Lincoln, NE, where EI ≥ 20 would decrease to 6.3% (NCAR273 CCSM), compared to 59.8% under current climate conditions (CRU).

As indicated, there were regional differences across North America in output of the bioclimate model for *M. sanguinipes* when the three different GCMs were applied (Figures 2–4). The application of CSIRO MARK 3.0 climate data resulted in a northward shift of areas predicted to have
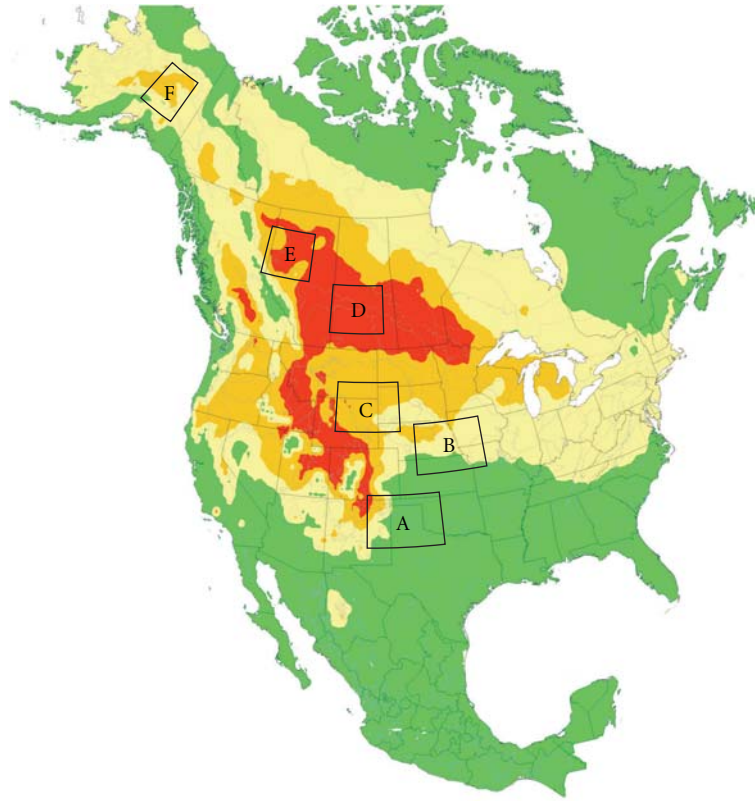
FIGURE 3: Predicted distribution and abundance (EI) of *Melanoplus sanguinipes* for 2080 (MIROC-H) at six regions: (A) Lubbock, TX; (B) Lincoln, NE; (C) Gillette, WY; (D) Saskatoon, SK; (E) Peace River, AB; (F) Fairbanks, AK. Green = "Unfavourable" (EI = 0–5); Tan = "Suitable" (EI = 5–20); Orange = "Favourable" (EI = 20–30); Red = "Very Favourable" (EI $\geq$ 30).

reduced suitability for grasshopper populations within the southern Great Plains, relative to current climate conditions (CRU). There was a significant reduction in EI values in states such as Colorado, Wyoming, and Missouri (Figure 2). In northwest Texas, the EI values were predicted to decrease to less than 10. In more northern regions, however, EI values were predicted to be higher in Alaska, northern Alberta, and Saskatchewan, relative to current climate conditions (CRU). Output based on the MIROC-H dataset resulted in a northwest shift of regions with EI $\geq$ 20 (Figure 3). Compared to current climate data (CRU), the MIROC-H GCM predicted that the overall area suitable for *M. sanguinipes* in the USA would be less than under current climate conditions. However, the suitable areas along the Rocky Mountains were observed to increase somewhat. The MIROC-H dataset predicted large EI increases across most of the Canadian prairies, and extending northwest to include a continuous area northwest to Peace River, Alberta. Of the three GCMs, MIROC-H output resulted in the largest, continuous areas with EI $\geq$ 20. Unlike CSIRO MARK 3.0 and MIROC-H, NCAR273 CCSM predicted a reduction in EI values for eastern North America. This GCM also predicted increased EI values in the interior of British Columbia.

In order to assess the potential impact of climate change in a more regional context, the resulting database was queried to analyze data at six regional locations between Lubbock, Texas, and Fairbanks, Alaska. Overall, the largest differences in EI values were observed at northern and southern regions of North America. The shifts in EI values were less in central locations. Compared to current climate (CRU), EI values derived from GCMs resulted in increased EI for the areas surrounding the three northern regions Saskatoon, Peace River, and Fairbanks (Figures 1–4, Table 2). The magnitude of the increase in EI values, based on regional means, was 252%, 77%, and 33% greater for Fairbanks, Peace River, and Saskatoon, respectively, than those under current climate conditions. As a result, warming conditions were predicted to result in increased potential for *M. sanguinipes* outbreaks in these three regions. Outbreaks of *M. sanguinipes* have been recently reported in northern areas of North America. This species has been reported to be a sporadic, potentially damaging grasshopper pest of small grain crops in Alaska [27] and recent outbreaks of grasshoppers have been reported in the Peace River region of Alberta [28]. The three southern locations (Lincoln, Gillette, and Lubbock) had lower EI values when GCMs were used as inputs into the model. Relative to the EI values under current climate, the regional mean EI values for Gillette, Lincoln, and Lubbock were predicted to be 23%, 29%, and 69% less, respectively. The regional responses to model input varied for the three GCMs (Table 3). The MIROC-H GCM resulted in the largest increase in EI for the Peace River and Saskatoon regions,
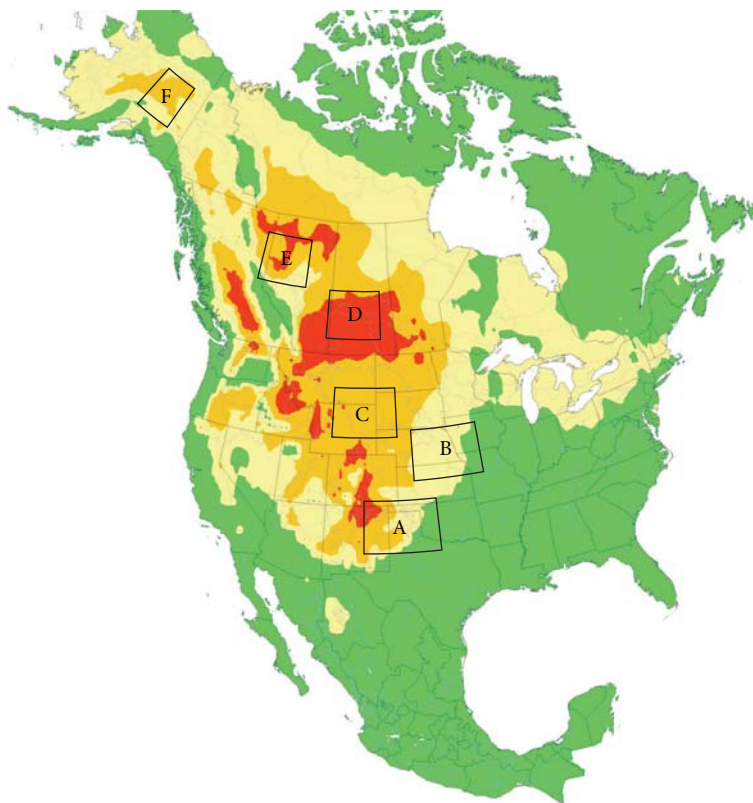
FIGURE 4: Predicted distribution and abundance (EI) of *Melanoplus sanguinipes* for 2080 (NCAR273 CCSM) at six regions: (A) Lubbock, TX; (B) Lincoln, NE; (C) Gillette, WY; (D) Saskatoon, SK; (E) Peace River, AB; (F) Fairbanks, AK. Green = "Unfavourable" (EI = 0–5); Tan = "Suitable" (EI = 5–20); Orange = "Favourable" (EI = 20–30); Red = "Very Favourable" (EI ≥ 30).

while the NCAR273 CCSM model resulted in the largest increase for the Fairbanks region. Of the three more southern regions, Lubbock exhibited the largest decrease in EI values for MIROC-H.

The weekly temperature index (TI) describes the weekly response of *M. sanguinipes* to the daily temperature cycles that occur during the growing season. *Melanoplus sanguinipes* overwinters in the egg stage. The timing and duration of spring hatch is influenced by the level of embryonic development going into winter, natural enemies, and soil temperature and moisture [29, 30]. In northerly regions, *M. sanguinipes* produces only one generation per year; in more southerly areas, a small proportion of the eggs oviposited do not enter diapause and may result in a lesser second generation. This species prefers warm, dry weather conditions. Warm temperatures early in spring favour nymphal development and in turn the timing of adulthood. Conversely, cool and wet conditions in spring results in increased nymphal mortality and delayed development. Crop loss due to feeding damage can occur throughout the growing season. Newly emerged seedlings in spring are most vulnerable, however, gradual plant defoliation may also contribute to decreased crop yield and quality [14, 16]. Later in the growing season, an extended, warm fall influences the longevity of adults, allowing them to continue reproducing until freeze-up [29, 30]. As a result, economic infestations

are often associated with a prolonged period of consecutive seasons with above-normal temperatures [29]. Intermittent warm seasons tend to result in fluctuating populations [31, 32]. The GCM datasets, associated with temperatures that are warmer than CRU values, resulted in increased TI values for northern regions and reduced TI for southern regions. Olfert and Weiss [17] reported that incremental scenarios of +2°C and +4°C resulted in increased TI values and increases in both EI and the potential area of Canada that would potentially be exposed to grasshopper outbreaks. At Fairbanks, TI values increased from 12.0 (CRU) to 20.1 (NCAR273 CCSM), resulting in more favourable temperatures during the growing season. Changes in central North America were less dramatic. Temperature indices in the Saskatoon region were predicted to increase from 30.7 (CRU) to 37.8 (NCAR273 CCSM). Excessively warm temperatures have been shown to hinder grasshopper populations [29, 33]. Output indicates that increased temperatures would result in higher heat stress (HS) values in northern Texas and Nebraska.

The growth index (GI) is a weekly thermo hydrological index that describes conditions that are favourable for growth. CLIMEX outputs the number of weeks where the growth index is nonzero, effectively determining the length of the growing season. Growing season length and cold stress accumulation are two factors that limit the potential

TABLE 3: Baseline (CRU) and general circulation model (NCAR273 CCSM, MIROC-H, and CSIRO MARK 3.0) scenarios and percent of area with EI values greater than, or equal to, 20 for *Melanoplus sanguinipes* at six locations in North America.

Location	GCM Scenario	% of area with EI ≥ 20
Fairbanks, AK	NCAR273 CCSM	57.1
	CSIRO MARK 3.0	48.2
	MIROC-H	49.1
	CRU	0
Peace River, AB	NCAR273 CCSM	75.6
	CSIRO MARK 3.0	85.2
	MIROC-H	94.1
	CRU	19.3
Saskatoon, SK	NCAR273 CCSM	100
	CSIRO MARK 3.0	100
	MIROC-H	100
	CRU	92
Gillette, WY	NCAR273 CCSM	100
	CSIRO MARK 3.0	100
	MIROC-H	88.1
	CRU	100
Lincoln, NE	NCAR273 CCSM	6.3
	CSIRO MARK 3.0	25.9
	MIROC-H	23.2
	CRU	59.8
Lubbock, TX	NCAR273 CCSM	40.7
	CSIRO MARK 3.0	24.4
	MIROC-H	12.6
	CRU	98.5

for population growth in the Fairbanks region. Increased temperatures were predicted to not only decrease the rate of cold stress accumulation, but to also increase both the diapause index (DI) and the length of the growing season from 14 weeks to 17-18 weeks. The growing season in the Peace River region was predicted to increase from 19 weeks to 22 weeks and would result in a growing season that is similar to the current growing season in the Saskatoon region. Mills [34] predicted that regions north of 55°N and west of 110°W have soils that are suitable for agricultural production and that climate change could positively impact small grain production in the area. This would suggest that *M. sanguinipes* populations could become established in these new agricultural areas in the event that they become accessible in the future. In southern regions, however, mean GI values and the number of weeks where GI values were positive decreased. Output indicated that prolonged periods of warm temperatures during the growing season could limit potential for grasshopper population growth. Extreme heat and drought tends to reduce crop growth while increase grasshopper feeding activity. Mukerji et al. [32] reported that increased competition for food can also result in population decline due to high mortality because of starvation.

In conclusion, bioclimatic models have proven useful for studies investigating the potential impact of climate on insect populations. However, some cautions have been expressed regarding the utilization of this approach including: (i) biotic interactions may not remain the same over time (adaptation can, and is likely to, occur); (ii) genetic and phenotypic composition of populations may change over time and space; (iii) most species have some limitation to dispersal [35, 36]. In the instance of *M. sanguinipes*, the impact of biotic factors such as natural enemies (e.g., diseases, parasites) must also be considered. For example, termination of several grasshopper outbreaks in Canada were attributed to cool, wet weather and epizootics of *Entomophthora grylli* Fres. [20, 37]. Even though conditions may be predicted to be conducive to grasshopper populations under climate change, diseases could result in population decline. In these instances, bioclimate and GCMs may not account for changes in population, and may overestimate populations. To address these naturally occurring phenomena, bioclimate modeling of grasshopper populations will benefit from a multitrophic approach (host plants—grasshoppers—natural enemies).

Acknowledgment

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Review Article

Density-Dependent Phase Polyphenism in Nonmodel Locusts: A Minireview

Hojun Song

Department of Biology, University of Central Florida, 4000 Central Florida Boulevard, Orlando, FL 32816-2368, USA

Correspondence should be addressed to Hojun Song, song@mail.ucf.edu

Although the specific mechanisms of locust phase transformation are wellunderstood for model locust species such as the desert locust *Schistocerca gregaria* and the migratory locust *Locusta migratoria*, the expressions of density-dependent phase polyphenism in other nonmodel locust species are not wellknown. The present paper is an attempt to review and synthesize what we know about these nonmodel locusts. Based on all available data, I find that locust phase polyphenism is expressed in many different ways in different locust species and identify a pattern that locust species often belong to large taxonomic groups which contain mostly nonswarming grasshopper species. Although locust phase polyphenism has evolved multiple times within Acrididae, I argue that its evolution should be studied from a phylogenetic perspective because I find similar density-dependent phenotypic plasticity among closely related species. Finally, I emphasize the importance of comparative analyses in understanding the evolution of locust phase and propose a phylogeny-based research framework.

1. Introduction

The contemporary definition of locusts is fairly strict and narrow. Pener [1] defined locusts as grasshoppers that belong to Acrididae (Orthoptera: Caelifera) that meet two criteria: (1) they form at some periods dense groups comprising huge numbers, bands of hoppers, and/or swarms of winged adults which migrate; (2) they are polyphenic in the sense that individuals living separately differ in many characteristics from those living in groups. There are a number of grasshopper species that satisfy the first criterion and thus often loosely called locusts [2–5]. However, the second criterion, the expression of density-dependent phase polyphenism, is rarer [6] and has only been convincingly documented in the migratory locust, *Locusta migratoria*, the brown locust, *Locustana pardalina*, the desert locust *Schistocerca gregaria*, the Central American locust, *S. piceifron*s, the South American locust, *S. cancellata*, and the red locust, *Nomadacris septemfasciata*, and to the lesser degree in the Moroccan locust, *Dociostaurus maroccanus*. In these species, color, behavior, morphology, biochemistry, and life history traits are strikingly affected by the change in local population density [2]. Those species that cause tremendous agricultural

damage but do not express visible phase polyphenism are often referred to as locusts, but whether they strictly fit the definition of "locusts" remains rather ambiguous. Uvarov [5, pages 142–150] dedicated a chapter titled "Antecedents of gregarious behaviour" to discuss these borderline species. Pener and Simpson [2] also listed 23 acrid species that show elements of density-dependent polyphenism and briefly mentioned phase-like expressions in those species not typically categorized as "true locusts."

It is difficult to prove whether a given grasshopper species displays density-dependent phase polyphenism. It is because the presence of density-dependent phase polyphenism is something that has to be tested through explicit experiments [7], especially when its expression is not readily visible. A species in question has to be reared in both isolated and crowded conditions in a carefully controlled manner, and the resulting phenotypes have to be quantified and statistically compared [8]. Also, the expressions of density-dependent polyphenism may be subtle and not manifest in an extreme way found in model locust species such as *S. gregaria* and *L. migratoria*. A good example of this can be illustrated in the Australian plague locust, *Chortoicetes terminifera*, which is convincingly demonstrated to display a strong form

of density-dependent behavioral polyphenism without the change in color [9]. Just because extreme manifestation of many phase-related characters occurs in model locust species, we cannot expect other locust species to express the same traits. After all, these locust species are the product of their own evolutionary history and finely adapted to their local environments [10]. If we accept the fact that locust phase polyphenism evolved multiple times [4], we also have to accept the fact that there are many ways to become locusts. It is important to realize that many traits associated with locust phase polyphenism do not necessarily evolve as a whole [4, 11]. Locust phase polyphenism is an ultimate expression of many different phenotypically plastic responses that are affected by the change of local population density. Song and Wenzel [11] showed that the evolution of density-dependent color plasticity precedes the evolution of behavioral plasticity in Cyrtacanthacridinae and that the physiological mechanisms necessary to produce density-dependent color morphs are phylogenetically conserved in the subfamily. Thus, understanding the phylogeny is exceedingly important in understanding the evolution of locust phase polyphenism.

Tremendous advances have been made in understanding the mechanism of phase transformation in *S. gregaria* and *L. migratoria* [2], but not much is known about the density-dependent phase polyphenism of nonmodel locust species. The present paper is an attempt to review all available literatures regarding the effect of population density in nonmodel locust species. I do not dwell on *S. gregaria* and *L. migratoria* because these model species have been the subject of several recent reviews [2, 12–14], but I only mention them when comparison and contrast with nonmodel species become relevant. When discussing each species, I try to incorporate available taxonomic and phylogenetic information [15]. Finally, I propose a robust research framework that incorporates a phylogenetic approach in studying the evolution of density-dependent phase polyphenism.

2. Expression of Density-Dependent Phase Polyphenism of Nonmodel Locusts

In this section, I review taxonomy, phylogeny, and the existence and expression of density-dependent polyphenism in nonmodel locust species across Acrididae. There is an enormous body of literature dedicated to biology, ecology, population dynamics, and pest management of these species, much of which is reviewed in Uvarov [5, 16], COPR [17], and others. I do not attempt to review these topics again unless they are relevant for discussion. Data presented in the following sections are summarized in Tables 1 and 2.

2.1. Locust Species in Schistocerca. The genus *Schistocerca* Stål, 1873 contains about fifty species and is widely distributed in the New World. It is difficult to pinpoint the exact number of species in the genus because the most comprehensive revision of the genus by Dirsh [18] made numerous synonymies based on an obscure morphometric species concept, which are now considered to be incorrect.

Harvey [19] revised the Americana complex based on a series of hybridization experiments, and Song [20] revised the Alutacea group based on morphological characters. A large complex of species which is currently synonymized under *S. nitens* needs to be examined thoroughly. *Schistocerca* is also well known for its transatlantic disjunction distribution in which the desert locust *S. gregaria* is the only Old World representative of the genus. A considerable amount of controversies and debates have centered on the origin of the desert locust [21, 22].

Schistocerca occupies a rather unique position in the study of locusts because it contains multiple locust species. The desert locust *S. gregaria* is of course the most well known of all locusts in terms of both swarm dynamics and the mechanism of phase transformation [2]. The Central American locust *S. piceifrons* and the South American locust *S. cancellata* are important swarming locust species in the New World, and the Peru locust *S. interrita* has recently been recognized as a locust. There have been reports of the American grasshopper *S. americana*, which is closely related to other swarming species in the genus, being able to form hopper bands and adult swarms [62], but no conclusive evidence exists to show that it is a locust [63]. It is important to realize that the swarming species in *Schistocerca* do not form a monophyletic group. Based on hybridization studies and phylogenetic studies, it is recognized that swarming *S. piceifrons* is sister to nonswarming *S. americana* [19, 22, 64], and swarming *S. cancellata* is sister to nonswarming *S. pallens* [19, 21, 22, 26]. In other words, locust phase polyphenism appears to have evolved multiple times even within the same genus. Many nonswarming sedentary *Schistocerca* species are capable of expressing density-dependent color polyphenism [65–69], suggesting that color plasticity is a phylogenetically conserved trait in the genus [11]. Interestingly, an isolated population of *S. gregaria* in South Africa is not prone to gregarization and is often referred to as the subspecies *S. gregaria flaviventris* [27]. Schimdt and Albütz [70] also found that a population of *S. gregaria* from Canary Island expressed much reduced phase traits even after intense crowding. Similarly, a Chilean population of *S. cancellata* is also not prone to gregarization [27]. These examples suggest that density-dependent behavioral plasticity is not a fixed trait for these locust species, and it may be reduced or lost due to adaptation to local environments or drift [71].

Schistocerca piceifrons (Walker, 1870) is distributed throughout Central America and the northern part of South America [19, 23, 24]. Two subspecies are recognized, the nominal subspecies and *S. piceifrons peruviana* which occurs in high elevations of Peru and Ecuador [24, 29, 72]. Recently, a migrant population was found on Socorro Island (Mexico) in the Pacific Ocean [73, 74]. In Mexico, where the locust is commonly referred to as langosta voladora, there are two generations, spring and fall, and the fall generation adults go through a reproductive diapause during the winter dry season [23]. *Schistocerca piceifrons* is found where there is between 100 and 250 cm of annual rainfall, distinct dry winter season, and no cold season. It prefers semixerophytic mosaic vegetation and feeds on a wide variety of herbaceous plants. It is a typical swarming

TABLE 1: Expressions of density-dependent phenotypic plasticity of the species included in this paper. When there is conclusive evidence on presence or absence of density-dependent phenotypic plasticity, it is noted as such. Asterisk denotes the possibility based on inconclusive and anecdotal evidence. Unknown denotes the lack of quantitative data.

Species	Density-dependent phenotypic plasticity				
	Nymphal color	Morphometrics ratios	Physiology	Behavior	References
Cyrtacanthacridinae					
Schistocerca gregaria	present	present	present	present	[2, 16]
Schistocerca piceifrons	present	present	present	present*	[23–25]
Schistocerca cancellata	present	present	present	present*	[19, 26–28]
Schistocerca interrita	present*	present*	unknown	unknown	[29–32]
Nomadacris septemfasciata	present	present	present	present*	[16, 33–35]
Patanga succincta	present	present	present	unknown	[17, 36, 37]
Austracris guttulosa	absent	absent	absent	unknown	[17, 36–40]
Anacridium melanorhodon	present	absent	absent	unknown	[41, 42]
Oedipodinae					
Locusta migratoria	present	present	present	present	[2, 16]
Locustana pardalina	present	present	present	present*	[5, 16, 33, 43]
Oedaleus senegalensis	present*	unknown	unknown	unknown	[41]
Gastrimargus musicus	present	present	unknown	present*	[44]
Pyrgodera armata	present*	unknown	unknown	unknown	[45]
Chortoicetes terminifera	absent	present	present	present	[9, 46]
Austroicetes cruciata	absent	present	unknown	unknown	[46]
Aiolopus simulatrix	present*	unknown	present*	unknown	[41, 47]
Ceracris kiangsu	unknown	unknown	unknown	unknown	[17]
Calliptaminae					
Calliptamus italicus	absent	present	present	present*	[48–51]
Gomphocerinae					
Dociostaurus marrocanus	present	present	present	present*	[5, 16, 52, 53]
Rhammatocerus schistocercoides	present*	present*	unknown	unknown	[54, 55]
Gomphocerus sibricus	absent	absent	unknown	unknown	[5, 56]
Melanoplinae					
Melanoplus sanguinipes	present	absent	unknown	unknown	[5, 56–58]
Melanoplus differentialis	unknown	absent	unknown	unknown	[59, 60]
Proctolabinae					
Coscineuta virens	absent	absent	unknown	unknown	[61]

locust with distinct density-dependent phase polyphenism in color, morphology, and other life history traits [24, 25]. In terms of color, nymphs are green at low density, but at high density they develop extensive black pattern in head, pronotum, wingpads, abdomen, and legs with pink or peach-red background [24, 25].

Schistocerca cancellata (Serville, 1838) is distributed in the southern half of South America, including Argentina, Bolivia, Paraguay, Uruguay, Chile, and southern Brazil [17]. It used to be known as *S. paranensis*, which previously referred to the locust in the New World, but hybridization experiments confirmed that there were two locust species in the New World, the Central American locust *S. piceifrons* and the South American locust *S. cancellata* [19, 26, 64]. It is adapted to temperate and subtropical climate, and there is an annual cycle of migration and breeding within the invasion area that is strongly influenced by weather and its seasonal variations [19, 27]. There are several permanent zones of

breeding, which consist of an area of desert or semidesert within an annual rainfall of over 500 mm [17]. The species matures and oviposits in areas where there has been rain. The species used to be a major plague species in the first half of the 20th century [75], but in recent years, large-scale infestations have become infrequent [27], and outbreaks are limited to the semiarid areas in north-west Argentina [76], possibly due to very effective control measures. The South American locust is a classic swarming species with pronounced density-dependent phase polyphenism similar to the congeneric *S. gregaria* [19, 28].

Schistocerca interrita Scudder, 1899, has been known as a nonswarming grasshopper occurring in Peru for a long time [77]. During 1983 and 1984 after the "El Niño" phenomenon, a severe outbreak of *S. interrita* reaching a proportion of a plague was reported in the northern coast of Peru [30]. It has been hypothesized that when there is abundant rainfall due to unusual events such as El Niño,

TABLE 2: Expressions of swarm dynamics and ecological characteristics of the species included in this paper. When there is conclusive evidence on presence or absence of a given phenomenon, it is noted as such. Asterisk denotes the possibility based on inconclusive and anecdotal evidence. Unknown denotes the lack of quantitative data.

| Species | Swarm dynamics | | | | Ecological characters | |
	Hopper band	Adult swarm	Group mating	Group oviposition	Habitat preference	Food preference
Cyrtacanthacridinae						
Schistocerca gregaria	present	present	present	present	arid and semiarid land	herbivorous
Schistocerca piceifrons	present	present	present	present	semixerophytic mosaic vegetation	herbivorous
Schistocerca cancellata	present	present	present	present	desert or semidesert with annual rainfall of over 500 mm	herbivorous
Schistocerca interrita	present	present	present	present	dry wooded area	herbivorous
Nomadacris septemfasciata	present	present	absent	absent	treeless grassland with seasonal flood	graminivorous
Patanga succincta	absent	present	absent	absent	grassland	graminivorous
Austracris guttulosa	absent	present	absent	absent	grassland	graminivorous
Anacridium melanorhodon	present	present	absent	absent	dry open woodland near Acacia	arborivorous
Oedipodinae						
Locusta migratoria	present	present	present	present	variable	graminivorous
Locustana pardalina	present	present	present	present	arid land	graminivorous
Oedaleus senegalensis	present	present	unknown	unknown	drier savannah	graminivorous
Gastrimargus musicus	present	present	present	present	costal and subcostal regions of Australia where annual rainfall is greater than 500 mm	graminivorous
Pyrgodera armata	present	absent	unknown	unknown	alluvial plains and adjoining hills with clay or stony soils	herbivorous
Chortoicetes terminifera	present	present	present	present	semiarid land	graminivorous
Austroicetes cruciata	present	present	present	present	drier and more open grasslands and semideserts with 200–500 mm annual rainfall	graminivorous
Aiolopus simulatrix	present	present	present*	present*	grassland	graminivorous
Ceracris kiangsu	present	absent	unknown	unknown	bamboo forest	monophagous on bamboo
Calliptaminae						
Calliptamus italicus	present	present	present	present	dry steppe zones	herbivorous
Gomphocerinae						
Dociostaurus marrocanus	present	present	present	present	semiarid steppe or semiarid desert	graminivorous
Rhammatocerus schistocercoides	present	present	present	present	shrub-like and wooded savannas	graminivorous
Gomphocerus sibricus	present	present	unknown	unknown	forest margins	graminivorous
Melanoplinae						
Melanoplus sanguinipes	present*	present	unknown	unknown	grasslands and meadows	graminivorous/ forbivorous
Melanoplus differentialis	present	present	unknown	unknown	tall herbaceous vegetation growing in wet meadows	graminivorous/ forbivorous
Proctolabinae						
Coscineuta virens	present	present	present	present	forest	herbivorous/ forbivorous

Lambayeque desert becomes a suitable breeding ground for *S. interrita*, which eventually leads to an exponential population growth [30, 31]. An anecdotal report of a locust swarm in Lambayeque is known from 1578, which can be probably attributed to *S. interrita* [31], but the most recent upsurge occurred in 1997–2003 in Lambayeque and Cajamarca of northern Peru. *Schistocerca interrita* is adapted to dry wooded area at the elevation of 3500 m above sea level, and population dynamics and basic ecology have not been thoroughly studied (see [29, 31]). At low density, nymphs are green, but they develop black pattern with yellow background at high density. Unlike the gregarious nymphs of *S. piceifrons* which develop broad black patterns in the lateral face of the pronotum, the gregarious nymphs of *S. interrita* develop black patterns with clearly defined margins, so that the lateral face of pronotum has a distinct yellow triangle [32]. Both hopper bands and adult swarms are known in this species and sexually mature adults turn yellow.

2.2. Locust Species in the Nomadacris-Patanga-Austracris-Valanga Complex. Within Cyrtacanthacridinae, *Nomadacris* Uvarov, 1923, *Patanga* Uvarov, 1923, *Austracris* Uvarov, 1923, and *Valanga* Uvarov, 1923 form a monophyletic group based on morphological characters including male genitalia, male subgenital plate, and male cerci [11]. The taxonomic history of this group is unnecessarily confusing, which I discuss in detail because I think it is relevant in discussion of the evolution of locust phase polyphenism in this group. Uvarov [78] first described the genus *Patanga* based on the shape of hind femora, prosternal process, and male subgenital plate. The other three genera were described later in the same publication. Dirsh [79] first suggested that the type species, *Gryllus (Locusta) succinctus* Johansson, 1763, Uvarov [78] used to describe as *Patanga* did not correspond to its original description by Johansson. He noted that there was an available name (*Acridium assectator* Fischer von Waldheim, 1833) matching Uvarov's [78], and Linneaus' original description matched that of *Acridium nigricorne* Burmeister, 1838, which was a type species of yet another genus *Valanga*. Uvarov [80] soon published a rebuttal, and Melville [81] carefully summarized this affair. The final opinion from ICZN was published in 1973 in favor of keeping nomenclatural stability [82]. Nevertheless, Dirsh [83] published a revision of *Cyrtacanthacris* and synonymized *Nomadacris*, *Valanga*, *Patanga*, and *Austracris* under *Cyrtacanthacris* on the ground of morphological similarities. Jago [84] criticized Dirsh's action and reinstated the ranking of genera synonymized by Dirsh [83]. In doing so, he suggested that *Nomadacris*, *Patanga*, and *Austracris* were congeneric and lowered the taxonomic ranking to subgenera under *Patanga*, which had a priority. He also argued that the genus *Valanga* should be maintained in line with the opinion of the ICZN [82]. Thus, Jago's [84] action resulted in three genera: *Cyrtacanthacris*, *Valanga*, and *Patanga*. *Nomadacris septemfasciata* was, however, one of the most important locust species, and there were numerous agricultural reports using that name. In order to promote taxonomic stability, Key and Jago [85] proposed to make *Nomadacris* have a priority over *Patanga*, on the ground of Jago [84] being the first reviser. Thus, *Patanga* and *Austracris* were considered subgenera of *Nomadacris*. Later, Key and Rentz [86] asserted that the Australian representatives were morphologically distinct and removed *Austracris* from synonymy.

All this taxonomic confusion is due to the fact that these four genera are very closely related. Because of the conventional usage of the names, I use the generic name *sensu* Uvarov [78], but it is certainly possible to consider these four genera congeneric. This leads to a very interesting point in terms of the evolution of locust phase polyphenism. Just like *Schistocerca*, which has a few swarming locust species, but mostly sedentary species, this generic complex also has the mixture of swarming and nonswarming species. Just like *S. gregaria* which is the only African representative of the genus, which happens to express the most extreme form of locust phase polyphenism of all *Schistocerca* locusts, *N. septemfasciata* is the only African representative of the generic complex, which also happens to express the most extreme form of locust phase polyphenism in the complex. This is a fantastic case of parallel evolution. Locust species in *Schistocerca* and this generic complex are very similar in terms of their color pattern and the same is true among the sedentary species in these two groups. However, the exact expressions of locust phase polyphenism are distinctly different between the two.

The red locust, *Nomadacris septemfasciata* (Serville, 1838), is distributed in most of Africa, south of Sahara, and in Madagascar [17]. Seasonal and annual variation of flood gives rise to unstable mosaic of very tall grasses and sedges and short grasses where *N. septemfasciata* thrives. Several studies were carried out in the Rukwa Valley, Tanganyika (Tanzania), one of three known outbreak areas of the red locust [87–91]. Several studies have emphasized the importance of physical structure of vegetation in concentration of individuals [88–90], and both nymphs and adults are known to roost on stems of *Echinochloa pyramidalis*, the dominant tall grass and *Cyperus longus*, the dominant short grass species [90]. The red locust is a classic swarming locust that expresses an extreme form of density-dependent phase polyphenism [5, 33]. Isolated nymphs are green, but crowded nymphs develop extensive black pattern with orange frons and yellow background [41]. Adult morphometrics, number of instars, and the rate of sexual maturation are all affected by the change in population density [5, 34, 35]. Both hopper bands and adult swarms are welldocumented [90, 92], but group mating and group oviposition have not been documented from this species. Adults go through a very long reproductive diapause up to 8 months [17, 87], and the particular stage of sexual maturation can be determined by examining the color of hind wing, which changes from transparent to pink to purple red [92].

The Bombay locust, *Patanga succincta* (Johannson, 1763) is widely distributed in southwestern Asia (India, Philippines, Indonesia, Malaysia, Thailand, Japan, and China) [17, 93]. No major swarm has been reported since 1908 although small populations seem to be consistently found [94]. Adults of *P. succincta* form a typical swarm, but it is not clear from the literature whether this species also exhibits hopper bands. Douthwaite [95] observed nymphal behavior in Thailand.

Nymphs favored grass species such as *Imperata* and maize, which co-occurred with low vegetation such as *Brachiaria*. He observed that nymphs move vertically on maize where they mostly fed. The vertical movement was rapid, but it was not synchronized among other individuals in the population. Feeding occurred during warm weather and nymphs climbed up the maize and descended to *Brachiaria* which they used as a shelter. Even when the population density is high, the hoppers move little [17]. Isolated nymphs are green, and crowded nymphs develop black mottles with yellowish orange or fawn background, but not extensive black patterns observed in other locust species [36, 37]. Morphometric ratios in adults do seem to be affected [36]. Both group mating and group oviposition are not reported from this species.

The spur-throated locust, *Austracris guttulosa* (Walker, 1870), is distributed throughout Australia and adjacent regions [96]. It is a tropical, ambivorous species, adapted to monsoon climate with a long dry season [97]. Although it feeds on a wide variety of plants, grass is preferred. Immature adults form a migrating swarm. The size of a typical swarm can be very large and dense, and it can travel up to 400–500 km in a week [38]. Although adults exhibit impressive migratory swarms, *A. guttulosa* does not exhibit many traits that are commonly associated with locust phase polyphenism [38]. For example, nymphal color does not become conspicuous upon crowding although density-dependent green/brown polymorphism appears to occur [39], adult morphometric ratios remain constant upon crowding [40], nymphs have never been observed moving in dense bands despite high local densities [38], and oviposition never occurs collectively in egg beds, suggesting the lack of group oviposition [38].

2.3. Anacridium melanorhodon. The genus *Anacridium* Uvarov, 1923, contains 13 valid species widely distributed in Africa and southern Europe [98]. The identity of *A. javanicum* which was described from a single female specimen from Java is questionable, and it might be a specimen belonging to *Valanga* which might have been mistaken as *Anacridium*. The Sahelian tree locust, *A. melanorhodon* (Walker, 1870), is distributed in the Sahelian zone in Africa. Two subspecies are known, the nominal subspecies occurring in the west and *A. melanorhodon arabafrum* occurring in the east through Arabia to Iran [17]. It is an arboricolous species, intimately associated with various *Acacia* species. In the field, especially in winter, swarms occasionally occur. A typical swarm of *A. melanorhodon* is small, less than one square kilometer, but a swarm as large as 20 km in length has been observed [42]. One of the characteristics of *A. melanorhodon* is its nocturnal habit. Most feeding and flight activities occur at night, and the species is locally known as sari-el-lel, which means the night wanderer. Both adults and nymphs roost on *Acacia* trees or other available tall trees. This roosting behavior seems to lead to the concentration of population, which in turn leads to the development of swarms. No characteristic group oviposition as in *S. gregaria* was observed, but the egg pod density can be high due to the structure of vegetation [42]. Hatchlings from such

high-density places gradually concentrate into groups and bands. Cohesive and directional marching behavior has been observed, but the density of hopper bands can be as low as one individual per square meter. Crowded nymphs develop black mottles with yellow background while isolated nymphs are green [41]. Adult morphometric ratios are not affected by population density [42]. The congeneric *A. wernerellum* is known to behave like a locust in rare circumstances [42], and its response to density is probably similar to *A. melanorhodon*.

2.4. Locust Species in the Oedipodine Tribe Locustini. The oedipodine tribe Locustini is of particular interest because it contains several species prone to density-dependent phenotypic plasticity including the migratory locust, *Locusta migratoria*, the brown locust, *Locustana pardalina*, the Senegalese grasshopper, *Oedaleus senegalensis*, the yellow-winged locust, *Gastimargus musicus*, and the Iranian grasshopper, *Pyrgodera armata*. Although there is no phylogenetic work focusing on this tribe as a whole, a recent molecular phylogenetic study by Fries et al. [99] included three genera of this tribe, *Locusta*, *Gastrimargus*, and *Oedaleus* and found that these form a strong monophyletic group. It is unclear how closely the locust species are related within Locustini, but it is intriguing that several major locust species belong to a relatively small tribe, which could suggest that some components of density-dependent phase polyphenism might be phylogenetically conserved in this clade, similar to the cases in Cyrtacanthacridinae.

The monotypic genus *Locustana* Uvarov, 1921, contains the brown locust, *L. pardalina* (Walker, 1870), which is one of the major locust species in southern Africa that thrives in the semiarid Karoo region [17]. Because of its agricultural importance, the brown locust has been studied very thoroughly in terms of its life history and swarm dynamics [100]. It is a classic swarming locust, capable of expressing extreme phase characteristics in color, behavior, morphology, and physiology [5, 33, 43]. The phase characteristics of the brown locust were thoroughly investigated early by Faure [33], just soon after the initial formulation of the phase theory [101]. Isolated nymphs are variable in color and exhibit a strong case of homochromy. Green color of the isolated nymphs is associated with high humidity. Crowded nymphs develop characteristic orange and black coloration. Adult morphometric ratios are also strongly affected by crowding. The brown locust displays typical hopper bands and adult swarms, group mating and group oviposition.

The genus *Oedaleus* Fieber, 1853, currently contains 27 valid species, widely distributed across the Old World, from Africa to Asia and to Australia. Ritchie [102] published the most comprehensive revision to date, in which he discussed the taxonomy and biogeography of the genus in detail. This genus is closely related to another genus of interest, *Gastrimargus* [102]. Several species in *Oedaleus* are economically important pests, but the Senegalese grasshopper, *O. senegalensis* (Krauss, 1877), stands out as the most devastating species [17]. The biology and ecology of this species was recently reviewed by Maiga et al. [103]. This species is widely distributed throughout the tropical and subtropical

regions, and it is often associated with mesoxerophilic habitats and can be categorized as graminivorous [17]. Marching hopper bands and loose swarms of this species have been frequently reported [104], but no quantitative study on behavioral phase is available. Normal green-brown polymorphism similar to other oedipodines is reported from *O. senegalensis* [105], but it is not clear if density-dependent color change does occur. Ritchie [105] reported that the nymphs in high-density population show a characteristic brown and black coloration. Launois and Launois-Luong [106] declared that *O. senegalensis* is a true grasshopper because it does not exhibit changes in physiological changes often associated with typical locusts, but gregarious behavior appears to be similar to the locust species. Another member of the genus, *O. decorus asiaticus* Bei-Bienko, 1941, which occurs widely in Asia, is known to exhibit migratory behavior [107]. Recently, Cease et al. [108] showed that rearing density significantly affected physiological responses in this species but failed to demonstrate a direct correlation among rearing density, color plasticity, and behavioral plasticity.

The genus *Gastrimargus* Saussure, 1884, currently contains 23 species and 8 subspecies, widely distributed in the tropical grassland of Africa, Asia, and Australasia. Ritchie [109] published the most comprehensive revision to date, in which he discussed the taxonomy and biogeography of the genus in detail and contrasted with the genus *Oedaleus* which he revised earlier [102]. *Gastrimargus* favors more humid habitats than *Oedaleus* although both genera are graminivorous [109]. Of the 23 species, only three species are reported to be of any economical importance, and they are *G. africanus*, *G. marmoratus*, and *G. musicus* [17]. Of these, only the yellow-winged locust, *G. musicus* (Fabricius, 1775), is known to express density-dependent phase polyphenism [44]. This species is endemic to coastal and subcostral Australia, where rainfall exceeds 20 inches annually. The most thorough and the only study of the biology and ecology of *G. musicus* was done by Common [44], and no subsequent study was followed despite its pronounced phase expressions. Isolated and crowded locusts differ in terms of color, morphometric ratios, and behavior. This species displays typical hopper bands, adult swarms, group mating, and group oviposition. Based on the specimens collected from an extensive outbreak that occurred in central Queensland between 1939 and 1947, Common [44] tested the existence of locust phase polyphenism in *G. musicus* and documented that solitarious nymphs have variable color with green/brown polymorphism and gregarious nymphs are medium to dark brown. He also commented that solitarious populations are often patchily distributed in native pastures, and the outbreak in central Queensland was a result of population buildups over several years under favorable environmental conditions.

The monotypic genus *Pyrgodera* Fischer von Waldheim, 1846, contains the Iranian grasshopper, *P. armata* Fischer von Waldheim, 1846, which is a peculiar grasshopper, easily identified by its high, arched, and laminate pronotal crest, distributed in the Mediterranean regions [45]. It is a minor pest in this region [17] but included in this paper because it is reported to have plastic response to change in population density [45]. Popov [45] encountered an unusual population of *P. armata* in South Iran, which showed a tendency to express different phenotypes at high density. The nymphs of this species are typically green at low density, but he found an aggregation of nymphs that have orange and black patterns, similar to the gregarious nymphs of a typical locust. These colored nymphs in high density formed a small marching band, where other nymphs with conspicuous color would join the band and the green nymphs would remain indifferent to the band. The orange and black pattern continued into the adult instar. Although this species does not develop into a full-blown locust swarm, Popov's observation is indicative of the species expressing density-dependent phenotypic plasticity in terms of both color and nymphal behavior.

2.5. Chortoicetes and Austroicetes. *Chortoicetes* Brunner von Wattenwyl, 1893, and *Austroicetes* Uvarov, 1925, are not placed in any tribe within Oedipodinae because they are quite divergent from other members of the subfamily. Fries et al. [99] included both of these genera in their study and found that these two Australian genera form a strong monophyletic group but not related to any other groups within the subfamily. Thus, it is possible to conclude that these two genera are sister to each other but occupy rather an isolated position in Oedipodinae [46].

The Australian plague locust, *C. terminifera* (Walker, 1870), is the most economically important pest species in Australia [17]. It is found throughout Australia, and its outbreaks are both localized and widespread [96]. Due to its agricultural importance, the life history and population dynamics have been thoroughly studied [110]. The genus *Chortoicetes* currently contains two species, the nominal species *C. terminifera* and *C. sumbaensis* which was initially described as *Aiolopus sumbaensis* by Willemse [111] based on a female specimen collected from the Indonesian island of Sumba. Hollis [112] transferred this species to *Chortoicetes* based on tegminal venation, but there was no distinct character to warrant a specific status separate from *C. terminifera* other than size differences and wing patterns. Although it is difficult to confirm, I suspect that it was a migrant individual of *C. terminifera* that somehow colonized Sumba, which means that the genus should be considered monotypic. Although *C. terminifera* displays all the behavioral traits typically associated with locusts, including hopper bands, adult swarms, group mating, and group oviposition [96], it does not change color in response to change in population density [46]. Key [46] showed that adult morphometric ratios are affected by crowding, but the degree of transformation is not as pronounced as other typical locusts. Recently, Gray et al. [9] demonstrated that *C. terminifera* expresses strong behavioral phase polyphenism, and Cullen et al. [113] showed that the behavioral phase transformation is triggered by tactile stimulation of the antennae. These new studies based on quantitative behavioral assay techniques collectively show that density-dependent phase transformation does not necessarily involve change in color.

The genus *Austroicetes* is probably sister to *Chortoicetes* and contains 9 valid species. Some members of this genus

can cause severe damages to crops, but the small plague grasshopper (or sometime small plague locust), *A. cruciata* (Saussure, 1888), used to be considered the worst grasshopper pest in Western Australia [17]. This species occasionally forms hopper bands and loose adult swarms when population density becomes high. Key [46] demonstrated that this species and the congeneric *A. nullarborensis* were capable of displaying density-dependent polyphenism in color, adult morphometrics, and behavior.

2.6. Aiolopus simulatrix. The oedipodine genus *Aiolopus* Fieber, 1853, currently contains 14 species widely distributed throughout the Old World and Australia. Since the revision by Hollis [114], a number of new species have been added to the genus, but this genus still needs to be fully revised. Within *Aiolopus*, four species (*A. simulatrix*, *A. strepens*, *A. longicornis*, and *A. thalassinus*) are recognized as economically important species, but the Sudan plague locust, *A. simulatrix* (Walker, 1870), is the most devastating species of grain and other crops. Joyce [115] described the biology and behavior of *A. simulatrix* (as now synonymized *A. savignyi*) from East Central Sudan. It forms impressive migratory swarms, but the existence of hopper bands is not well recorded. Nymphs do exhibit density-dependent color plasticity in which nymphs in low density are brown, green, and of a mixture of two colors, whereas crowded nymphs develop a dark pigmentation in pronotum, wingpads, and hind femora [41]. Although there has not been an explicit experiment to study the effect of density in *A. simulatrix*, Heifetz and Applebaum [47] did such an experiment in a related species *A. thalassinus*. They found that crowding did not result in changes in morphometric ratios or color but affects behavior and other physiological responses such as CO_2 release and carbohydrate and lipid levels. Thus, it is possible that *A. simulatrix* may respond similarly to the change in density if it is subjected to a controlled experiment.

2.7. Calliptamus italicus. The genus *Calliptamus* Serville, 1831, currently contains 15 extant species, and it is widely distributed from northern Africa to Europe and into Russia and China. Of the 15 species, only *C. italicus* (Linnaeus, 1758) is known to swarm, and it is the only known swarming locust in the subfamily Calliptaminae [17]. It forms narrow and long hopper bands (6–2800 m in length, 3–70 m in width) [116], and the adults form typical migrating swarms. Unlike the classic locusts, nymphal color is not affected by change in the population density [48], but nymphal behavior does appear to be affected [49] although quantitative behavioral assays have not been applied to this species. This species exhibits physiological responses to the change in density because the locusts reared in a crowded condition mature more rapidly than the ones reared in an isolated setting [5]. Adults also respond morphometrically, and gregarious adults have much longer tegmina than solitarious adults [50, 51].

2.8. Dociostaurus marrocanus. The gomphocerine genus *Dociostaurus* Fieber, 1853, contains three subgenera and 26 species and is widely distributed in the palearctic region. The Moroccan locust, *D. marrocanus* (Thunberg, 1815), is the only species in the genus known to express an extreme form of density-dependent phase polyphenism in color and morphology in both nymphal and adult stages [5]. Isolated nymphs are yellowish or olive brown with three very distinct black spots on the upper part of hind femora, but crowded nymphs develop orange color in the head and pronotum with faded or no black spots on the hind femora [52]. Gregarious adults are larger in size and have longer tegmina and shorter hind femora than the solitarious ones [53]. It used to be very difficult to rear *D. marrocanus* in a colony setting [117], but recently there has been an advance in this aspect [118]. Characteristic hopper bands and adult swarms are well documented in this species [5, 17, 52]. This species is highly polyphagous and causes significant agricultural damages in the many countries in the Mediterranean zone [119]. However, the Moroccan locust appears to be very selective in terms of its habitat preference; it is often associated with an ecotonal zone between foothills and valleys, at a range of altitudes of 400–800 m above sea level, with dry-steppe vegetation [117]. The habitat destruction has decreased the severity of outbreak in several developed countries so much, so that the locusts never produce swarms in some cases. Nevertheless, this species is still a major pest species in Afghanistan, Iran, Algeria, Morocco, Uzbekistan, and southern Kazakhstan [117].

2.9. Rhammatocerus schistocercoides. The gomphocerine genus *Rhammatocerus* Saussure, 1861, currently consists of 18 species, mostly distributed in the Central and South America. The status of many species is uncertain and the genus is in need of a taxonomic revision although several species in this genus are agriculturally important pest species, and the Mato Grosso grasshopper, *R. schistocercoides* (Rehn, 1906), stands out as the most serious one. It is found in the shrub-like and wooded savannas in South America, and two of the most affected areas include the Brazilian States of Mato Grosso and Rondonia and the Colombian States of Casanare, Meta, and Vichada [54]. The Mato Grosso grasshoppers regularly form very impressive hopper bands [120] and adult swarms [121], but the effect of population density has not been systematically studied. It is unclear if isolated nymphs would behave any differently from crowded ones. Ebratt et al. [55] reared nymphs in isolated and crowded settings and reported that nymphs were green at low density, but red or brown at high density, which also corresponded with the change in morphometric ratios. However, Pierozzi and Lecoq [54] did not find any morphometric differences in the adults collected from high and low densities and suggested that this species should be considered a grasshopper, not a locust, although they recommended that a more thorough investigation on the expression of locust phase needs to be done in this species. This species is highly variable in terms of color, and Lecoq and Pierozzi [122] documented the color change from brown to green upon sexual maturation.

3. Other Pest Grasshopper Species

Pener and Simpson [2] list 23 acridid species that show elements of density-dependent polyphenism, which is an

extended list from Song [4]. In addition to *S. gregaria* and *L. migratoria*, the species that I discuss in the previous section are the ones that exhibit cohesive migration groups and density-dependent phenotypic plasticity although the degree of expression is quite variable across species. The Rocky Mountain locust, *Melanoplus spretus* (Walsh, 1866), used to be the most devastating locust species in North America before it abruptly became extinct in the early 20th century [123]. It is likely that *M. spretus* displayed locust phase polyphenism [124], but most of the data collected for that species predate the formulation of the phase theory [125], and therefore I do not discuss this species in this paper. In this section, I talk about the remaining four species and one species not mentioned by Pener and Simpson [2].

3.1. Melanoplus. The melanopline genus *Melanoplus* Stål, 1873, is one of the largest acridid genera containing 243 valid species. No comprehensive revision of this genus is available to date. Many species have very narrow geographic ranges, but some occur throughout North America. Two species that are reported to have density-dependent polyphenism by Pener and Simpson [2] are the migratory grasshopper, *M. sanguinipes* (Fabricius, 1798), and the differential grasshopper, *M. differentialis* (Thomas, 1865). Both species have been reported to display hopper bands and adult swarms that migrate under a very high-density condition in the first half of the 20th century [57, 59, 126]. Crowding does induce melanization in nymphs [58] in *M. sanguinipes*, but morphometric ratios are not affected. A large body of literature is devoted to the biology and ecology of these two species due to their economical importance [60], but none of the available studies has definitely demonstrated the existence of locust phase polyphenism in these species. Therefore, it would be fair to categorize them as outbreak grasshoppers.

3.2. Gomphocerus sibiricus. The gomphocerine genus *Gomphocerus* Thunberg, 1815, contains 8 valid species mostly distributed in the Old World, except one Brazilian species *G. semicolor*, whose taxonomic status is questionable. Among these, the Siberian locust, *G. sibiricus* (Linnaeus, 1767) (which was sometimes referred to as *Aeropus sibiricus* before *Aeropus* was synonymized under *Gomphocerus*), is one of the most economically important pest species in Russia [5]. This species is restricted mainly to xerophilous forest margins [56] and is prone to outbreak. However, there is no documented report of *G. sibiricus* responding to population density, suggesting that its common name has been misapplied.

3.3. Ceracris kiangsu. The genus *Ceracris* Walker, 1870, contains 12 described species which are distributed throughout China. The Orthoptera Species File currently places the genus in the tribe Parapleurini of the subfamily Oedipodinae [127], but Chinese researchers have always placed it under Arcypteridae [128], which is a junior synonym of the tribe Arcypterini of Gomphocerinae. The genus includes a few economically important species, and the yellow-spined bamboo locust, *C. kiangsu* Tsai, 1929, is known to be the most important agricultural pest of bamboos [129]. Earlier

studies described the nymphs and adults to be gregarious [130, 131] and also reported the migrating bands of the late instar nymphs [131]. These earlier studies led Song [4] and Pener and Simpson [2] to include *C. kiangsu* as one of the species exhibiting a certain level of density-dependent phase polyphenism, but in fact, there is no definitive report of this species being able to change color, morphology, or behavior in response to change in population density. Based on published data, it is possible to deduce that *C. kiangsu* specializes in feeding on bamboo, and its life history is intimately associated with the bamboo forest. Recent studies have shown that *C. kiangsu* is attracted to human urine possibly to supplement sodium and nitrogenous compounds which are lacking in bamboos [132], and some have advocated the use of human urine to bait and control this pest [133]. All available data point to a conclusion that *C. kiangsu* is an outbreak species but does not fit the definition of a locust.

3.4. Coscineuta virens. The genus *Coscineuta* Stål, 1873, currently contains 8 valid species, and it is the only member of the basal proctolabine tribe Coscineutini [134]. *Coscineuta* is widely distributed in South America, but the Moruga grasshopper, *C. virens* (Thunberg, 1815), is currently restricted to the southeastern region in Trinidad. Other specimens of this species are known from Guyana and Uruguay, but there is no report of recent occurrence [61]. The Moruga grasshopper, also locally known as Courtac, has been a principal acridid pest of Trinidad feeding on a wide variety of crops including citrus, coffee, cocoa, mango, cassava, and several vegetables [61]. This species is of particular interest because it is known to be gregarious in all stages of life. Nymphs are characteristically colored black and yellow, reminiscent of typical pyrmorphid nymphs, and form very dense and mobile marching bands. Because of this locust-like behavior, Popov et al. [61] examined the existence of density-dependent phase characteristics in this species but found that this species was not affected by isolation or crowing in any meaningful way. In fact, the species appeared to be always in the "gregarious phase" at least in terms of behavior. No followup study has been done on this interesting species of grasshopper.

4. Evolution of Density-Dependent Phase Polyphenism in Acrididae

Locust phase polyphenism has evolved multiple times within Acrididae. The convergent evolution of this phenomenon should not be understated. Only a handful of species are capable of expressing locust phase polyphenism out of more than 6400 valid species of Acrididae. In other words, only about 0.29% of known acridids (19 legitimate locust species out of 6444 valid acridid species) can be categorized as locusts. The proportion of the locusts that express full-blown phase polyphenism is even smaller. Based on the present paper, it is possible to conclude that locust phase polyphenism has evolved only in four acridid subfamilies, Cyrtacanthacridinae, Oedipodinae, Gomphocerinae, and Calliptaminae, out of 24 currently recognized subfamilies.

Within each subfamily (except Calliptaminae which only contains one locust species), it has evolved multiple times. Although the ultimate expression of locust phase, density-dependent phenotypic plasticity leading to gregarization and migration, is similar across different locust species, the specific mechanisms behind phase transformation are quite variable. In fact, the deep understanding we have gained through studying *S. gregaria* and *L. migratoria* is probably not directly applicable to many nonmodel locust species. This perspective is quite different from a traditional view of studying locusts in which researchers used to look for specific *physiological* phase characteristics such as changes in color and morphometric ratios in the species in question to determine whether it is a "true locust" or not [135]. The more appropriate view in light of the contemporary definition of locusts should be based on the presence of *any* density-dependent phenotypic plasticity whether the expression is morphology, physiology, or behavior, or any combination of these.

From a taxonomic point of view, an interesting general pattern emerges from the present paper. Typically, locust species often belong to larger taxonomic groups in which most species are not locusts. For example, the Italian locust is the only locust species out of 15 *Calliptamus* species, and the Moroccan locust is the only locust out of 26 *Dociostaurus* species. *Schistocerca* contains only four locust species out of 50 species, all of which are nonswarming sedentary species. This pattern can also be extended to monotypic genera such as *Locusta* and *Locustana*, both of which belong to Locustini which contains 72 species, most of which are sedentary grasshoppers. Similarly, the monotypic genus *Chortoicetes* forms a monophyletic group with *Austroicetes* which includes nonswarming species. There is no known case of every species of a given taxonomic group being locusts. Every species in a given taxonomic group (whether a genus or a tribe) is closely related phylogenetically and must be very similar to each other morphologically, biologically, and ecologically. But, only a small proportion of a given taxonomic group expresses locust phase polyphenism. What makes some species locusts while other species in the same taxonomic group remain as regular grasshoppers? Do the nonswarming species in these taxonomic groups have the potential to develop locust phase polyphenism?

These are certainly very difficult questions to answer, and the obvious answer would be "we do not know." Locusts are exceptionally adapted to their local environments, and these locust species may simply have the best combination of the traits that make them the most successful, compared to other species in the same taxonomic groups, or there may be some species that are capable of becoming locusts, but the environmental conditions are simply not conducive to the expression of locust phase polyphenism, and we cannot know whether one would be a locust or not a priori. For example, the recent outbreak of *S. interrita* was not anticipated because the species was not known to be a locust, but the El Niño phenomenon created an exceptionally favorable environment for the species to express its hidden potential to express locust phase polyphenism [29].

In addition to the general pattern that only a small proportion of species in a given taxonomic group expresses locust phase polyphenism, there is another interesting pattern which is not readily noticeable unless one understands the phylogeny of these locusts. Although locust phase polyphenism has evolved convergently, its evolution does not appear to be totally random especially when the phase characteristics of closely related locusts are examined. There are four cases in which there are multiple locust species occurring in supposedly monophyletic groups. They are the locust species in the *Schistocerca*, *Nomadacris-Patanga-Austracris-Valanga*, Locustini, and *Chortoicetes-Austroicetes* clades. Phase-related characters are remarkably similar across different locust species within each monophyletic group (Tables 1 and 2). For instance, the locust species within *Schistocerca* all exhibit a similar form of density-dependent phenotypic plasticity in color, morphology, physiology, and behavior. They all behave very similarly at high population density and prefer dry habitat and herbaceous plants. Although in the same subfamily, the locust species in the *Nomadacris-Patanga-Austracris-Valanga* clade behave quite differently from *Schistocerca*. Adult swarms are prominent in this clade, but hopper bands are only weakly or not at all expressed. These species exhibit neither group mating nor group oviposition, and they distinctly prefer grassland habitats and grasses. The locust species in Locustini also favor grasses but have broader habitat preferences. They all express typical swarm dynamics both as nymphs and as adults and show pronounced density-dependent phenotypic plasticity in many traits. The *Chortoicetes-Austroicetes* clade belongs to the same subfamily as Locustini, thus the locust species in this clade show similar ecological characteristics but do not change color at high density.

Throughout the locust literatures, comparisons among the locust species belonging to different taxonomic groups have seldom been made. The reason for this lack of comparative studies may be due to the fact that several of these locust species are monotypic and thus assumed to be somewhat unique. Although different locust species may not always form a monophyletic group within each clade, it is important to understand that the evolution of locust phase polyphenism is shaped by the shared ancestry and the adaptation to local environmental conditions. For example, Song and Wenzel [11] showed that *N. septemfasciata*, *P. succincta*, and *A. guttulosa* form a monophyletic group based on morphological characters and that the individual components of locust phase polyphenism evolve at different times and its full expression is achieved when these components are expressed together. Because of the shared ancestry, these locust species exhibit the same density-dependent plastic responses, but they also exhibit unique traits and ecological adaptations because they are specifically adapted to their local environments. Another example can be found in *Schistocerca*. Many sedentary species in the genus *Schistocerca* display density-dependent color plasticity [65–69], which indicates that the physiological mechanisms behind this plastic reaction norm may be a phylogenetically conserved ancestral trait. Thus, the development of conspicuous nymphal coloration in the gregarious phase of *S. gregaria* is

not a novel trait in locusts, but an expression of ancestral phenotypic plasticity [4]. These examples are, however, based not on experimental data, but on the fragmentary reports published in various literature sources [11]. Nevertheless, it demonstrated the importance of a phylogenetic perspective in understanding the evolution of locust phase polyphenism.

5. A Call for a Phylogeny-Based Research Program in the Study of Locust Phase Polyphenism

For the last century since the formulation of the phase theory, especially for the last two decades, tremendous advances have been made in the study of locust phase polyphenism using *S. gregaria* and *L. migratoria* as model systems. Despite the deep understanding we have gained based on a model-based approach, we know surprisingly little about other nonmodel locust species. In this paper, I show that many of the nonmodel locusts exhibit different forms of locust phase polyphenism and what we know about the model species do not necessarily translate to these nonmodel species. As a parallel illustration, we have accumulated an enormous body of information on the making of a fruit fly, *Drosophila melanogaster*, a very specialized dipteran species, but this does not mean that we have learned everything about the extremely diverse order of Diptera, nor does it mean what is known about the fruit fly is directly applicable to other flies. The model-based approach in studying locust phase polyphenism is undoubtedly invaluable, but a much richer understanding of this phenomenon can be gained if it is complemented with a phylogenetic approach.

Applying a phylogenetic perspective to the study of speciation, adaptation, behavioral ecology, and character evolution has often resulted in deeper and more comprehensive understandings of the subject [136]. A phylogeny-based research framework in locust phase polyphenism can allow us to investigate relevant questions such as reconstructing ancestral state of individual components of locust phase, tracing the origin and transformation of different phase-related traits, and testing correlations between different phase-related traits. This approach can predict that non-swarming species might be capable of expressing phase polyphenism when favorable environmental conditions arise and also help form testable hypotheses on the phase expressions of nonmodel locust species that are closely related to the model species. For instance, what we know about *S. gregaria* can form a basis for studying other locust species in *Schistocerca* because of their phylogenetic relationships. Take the mechanoreceptors present in the outer face of hind femora for an example. The behavioral phase transformation can be achieved by stimulating these mechanoreceptors in *S. gregaria* [137]. An informed null hypothesis then may be that *S. piceifrons* or *S. cancellata* can also respond to density in a similar way. Cullen et al. [113] recently showed that the tactile stimuli are sensed by the antennal receptors in *C. terminifera*, rather than hind femora. This suggests that what is known about *S. gregaria* might not apply to *C. terminifera*, but what we gain from studying *C. terminifera*

can form a basis for studying *Austroicetes cruciata* because of their phylogenetic relationships. It is thus possible to predict that *A. cruciata* is likely to respond to antennal stimulation rather than leg stimulation. Likewise, what we know about *L. migratoria* is a good starting point for understanding the locust phase polyphenism in *L. pardalina*, *G. musicus*, and *O. senegalensis* because they all belong to Locustini. By studying both similarities and differences among different locust species in the same monophyletic groups, we can gain greater understanding of the evolution of locust phase polyphenism.

This phylogeny-based research program certainly has several challenges. Reconstructing a robust phylogeny is always a difficult endeavor laden with problems of taxon and character sampling, and numerous assumptions about phylogenetic reconstruction methods. For locust research, the problem is exacerbated because the use of mitochondrial genes, which is commonly employed in inferring the relationships among closely related species, is difficult because Acrididae is known to be severely affected by nuclear mitochondrial pseudogenes [138–140]. Generating data on density-dependent phenotypic plasticity in explicitly controlled laboratory settings for all species in a given monophyletic group is extremely challenging. Even the cost of maintaining colonies of different species would be prohibitively high. Thus, this research program would necessarily have to be a long-term international collaborative project.

Despite all these difficulties, I would still argue that this phylogeny-based approach would considerably expand upon the insights we have gained from the current model-based approach. In this paper, I have identified four candidate monophyletic groups which contain multiple locust species and many nonswarming species. Of these, I argue that the locust research community should initially focus on *Schistocerca* and Locustini. We can take advantage of what we have learned so far based on the study of *S. gregaria* and *L. migratoria* and begin to understand the evolution of locust phase polyphenism in other locust species in these two groups with phylogeny-based, informed predictions. Exciting results from this research program will eventually form a basis for investigating other nonmodel locust species.

6. Conclusion

In this study, I have performed a literature review focusing on locust phase polyphenism of nonmodel locust species. The most striking finding is how little we know about these nonmodel locust species. So far, there have been only three locust species (*S. gregaria*, *L. migratoria*, and *C. terminifera*) that have been investigated using modern quantitative behavioral assay techniques [2, 8, 9]. We do not know what specific stimulus triggers phase transformation in other species. Endocrine responses, biochemical changes, and molecular expressions in response to change in density are completely unknown for most of the locust species. This lack of knowledge means that there are many new exciting findings and insights waiting to be discovered. The major

theme of this paper is that there are many ways to become locusts, and the evolution of locust phase polyphenism has to be understood through the lens of phylogeny. We have learned a great deal about the specific mechanisms of phase transformation of model locust species over the past few decades. Now, it is time to expand the study of locust phase polyphenism to these nonmodel locust species to gain a deeper understanding of this fascinating phenomenon.

Acknowledgments

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Research Article

Phase-Dependent Color Polyphenism in Field Populations of Red Locust Nymphs (*Nomadacris septemfasciata* Serv.) in Madagascar

Michel Lecoq,[1] Abdou Chamouine,[2] and My-Hanh Luong-Skovmand[1]

[1] *Cirad Acridologie, 34398 Montpellier, France*
[2] *Université de Toliara, BP 185, Toliara 601, Madagascar*

Correspondence should be addressed to Michel Lecoq, lecoq@cirad.fr

Pigmentation of the Red locust hopper, *Nomadacris septemfasciata* Serv., was studied in natural conditions in Madagascar in relation to population density. More than one thousand hoppers were collected and described according to a semiquantitative method. A typology is proposed, strictly reflecting the increase in population densities. This correctly translated the progressive evolution of a solitary state into a gregarious state, while passing through several intermediate transiens stages. According to their density, hopper populations consist of a mixture, in various proportions, of several pigment types. The gregarization threshold is estimated at 100,000 hoppers/ha. A slight black spot on the hind femur is the first sign of gregarization. These results should improve the reliability of the information collected by the Malagasy National locust centre when surveying this major pest. They question the rapidity of the gregarization process in natural conditions as well as the stimuli involved.

1. Introduction

Locusts are acridid species that exhibit density-dependant phase polyphenism and/or an ability to form marching hopper bands and/or flying swarms resulting in outbreaks and plagues. Individuals are either of two extreme phenotypes: solitarious or gregarious [1, 2]. This polyphenism is continuous and all the intermediate stages, transiens, congregans or dissocians, are found between the two extreme phases, depending on the direction of the transformation. Induction of phase transformation can occur at any stage of development of the locust including the larva and the imago. It can be strengthened through generations and is reflected by a suite of changes in behaviour, morphometry, color, development, fecundity, and endocrine physiology (see recent reviews in [3–7]). Better understanding of locust phase polyphenism has an obvious applied potential and could lead, in the future, to nonconventional locust control measures as a substitute for the chemical insecticides in use [5], but increasingly challenged because of their environmental impact [8, 9]. Currently, the precise characterization of the phases, and especially the intermediate transiens, is crucial for the effective implementation of preventive strategies against these locust pests, which require intervention as early as possible [10–13]. The transiens phase marks the first stages of the gregarization process. In the progressive development from remission periods to invasive periods, an understanding of the transiens phase can allow early detection and measurement of the degree of severity of the locust situation.

In nature, behavioural changes are often the first characteristic observed as a result of a gathering of individuals caused by external causes such as wind convergence, surface restrictions related to phenomena such as floods, and resource distribution [14–18]. This characteristic is difficult to precisely quantify for the intermediate transiens stages. Morphometry remains the best method to estimate the degree of phase transformation of an individual or a population. Morphometric charts can be used to monitor the gregarization process over generations [2, 3, 19]. In hoppers, only the color characteristics can be used. The coloring is one of the most obvious signs of the phase transformation in locusts [5]. Several studies have been carried out on the nature of the pigments involved, the underlying physiological mechanisms, and the influence of environmental conditions [2, 3, 20–23]. The color characteristics of the solitarious and gregarious phases have been shown numerous times (see,

e.g., Stower [24] for the Desert locust *Schistocerca gregaria* Forskål; Faure [25, 26] for the Red locust *Nomadacris septemfasciata* Serville 1838; Albrecht [20], Lecoq [27], Popov [28] for the Migratory locust *Locusta migratoria* L. 1758). The transiens phase remains, however, much less well documented, especially for the hoppers. Often, in the literature, the near infinite number of intermediate colors between the solitarious and the gregarious phases of these individuals is just mentioned. In the recent review by Pener and Simpson [5] the word transiens (or transient) appears 10 times only, when gregarious and solitarious are mentioned respectively, 560 and 440 times. Moreover, the phase transformation threshold is widely ignored. In nature, this threshold corresponds to the population density at which the interactions between individuals are large enough to allow the phase transformation process to start. It is sometimes given on the basis of an expert opinion without any results of specific observations [29]. The very validity of this concept is sometimes questioned because it also depends on the insect development stage and on the vegetation density [30]. This is crucial information from both an operational perspective to better manage locust preventive control and from a theoretical point of view to allow further detailed field studies on the phase transformation process determinism.

The various difficulties in the characterization of transiens are particularly noted for the Red locust. In this species, despite various studies that have contributed to describing the pigmentation of the solitarious and of the gregarious stages [25, 26, 28, 31–33], the transiens remains poorly characterized and the phase transformation thresholds have never been established. More generally, phase polyphenism in the Red Locust is poorly understood and has rarely been proven experimentally and—in comparison to Desert and Migratory locusts—just a few papers are available for this species (see for instance [34–36]). The main effects of increased density on *Nomadacris* as revealed by laboratory work, were summarized by Uvarov a long time ago [2], and further research is obviously required [5]. In practice, the information collected by the locust services on the transiens phase is often unreliable [37]. We propose to clarify the color characteristics of the hopper individuals of this species in relation to population density. This study aims to provide a better understanding of the phase transformation thresholds and to improve the implementation of monitoring and preventive control of this species. This work was carried out in the field in Madagascar where this locust is a major crop pest.

2. Materials and Methods

2.1. The Red Locust.
The Red locust is well known throughout central and southern Africa [38, 39]. Some isolated populations can also be found in the lake Chad basin, the central delta of the Niger river in Mali, and the Cape Verde Islands [40]. The species undergoes phase transformation and its outbreak areas are mainly located in the Great Lakes region of East Africa, in Tanzania, Zambia, Malawi and Mozambique [41, 42]. Since the last great invasion of 1929–1944, which affected most African countries south of the equator, the species is controlled by an international organization, IRLCO (International Red Locust Control Organization) [43]. Infestations are now less frequent and are mainly focused in the reproduction areas, far from the cultivated areas [44]. Large outbreaks occurred, however, between 1994 and 1996 [42, 43, 45, 46] and more recently in 2009 [47, 48].

In Madagascar, the Red locust is also a major pest and outbreaks are frequently observed with formation of hopper bands and swarms. No widespread invasion of the island has ever occurred as was frequently the case with the Migratory locust [49] whose last plague ravaged the Island between 1997 and 1999 [11]. The problem is now managed by the National Anti-Locust Centre as part of a crop protection strategy [40, 50, 51]. In Madagascar, the lifecycle of the Red locust has only been documented for the Betioky-Sud region, where this species produces just one generation per year [52–58], as in the rest of Africa. Mating and egg laying take place in November and December, at the onset of the rainy season, which lasts until April. Females generally lay eggs twice or three times, with a clutch of 20–100 eggs for gregarious locusts and 20–195 eggs for solitarious locusts. The eggs hatch after 24–36 days of incubation. The hoppers begin to appear in December. The hopper development passes by 6 instars for the gregarious individuals (1 to 6) and 7 instars for the solitarious (numbered 1, 2, 3, 4, 4a, 5, and 6 in order for the last instar to always carry the same number, the extra instar being before the reversal of the wing rudiments, between instar 4 and 5) [34]. The hopper development period lasts almost 2 months, ranging 50–70 days and the new generation of adults appears in April. They enter diapause to survive through the dry season (April–September), in refuge zones located away from breeding areas. Important seasonal migrations of solitary populations take place between dry season refuge zones (where population densities are low) and rainy season breeding zones (where the populations concentrate and reproduce and where outbreaks are frequently observed) [59]. Samples of hoppers were collected from this latter area, where the first manifestations of gregariousness may occur (behavioral changes in the parental adults, and behavioral, pigmentary, morphological changes etc. in the offspring).

2.2. Sampling and Description of Hoppers.
Red locust hoppers were collected in south-western Madagascar in a vast area well-known as the breeding area of this species. The samples were taken during two successive rainy seasons from January to March in 2007 and in 2008. During the two sampling periods, we continuously (each hour) recorded the air temperature and the relative humidity in one location in the sampling area (near Betioky-Sud). Both parameters were not very variable, during one sampling period as well as from one year to another (temperatures 2007/2008: min $22,7°C \pm 1,4/23,1°C \pm 1,5$; max $35,1°C \pm 3,1/37,0°C \pm 4,2$; average $27,8°C \pm 1,7/28,9°C \pm 2,3$; air humidity 2007/2008: min $39,8\% \pm 14,4/34,4\% \pm 17,7$; max $82,5\% \pm 7,9/80,2\% \pm 8,4$; average $64,1\% \pm 10,9/59,1\% \pm 13,3$).

The sampling sites were chosen based on the information provided by the National Anti-Locust Centre on the presence

of locust hoppers and their density. At each site, thirty hoppers were collected. The hopper density was evaluated by counting one hundred sample surfaces of one square meter each using a classical method commonly used by scouts from the locust centre [60, 61]. These hopper populations were derived from migrant adults arriving in the breeding area at the start of the rainy season and whose phase status was described broadly as solitarious as shown by survey data from the National Anti-Locust Centre (3741 observations conducted on the whole of south-western Madagascar in 2006 and 2007 on the parental populations). Some populations in densities above the gregarious threshold, however, were observed (13 in all, including 4 light swarms at a density of between 160,000 and 200,000 imagos per hectare).

For each hopper, the stage was determined by overall size, the size and the orientation of the wing pads, the number of eye stripes, and the color characteristics recorded using a standardized method. Only phase color (density) polyphenism and green/brown (humidity) polyphenism exist in the Red locust [5]. The latter is relatively limited as the hoppers of the single annual generation were still developing in relatively close conditions at the heart of the rainy season in lush vegetation. The proportion of green hoppers diminished late in the rainy season [57]. In cages, homochromy has sometimes been observed in solitarious hoppers [26]. Regarding the phase color polyphenism, the descriptions in the literature concern essentially solitarious and gregarious individuals [25, 26, 28, 31–33]. For the transiens phase, information is scarce and mainly concerns the transiens dissocians [31, 33].

The characters finally selected were the background color (GC) and the degree of melanisation of the cephalic capsule (H), the degree of melanisation of the compound eyes (E) (with more or less visible stripes), background color of the pronotum (GP) and the degree of melanisation of its dorsal carina (CP) and lateral sides (LP), the degree of melanisation of the wing pads (W), and the presence and extent of a black spot on the distal part of the upper outer carina of the posterior femur (F). The latter criterion was supposed to be one of the first signs of gregariousness when the population density increases. The black abdominal maculation, difficult to quantify, was not considered. These eight criteria were recorded in the field using a semi-quantitative method (Figure 1). For E, H, CP, W, LP, and F, the extent of black pigmentation was coded 0 for absence of black pigmentation, 2 for a well-marked black spot and 1 for an intermediate situation. General pigmentation was recorded as green, brown, or orange for the cephalic capsule (GC), and as green, brown, or yellow for the pronotum (GP). Each hopper was individually identified and photographed under standard conditions for later checking of the rating criteria.

2.3. Data Analysis. The results were analyzed using the Addinsoft XLSTAT data analysis software (1995–2010). The data table [hoppers × color variables] containing the value of the different variables (semi quantitative) for each of the hoppers observed was converted into a disjunctive table (each nominal variable comprises several levels and each of these levels is coded as a binary variable). The latter was subjected to a Multiple Correspondence Analysis (MCA) to highlight the relationships between the various color variables, on the one hand, and between the hoppers on the other hand, according to their similarity [62]. The hoppers and the variables were then classified according to their coordinates on the first factorial axes of the MCA using a hierarchical clustering method (Euclidean distance, Ward's aggregation method). A typology of the hoppers, from the most solitarious to the most gregarious, was constructed on the basis of the results of this classification. Finally, each class of hoppers was related to the population density value in which they were most frequently observed. This helped establish the phase transformation threshold, that is to say, the population levels from which one hopper class moves to another, solitarious forms to more and more gregarious forms (or more exactly, from population consisting of a mixture of different color types in varying proportions to another).

3. Results

3.1. Hoppers Pigmentation. A total of 1139 hoppers were collected and their color characteristics were described, respectively, 36, 129, 123, 283, 233, and 343 hoppers of 1, 2, 3, 4 (including 4a), 5, and 6 instars. These hoppers were collected in 42 localities where hopper densities were (on a very regular density gradient) less than one hopper (solitarious populations) to several hundred hoppers per square meter (gregarious hopper band) (Figure 2). For densities greater than 150 hoppers/m^2, no accurate count was possible and this class included densities ranging from 150 to several hundred hoppers per square meter.

The hoppers collected from low-density populations (less than one hopper per square meter) were characteristic of the solitarious phase with a general green background coloring on all parts of the body (sometimes slightly yellowish) and a lack of black pigmentation (Figure 3). The pigmentation was generally very similar in all individuals with low variability. Rare individuals with a general brown background color were sometimes observed and were regarded as solitarious individuals within the traditional framework of the green/brown polyphenism (as is the case with the Migratory locust, e.g.,). However, even if some of these individuals were found in low-density populations (<1/m^2), they were occasionally collected in relatively high-density populations of about 20–69 hoppers per square meter. Their status remains uncertain, but these hoppers (10 in all) represented only 0.9% of the individuals collected.

As the population density increased, changes in pigmentation and pigment diversity increased. More numerous yellowish or orange areas appeared as well as melanised areas. In high-density populations (100/m^2 and more), the pigmentation was typical of the gregarious phase, which has been described by various authors: the compound eyes were completely dark and the eye stripes were invisible, the cephalic capsule is almost completely melanised, the general background color of the hopper was bright orange and a large part of the body was marked with highly developed black spots (Figure 3). Between these two very contrasting solitarious and gregarious states, color changes

0   2

Head capsule

Pronotum

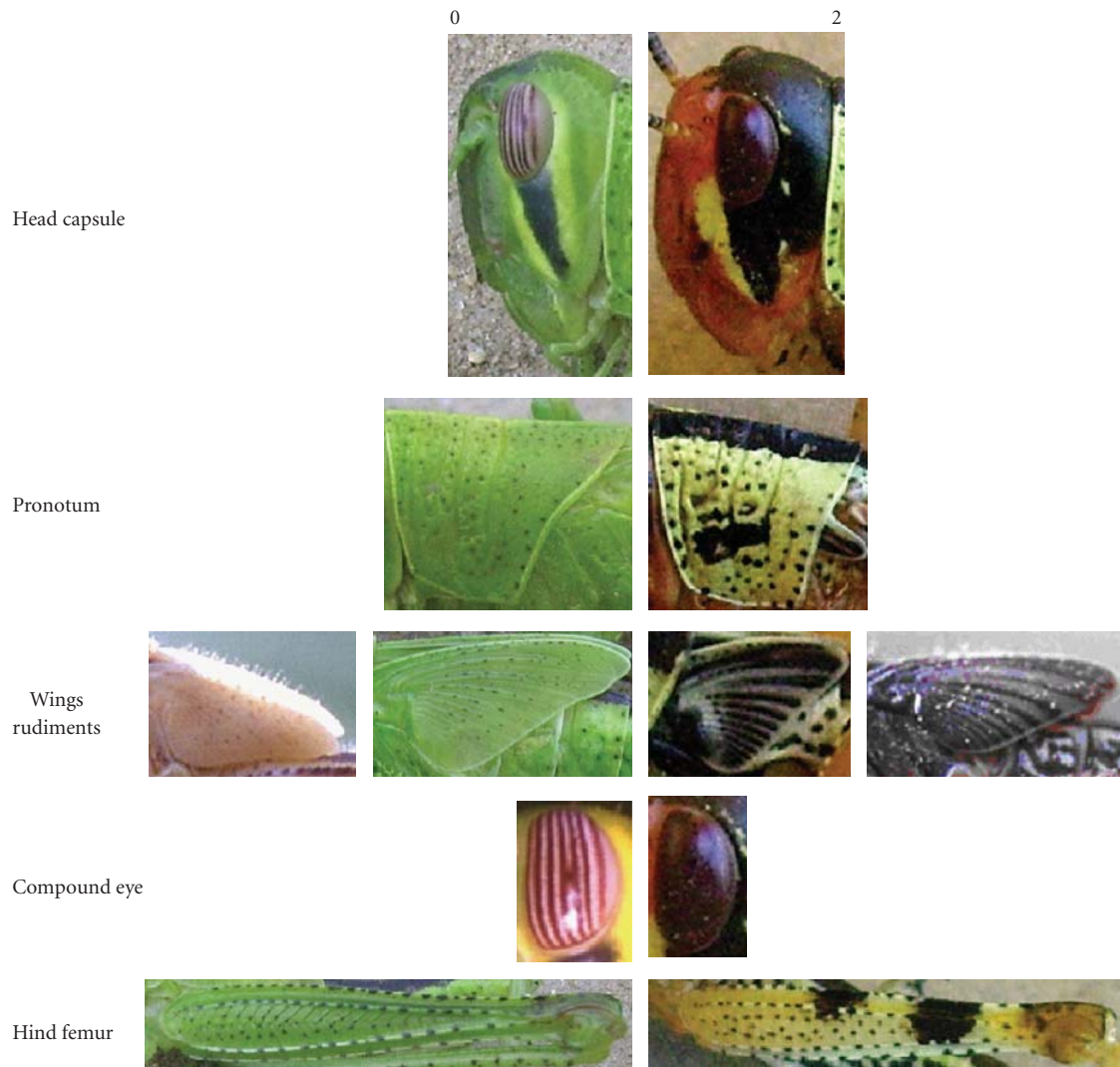Wings
rudiments

Compound eye

Hind femur

FIGURE 1: Color patterns and morphological variables selected to characterize the pigmentation of Red Locust hoppers. Note that the subocular stripe is a constant characteristic of the Red Locust but, in case of gregarisation, it tends to disappear under the general black pigmentation of the posterior part of the head. Photos: M. Lecoq, A. Chamouine and M.H. Luong-Skovmand.

became more pronounced and appeared gradually in relation to density, corresponding to individuals that could generally be described as transiens (Figure 3). These changes primarily concerned the femoral spot (F), the dorsal carina of the pronotum (CP), the compound eyes (E), and to a lesser extent, the cephalic capsule (H). With densities higher than $100/m^2$ the melanisation was well marked for all the variables (E, CP, LP, W, F equal to 2 in almost 100% of cases). A progressive change in the background color of the pronotum (GP)—from green to yellow from low to high densities—was also recorded, as well as a change from green to orange for the background color of the cephalic capsule (GC).

3.2. Hoppers Typology. MCA demonstrated that the data were highly structured with the first two factorial axes totaling almost 90% of the total inertia of the cloud of points (Figure 4). The plane determined by these first two

axes served to underline the correlation between hopper pigmentation and hopper population density (density was introduced in the analysis as an additional variable, that was not included in the calculation of the inertia of the cloud of points, but projected on the axes). The first axis alone groups 82.4% of the inertia. On this axis, there is an opposition between the absence of melanisation and the green colors, on the one hand, and a strong melanisation and yellow and orange colors, on the other hand. This differentiated the solitarious individuals very schematically from those with gregarious characteristics. Along this axis, the hopper density classes ranged regularly from low densities on the negative side of the axis to high densities on the positive side. Axis 2 groups 5.9% of the inertia and shows an opposition between extreme color characteristics (0 and 2 for melanisation, green and orange for background color) and the intermediate values
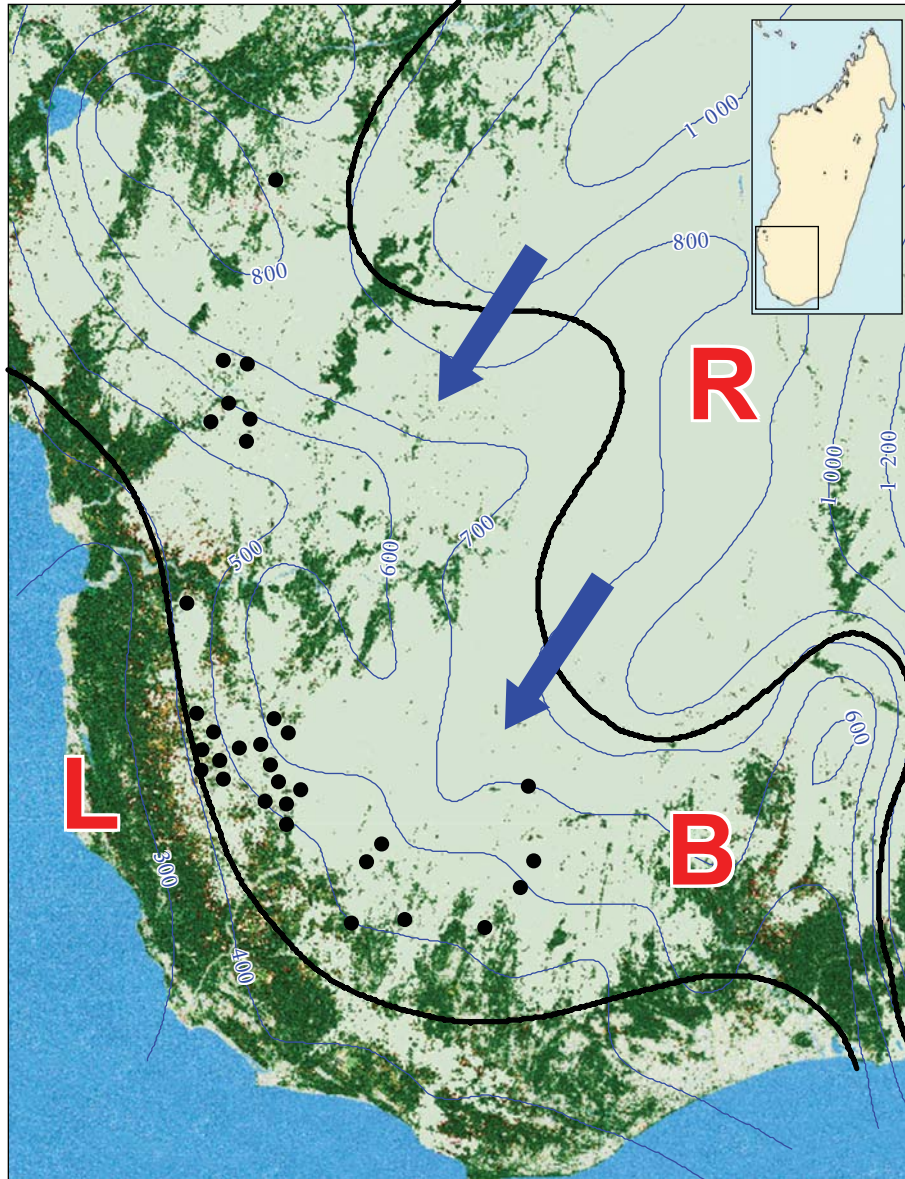
FIGURE 2: Location of the locust hoppers sampling sites in 2007 and 2008 in southern Madagascar. R: dry season refuge zone; B: breeding zone; L: unsuitable southernmost border zone. Green areas: dry forest. Blue lines: isohyets (mm). The arrows underline the orientation of the migrations of maturing adult populations at the beginning of rain season (according to Lecoq et al. [59]).

(1 for melanisation, green-orange, yellow and yellow-orange for the background color). This axis thus underlines the first demonstration of color polyphenism. Finally, axis 3 with only 2.9% of the inertia is entirely determined by individuals with a brown background. These results were valid regardless of the hopper instar. The same analysis (MCA) conducted either on older hoppers (4, 5 and 6) or on young hoppers (1, 2 and 3) led to exactly the same results as well as for tests conducted separately on data from 2007 and 2008 (results not shown).

Classification of individuals according to their coordinates on the first five factorial axes provided a hopper typology to distinguish 15 types. This could be correlated with population density where the hoppers were

collected. The color characteristics changed very gradually with increasing density. A regular gradient of color types existed from types 15, 8, and 13, showing the characteristics of low-density populations representing the solitarious types (especially the most abundant type 13), to types 6 and 9 that were found in populations where the density was higher than 60 hoppers/m^2, and more generally, those where the density exceeded 150 hoppers/m^2, and represented typically gregarious individuals. Between these two extremes, the other 9 types corresponded to intermediate situations concerning both color and density, and transiens-type hoppers (Figure 5). Each hopper class was not therefore associated with a specific population density, but its frequency increased and then decreased steadily with density. Thus, class 5 was

Solitarious

(a)
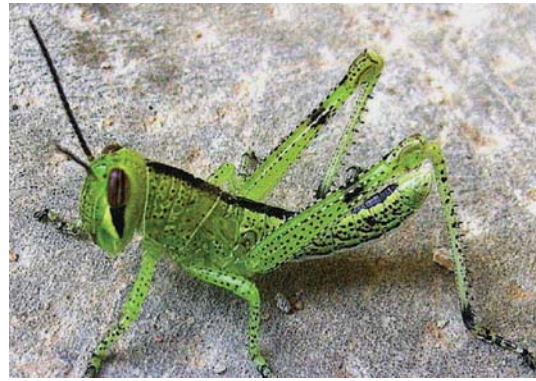
Solitaro-transiens

(b)

Transiens

(c)

Gregarious

(d)

(e)

FIGURE 3: Examples of Red Locust hopper polyphenism (above) and gregarious hopper band (below) observed in February 2008 in the southern part of Madagascar (Mahafaly plateau). Photos: M.H. Luong-Skovmand (solitarious and gregarious) and A. Chamouine (solitaro-transiens, transiens and hopper band).
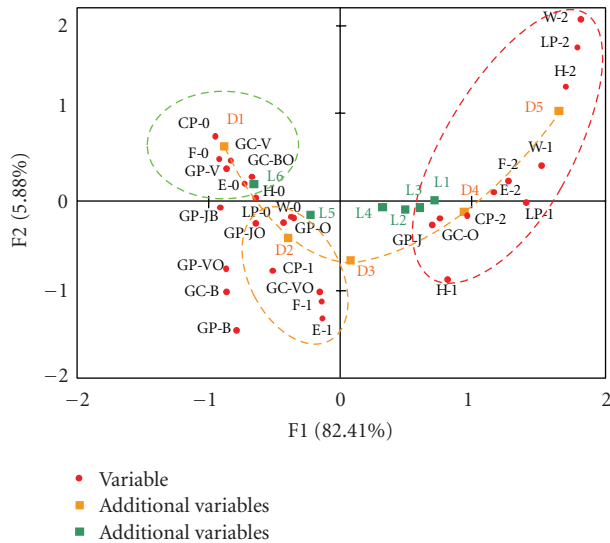
FIGURE 4: Result, in terms of the first two factorial axes, of the multiple correspondence analysis carried out on the table [individuals × variable pigment]. Ellipses surround variables characteristic of the solitary, solitaro-transiens/transiens, and gregarious populations. The brown individuals, from dubious status, isolate themselves on axis 3. Codification of the variables (red dots): (1) variables related to the black pigmentation (0, 1 or 2 according to the melanisation intensity): compound eye (E), cephalic capsule (H), median carina of pronotum (CP), wings rudiments (W); lateral black spot of pronotum (LP), black spot on hind femur (F); (2) variables related to the general color of the tegument (V, green; B, brown; O, orange; J, yellow): cephalic capsule (GC) and pronotum (GP). Variables introduced into the MCA as additional elements: D1 to D5, density of the hopper population (D1 < 10, D2 = [10–30], D3 = [30–70], D4 = [70–100], D5 > 100/m^2) (orange squares); L1 to L6, hopper instars (green squares).
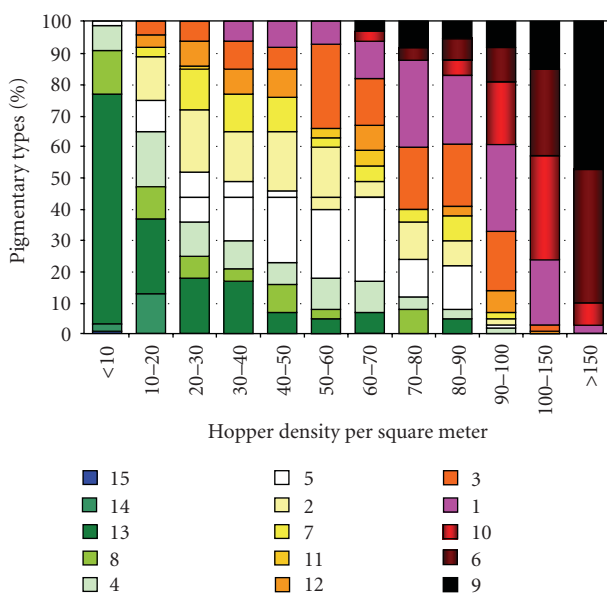

FIGURE 5: Relationship between the 15 color types and hopper densities. In X-coordinate: density classes; in ordinate: percentages of the various color types (1 to 15).

present at low levels for densities less than 10 hoppers/m^2, and it was more abundant in densities ranging from 20 to 30 hoppers, then steadily decreased in frequency. This type of hopper was not found at densities greater than 100 hoppers/m^2.

3.3. A Simplified Typology for Operational Purposes. In order to achieve a practical classification that is easy to use as part of locust population survey operations, the 15 color types were grouped into 4 types based on the classification results and according to their percentage of presence in the different density classes. The color types 15, 14, 13, 8, and 11, only present in low-density populations (<10/m^2), were grouped into a single type which gathered together, in their diversity, populations that were typically solitarious. Types 6 and 9 were virtually the only ones present in very high-density populations (>150/m^2) and could be regarded as representative of the gregarious populations. Types 4, 2, 5, and 7, which were very similar and predominated the medium-density populations, corresponded to solitaro-transiens populations. Finally, types 12, 3, 1, and 10, also similar, predominated the population at densities slightly greater (70–100/m^2) than for the previous types. These types could be grouped under the name transiens. These different types of hoppers can be distinguished easily and unambiguously on the basis of certain criteria for easy use in the field by the locust center scouts (Table 1). Thus, the appearance of the femoral spot signified the transition between solitarious and solitaro-transiens populations. Wing-pad melanisation distinguished solitaro-transiens and transiens hoppers. Finally, maximal melanisation of all body parts signified the onset of the gregarious type. Ultimately, the criteria used could easily assign each hopper to a particular phase category, either solitarious, solitaro-transiens, transiens, or gregarious.

The hopper populations consisted of a mixture of hoppers that may belong to different color types. The percentages of each category developed progressively: a high proportion of solitarious individuals were found in lower density populations and higher densities had increasing proportions of solitaro-transiens, transiens and then gregarious individuals. Solitarious, solitaro-transiens, transiens or gregarious populations could thus be classified on the basis of the dominant color types within the population.

3.4. Pigmentation and Population Density. Some color variables changed earlier than others to an increase in the hopper population density and could therefore be regarded as indicators of early signs of gregarization (Table 1). The eye stripes were still visible in half of the hoppers collected at a density of 30–70/m^2. The eyes were dark for most of the hoppers at a density of 70–100/m^2. Melanisation of the cephalic capsule, which started at 10–30/m^2, was especially marked at a density of 70–100/m^2. The background color of the cephalic capsule was green for most of the larvae at very low densities. The red-orange color became predominant only at a density of 30–70/m^2. Melanisation of the dorsal carina of the pronotum appeared at a density of 10–30/m^2 and half of the hoppers were strongly marked at a density

TABLE 1: Color characteristics of the four hopper types.

| Characters | Hopper types | | | |
	Solitarious $d < 10/m^2$	Solitaro-transiens $d = 10–70/m^2$	Transiens $d = 70–100/m^2$	Gregarious $d > 100/m^2$
E	0	0-1-2	1-2	2
H	0	0-1	0-1	2
GC	green or brown	green, green-orange, yellow or orange	orange	orange
CP	0-1	1-2	2	2
LP	0	0	0-1-2	2
GP	green or yellow	green or yellow	yellow	yellow
W	0	0	1	2
F	0	1	2	2

E: compound eye; H: cephalic capsule; GC: general pigmentation of the cephalic capsule; CP: median carina of pronotum; LP: lateral black spot of pronotum; GP: general pigmentation of the pronotum; W: wings rudiments; F: black spot on hind femur.

of 30–70/m^2. Conversely, the lateral pronotal spot was very pronounced in only one third of the hoppers at a density of 70–100/m^2. It was strongly marked in all the hoppers for densities greater than 100/m^2. The background color of the pronotum, mostly green in individuals in very low densities, turned yellow in the majority of hoppers at a density of 10–30/m^2. The darkening of the wing pad veins appeared later. It was significant in one third of individuals at a density of 70–100/m^2. Above a density of 100/m^2, all hoppers had strongly melanised wing pads. The femoral spot appeared at a density of 10–30/m^2 and it was predominant in half of the hoppers at a density of 30–70/m^2. It was present and strongly marked in all hoppers at high densities (>100/m^2). Finally, the first transiens hoppers appeared at a density of only 10–20 hoppers/m^2 (Figure 5).

4. Discussion

4.1. Characterization of the Hopper Phase. The results from our field study on Red Locust hopper pigmentation established a clear typology, which strictly reflected the increasing densities of the populations. This correlates with the results obtained by Gunn and Hunter-Jones [63] on the regular gradient of pigmentation in relation to hopper density in the Migratory locust under laboratory conditions. In our case, this gradient reflected the gradual development of individuals from the solitarious state to the gregarious state through several intermediate transiens stages. Up to nine transiens categories were distinguished. Finally, only two were selected for a practical classification to highlight the first key stage of the gregarization process represented by the solitaro-transiens individuals. For each density, hopper populations were composed of a mixture of several color types in varying proportions. The proposed criteria were simple and unambiguous. The information collected by the National Anti-Locust Centre in Madagascar on the phase status of hopper populations could thus become precise, reinforcing the reliability of the survey protocol on this species.

There was a possibility that environmental factors, other than population density, affected hopper coloration. For instance, temperature affects dark color patches in many acridids, especially in locusts [21]. In our case, temperature and humidity were not very variable during the sampling periods. The same results were obtained in 2007 and 2008 whatever the ecological conditions showing that population density was more important than any other factor—in our field conditions in Madagascar—to determine the coloration of hoppers of the Red Locust, contrary to an early statement by Lea and Webb in 1939 [64].

Our results confirmed (although only the pigmentation aspect was considered, which is just one component of phase polyphenism), that all hopper phases are present in Madagascar: the solitarious, all transiens-intermediate stages, and true gregarious hoppers were, in all respects, similar to those previously described in the literature, both in pigmentation and behavior (well-established and large, dense hopper bands of several hundred hoppers per square meter). These results therefore contradict the hypothesis by Roblot [65] and Roy [66], in force for almost half a century, according to which, as the environment is assumed to be less favorable to the Red locust in Madagascar as compared to Africa, only solitarious and transiens forms were able to exist on the island. This concept was so ingrained in the mentality, that the National Anti-Locust Centre in Madagascar deleted the term "gregarious" from the observation forms; only solitarious or transiens individuals were recorded. This is obviously the best way to avoid observing gregarious individuals. Our results complemented recent studies (based on morphometric measurements) showing that the gregarious phase amongst the imagos was indeed present in Madagascar from the extreme south to the extreme north of the country [67]. A new gregarious area has moreover recently been identified following major outbreaks that occurred from 1999 to 2003 in the far north, surely as a result of intensive deforestation leading to the creation of new suitable biotopes [67, 68].

4.2. The Gregarization Threshold in Red Locust Hoppers. Our results showed that the typology of hopper populations is strictly a reflection of hopper density. The color changes marking a first phase change were noted in the hoppers found in populations where the density is 10 hoppers

per square meter. The first real gregarious hoppers are found, occasionally, from 60–70 hoppers/m^2 and become predominant from 150/m^2. Thus, the gregarization threshold can be estimated at about 100,000 hoppers per hectare. To our knowledge, this is the first indication of this type in the Red locust. For adults, this threshold has been recently estimated to be around 5,000 individuals per hectare by Franc et al. [67]. In comparison, the threshold is estimated at 2,000 adults/ha for the Migratory locust [69]. For the Desert locust, the threshold is estimated at 250–500 hoppers per hectare and varies between 5 and 0.5 hoppers/m^2 from the first to the fifth instar [29]. For the Red locust, the threshold is probably very likely to be modulated according to the hopper instar. The value quoted above was an average for all of our sampling (1th to 6th instars). Presumably it was lower in the 6th instar and higher in the first, which should be verified on a larger sample.

The gregarization threshold may be reflective of the hopper environment, particularly the structure of the vegetation. The latter may be more or less heterogeneous and may promote local concentrations of populations. In general, the distribution of resources such as food, favorable areas of microclimate, and roosting sites are all factors that may help promote gregariousness as has been shown especially in the Desert locust [16–18]. However, the Saharan habitats of the Desert locust, a plurivoltin species, can be very diverse, both in space and time. On the contrary, the hoppers of the only annual generation of the Red locust in Madagascar varies between January and March, within the breeding area in the south-west, in a lush, dense vegetation (100% coverage, plant height between 40 and 80 cm on average) whose structure is very similar from one year to the other. We believe that the threshold concept takes on certain significance and is of considerable value for the local antilocust survey service, even if the figures are only a rough estimate.

Finally, it is interesting to compare our threshold values to those recorded experimentally for the density at which the coordinated marching behaviour of the gregarious populations appears. Collett et al. [18] has shown experimentally, in the third hopper instar of the Desert locust, coordinated movements that are well marked at densities above 74 hoppers/m^2. However, at densities below 18 hoppers/m^2, no coordinated movement is noted. Even if the species and conditions were very different from ours (hoppers in the field in dense vegetation compared to hoppers in a circular arena without vegetation), it is interesting to note that our observations give similar values with a phase transformation threshold estimated at 10 hoppers/m^2 and the emergence of real gregarious hoppers from densities of 60–70 hoppers/m^2. This could be the result of an identical "radius of influence", whatever the circumstances and regardless of the stimuli involved. Differences in the gregarization threshold for Migratory, Red and Desert locusts could therefore be the result of the respective structures of these three species' habitats. For adults, the lowest gregarization thresholds were indeed noted for the Desert locust living in habitats where vegetation is scarce and often in clumps and highest for the Red locust living in environments with much wetter, tall, and dense vegetation.

4.3. Phase Transformation Rapidity and Parental Antecedents. The fact that from solitarious parental populations we can obtain hoppers with perfectly gregarious color characteristics in the next generation may question the rapidity of the gregarization process in the Red locust. Can we consider a parental effect on our results? We know that phase characteristics are transmitted to offspring, a phenomenon well known in the Desert locust and the Migratory locust [70–74]. In Madagascar, the early stages of phase transformation are often initiated at the beginning of the rainy season when solitarious populations migrate from the dry season refuge areas to the rainy season breeding areas. Such a phenomenon is observed in the Migratory locust [49, 60] as well as in the Red locust [59]. These migrations often lead to sudden and rapid increases in adult densities allowing the appearance of the first behavioral manifestations of gregarization. The density shock suffered by females during laying can be inherited and affect the phase of the descendant and, in particular, the expression of color polyphenism in the hoppers.

Such a parental effect could explain the rapidity of the process observed in the hoppers. Even if the parent populations appear to have been mostly solitarious, observations conducted by the National Anti-Locust Centre have shown the presence of some population densities above the gregarization threshold and a few swarms. In early 2006, in the dry season, the average density in south-western Madagascar was 94 adults/ha (max 680). In the early rainy season of 2006-2007, the average density increased to 664/ha (with one swarm at 160,000/ha), then decreased to 272/ha in the early dry season of 2007 (with four swarms and nine cases where the density exceeded the gregarization threshold of 5,000 adults per hectare). All transiens or gregarious hoppers could descend from parent populations that have already experienced, to varying degrees, a density shock in their history when laying or early in their development over a number of generations. This is impossible to determine, but it would explain the wide range of phase conditions registered in our database.

4.4. Relative Importance of Various Stimuli in the Gregarization Process. The low densities from which the first transformation phase signs were noted in the Red locust raise questions about the nature of the stimuli involved. Progress has been made in recent years towards understanding the stimuli associated with crowding that evoke gregarious-phase characteristics in *S. gregaria*. The main focus has been on induction of gregarious behavior [5]. Simpson et al. [16, 17, 72, 75–78] have brilliantly shown in the Desert locust that mechanical stimuli appear to intervene initially; they are potent inducers of phase-transformation behavior and have a central role. The mechanoreceptors responsible are located on the outer face of the hind femur. Various authors have shown, however, especially in the Desert locust, that visual and olfactory stimuli (less active or completely inactive separately) can act synergistically and lead to both gregarious behavior and the development of black spots and yellowing of the cuticle, characteristic of gregarious hoppers [79–81]. A former experiment by Launois et al. [82],

on the Migratory locust suggests that the daily rhythm of solitarious adults activity collected in the field and tested using actography near the field, can be changed depending on the density of individuals in the experimental room without any tactile contact between them, suggesting the influence of olfactory or visual stimuli in the early stages of behavioral gregarization. More recently, Simpson's group has also shown that tactile stimulation (of the antennae in this case) is necessary to induce behavioural gregarization in the Australian plague locust, *Chortoicetes terminifera* (Walker, 1870) [83]. Thus convergent behavioral responses to crowding have certainly evolved, employing different sites of sensory input according to the species.

In our case, no apparent manifestation of behavioral gregarization (coordinated movements) seems apparent in hopper populations of the Red locust at densities equal to the gregarization threshold or 10–20 hoppers/m^2 only, far from the hundreds of individuals in gregarious or pregregarious hopper bands. During the rainy season, the hoppers developed in homogeneous, dense vegetation covering the entire ground at an average height of 40 to 80 cm between January and March. However, the first signs of gregarization occurred at these densities, at least the pigmentary signs. The probability of tactile contact in these conditions seems relatively low. Visual, olfactory or auditory signs could also be very important in the early stages of the gregarization process when locust densities are too low (and therefore when a natural tendency for repulsion still occurs) and vegetation density is too high to allow frequent contact between individuals. Of course, in nature, mechanical, chemical, visual and auditory stimuli are all present and must act synergistically. The importance of these various factors in the induction of gregarization in the Red locust needs to be clarified in natural conditions. An excellent knowledge of the transiens phase and of its first signs is thus of fundamental interest.

Acknowledgments

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Research Article

Diel Behavioral Activity Patterns in Adult Solitarious Desert Locust, *Schistocerca gregaria* (Forskål)

Sidi Ould Ely,[1,2] **Peter G. N. Njagi,**[1] **Magzoub Omer Bashir,**[3,4] **Salah El-Tom El-Amin,**[4] **and Ahmed Hassanali**[1,5]

[1] *International Centre of Insect Physiology and Ecology (ICIPE), P.O. Box 30772-00100, Nairobi, Kenya*
[2] *Centre National de Lutte Antiacridienne, BP 665 Nouakchott, Mauritania*
[3] *ICIPE Field Station, P.O. Box 1213, Port Sudan, Sudan*
[4] *Crop Protection, Faculty of Agriculture, Department of Crop Protection, University of Khartoum,*
  P.O. Box 32, Khartoum North, Shambat, Sudan
[5] *Chemistry Department, Kenyatta University, P.O. Box 43844-00100, Nairobi, Kenya*

Correspondence should be addressed to Sidi Ould Ely, sidiouldely@yahoo.com

The responses of adult solitarious desert locust to odors from a host plant were evaluated in a two-choice wind tunnel. Solitarious desert locusts collected from the field (Red Sea Coast) were more attracted to volatiles from potted *Heliotropium ovalifolium* in scotophase than in photophase. The attraction towards the host plant odors rather than to clean air, in both photophase and scotophase, concurs with previous observations on oviposition preferences near these plants. Diel behavioral activity patterns of adult solitarious desert locusts *Schistocerca gregaria* (Forskål) that were collected from the field in Port Sudan were investigated by monitoring, scanning, resting, taking off, and walking/running in a wind tunnel. Solitarious locusts that had been propagated in the laboratory for 20 generations were also observed for comparison. In both groups of locusts, insects were significantly more active after sunset and this activity attained peak level at 1-2 hours after dusk. Of the two groups, solitarious locusts collected from the field were significantly more active. In the scotophase, the former traversed distances that were about seven times those covered by laboratory-reared locusts. Overall, the results show that the repertoire of behavioral activities of solitarious locusts is maintained in laboratory-reared insects, albeit at a lower level. The implications of these observations in the behavioral ecology of the desert locust are discussed.

1. Introduction

Among the two phases (solitarious and gregarious) of the desert locust, *Schistocerca gregaria* (Forskål), the active solitarious locusts are primarily present during long drought periods and are mainly confined to some patchy habitats of the arid areas in the Sahel [1, 2]. A number of field observations on solitarious locusts suggest nocturnal behavior of this phase of the insect. They have been reported to be cryptic during the day, spending more time either resting on the ground or roosting within bushes and only fly when they are disturbed or flushed [3]. On the other hand, in warm weather, they have been reported to start flying after dusk and continue being active during the early part of the night

[4]. These night flights sometimes culminate into migrations of the solitarious locusts into distant habitats in swarms, like their gregarious counterparts, leading to unexpected locust infestations, and it has been suggested that they can fly distances of up to 1000 km [5–9]. There are also reports on seasonal movements of solitarious locusts between summer breeding areas in the Sahelian zone and winter-spring breeding habitats in the southern and central Sahara [10–15]. More recently, Riley and Reynolds [16] made an attempt to monitor migrating solitarious individuals flying at high altitudes at night using vertical-looking radar (VLR).

Host plants contribute significantly to locust and grasshopper dynamics because of dietary relationship between preferred host plants and grasshopper survival,

growth, and reproductive performance [17]. Moreover, preference for specific desert plants for oviposition is envisaged to play a significant role in initiating congregation of scattered solitarious locusts in the field [4, 18–21].

However, no definitive studies associated with the diel behavioral patterns of solitarious desert locusts have been reported, unlike gregarious locusts on which extensive information is available. Methodical attempts to address this gap are an important prerequisite for understanding the behavioral and population dynamics of the solitarious phase and, therefore, the subtleties that underlie the phase dynamics of the insect.

In the present study, we examined the behavioral responses (scanning, resting/walking/running, flying attempts, and distance moved) of field caught solitarious desert locusts that were exposed to odor plumes originating from potted *Heliotropium ovalifolium* during photophase and scotophase (artificially induced). The activity patterns of these insects were also monitored in detail in the laboratory. For comparison, we also studied the behavioral patterns of isolated locusts that had been reared in our laboratory for many generations.

2. Materials and Methods

2.1. Insects. Solitarious desert locusts aged between 3 and 4 weeks old were collected from the field around the Tokkar Delta on the Red Sea Coast of Sudan. Each locust was kept isolated in a 1L ice cream cup for about one week to adapt to the laboratory conditions prior to carrying out the observations. Each cup was ventilated through a small window in the lid that was covered with a piece of fine gauze. For comparison, 24-day-old solitary-reared locusts that had been kept in the laboratory for 20 generations (corresponding to five years) and fed on a mixture of desert plants at the ICIPE field station, Port Sudan were used. Both groups of locusts were kept in a room maintained at the ambient temperature and humidity and a 12L : 12D photoperiod which is roughly the same as in natural conditions at Port Sudan.

2.2. Wind Tunnel. The behavior of locusts was observed in a rectangular flat-bed wind tunnel (110 × 40 × 40 cm) made of clear Plexiglas for easy observation and to minimize the tendency of insects to climb up the walls (Figure 1). The wind tunnel had two openings (15 cm × 15 cm) with covers on the top side for the placement or removal of locusts. At the bottom of each end, a rectangular opening (25 cm × 2 cm) which was covered with a black muslin cloth formed the air inlet. Air was drawn into the wind tunnel and cleaned using activated charcoal (granular, 4–14 mesh; Sigma Chemical Co.) filters that lined up the air inlets. Subsequent extraction of the air was through a central port (10 cm × 2 cm) in the floor of the wind tunnel that was connected to an exhaust fan via a duct. The air speed recorded 1-2 cm above the floor of the wind tunnel during observations was 15–20 cm/s. When using potted plants (*Heliotropium ovalifolium*), small chambers (25 cm W × 2 cm H × 5 cm L) were replaced by bigger chambers (25 × 25 × 25 cm) that could fit the potted plant (Figure 1). Plants were hidden from insects tested by black sugar paper.

2.3. Behavioral Assays. Observations were carried out during photophase (10:00 h–16:00 h) and after sunset during scotophase (19:00 h–23:00 h) in Port Sudan. In experiments that were carried out in photophase, five 60-watt bulbs placed one meter directly above the wind tunnel illuminated the experimental section and there were no other sources of light in the room. An electric fan heater with a thermostat maintained the room temperature at a level similar to that recorded outdoors in sunshine (31.7 ± 3°C) during the day and 27.3 ± 1.2°C at night. The relative humidity was 55.1 ± 1.5% and 65.0 ± 3.9%, respectively. At the end of the day, the fan heater was switched off one hour earlier after opening windows of the bioassay room to allow for the equilibration of the indoor temperature with the one outside. Lights were also switched off and observations carried out with the aid of an Infrared Find-R scope viewing device (FJW Optical Systems Inc., USA). An additional 5-watt red lamp was placed over the wind tunnel to moderate the darkness in the room.

A solitarious male or female locust was held in a small perforated Plexiglas cage (10 cm × 4 cm × 4 cm) that had no base placed over the wire mesh covering the central exhaust port on the floor of the tunnel (Figure 1). The holding cage had a nylon string (4 mm thick) attached to the top and running through a small hole (5 mm diameter) in the top of the wind tunnel. The test insect was held under the cage for 2-3 minutes to allow it to acclimatize and the air evacuation system was switched on prior to starting the observations. To release the insect, the holding cage was pulled up and secured using the nylon string and the locust was then free to move toward the middle of the wind tunnel. The following behaviors of each locust from the two groups were monitored by the same person over the subsequent 30 minutes: (i) scanning—movement of the front part of the body from side to side (≈4–6° displacement) with the body anchored by the abdominal tip (these movements have been suggested to be important in estimating the distance to the nearest visible object in the insect's field of vision [22–24]); (ii) flight attempts—these were vigorous jumps that were presumed to represent onset of flight that was, however, curtailed by the walls of the wind tunnel; (iii) walking and the distance traversed—no attempt was made to evaluate the speed of the movement; (iv) resting—characterized by a locust that did not change position for 5 seconds or more; (v) mean distance traversed towards the plant source when potted *H. ovalifolium* was included. The data were recorded as either the proportion of insects performing a given behavior and/or the frequency of occurrence of the behavior. Each locust was tested only once and 40 males and 40 females of each group were observed (laboratoryreared and field-collected locusts). Occurrence of the behaviors and their frequencies were recorded using The Observer 3.0 (Noldus Information Technology BV. Wageningen, Netherlands).
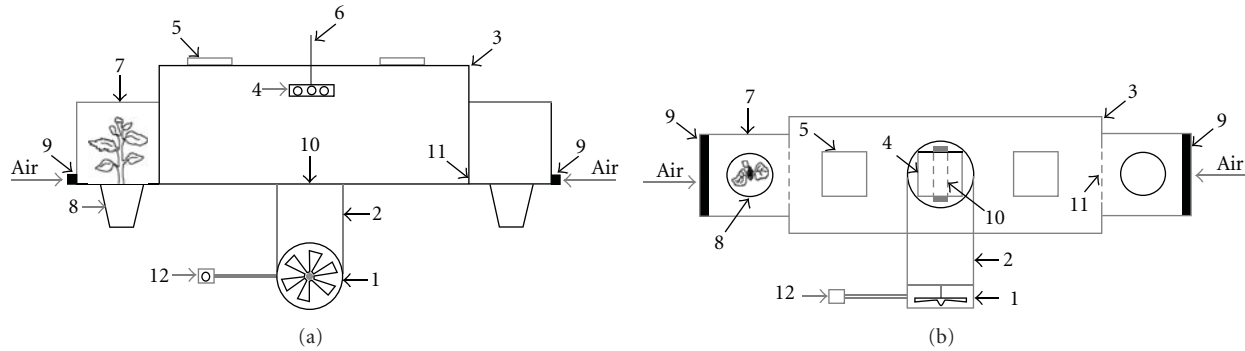
FIGURE 1: Diagram of the flat-bed wind tunnel used for testing plant volatiles. (a) Side view of the full length. (b) Top view. 1) Exhaust fan; 2) Cylindrical duct; 3) Wind tunnel chamber (transparent perpex); 4) Test insect holding box; 5) Doors for introduction and collection of insects; 6) Cord for pulling the insect box up; 7) Section for holding plant; 8) Potted desert plant; 9) activated charcoal filter; 10) wire mesh strip for air outlet; 11) wire mesh strip for air inlets; 12) Fan speed controller.

TABLE 1: Comparison of overall means ($\pm$SE) frequencies of walking, scanning, and jumping per insect for locusts caught from field in presence and absence of host plant (*Heliotropium* sp.) stimulus in photo- and scotophase. $N = 80$ insects used for each of the three behaviors.

| | | Behavioral activity (frequency of occurrence/insect) | | | | | |
| | | Scanning | | Jumping | | Walking | |
Sex	Stimuli	Photophase	Scotophase	Photophase	Scotophase	Photophase	Scotophase
Males	None	25.7 ± 2.4^a	47.5 ± 3.4^{ab}	4.5 ± 1.1^a	15.3 ± 2.8^a	21.8 ± 2.3^a	43.3 ± 2.9^a
Females	None	20.5 ± 1.6^{ab}	39.9 ± 3.4^a	1.8 ± 0.7^b	4.4 ± 1.4^c	16.9 ± 1.5^{bc}	37.0 ± 3.0^{ab}
Males	Host plant	30.9 ± 4.5^a	45.9 ± 3.8^{ab}	4.9 ± 1.2^a	26.2 ± 4.3^b	37.9 ± 5.2^b	47.9 ± 4.8^a
Females	Host plant	23.2 ± 4.3^b	52.1 ± 4.8^b	3.9 ± 1.1^{ab}	3.4 ± 0.7^c	15.8 ± 2.8^c	32.8 ± 4.7^b

Means with the same superscript letter in each column for each behavior are not significantly different (LSD test, $P < .05$).

2.4. Statistical Analysis. Data were analyzed using SAS (SAS Institute Inc., V 8.02, Cary, North Carolina, USA). For the wind tunnel experiments, separation of means of the frequencies of the behaviors studied between the laboratory-reared and field-collected solitarious locusts was carried out using Least Significance Difference (LSD) test for equal replications ($P < .05$). Student-Newman-Keuls multiple range test at $P < .05$ was used to analyze behavioral activity of solitarious locusts from the field. Tukey's studentized range test, at $P < .05$, was used to compare distance traversed by locusts during photo- and scotophases. The comparative behavior of lab and field locusts was analyzed using Student-Neuman-Kuels multiple range test, $P < .05$. The Student's *t*-test was used to evaluate differences between photophase and scotophase while the χ^2 test was applied to determine the significance in the proportion of insects attempting to take off.

3. Results

3.1. Behavior of Solitarious Locusts from the Field in Presence of Potted Host Plant. Males showed significantly more activity in the presence of host plant odors during scotophase relative to photophase compared to females, which showed less activity (Table 1, Figure 5). The mean distance traversed and the proportion of males and females that reached the target were recorded (Table 2); both sexes traversed significantly greater distance toward the source of stimulus compared

to the clean air side and a significant proportion of these reached the source (Table 2).

3.2. General Behavioral Activity of Solitarious Locusts from the Field. Solitarious locusts that had been caught from the field and kept under laboratory conditions for a week were mainly more active after dusk than during the day or later hours in the night. After dusk, there was a considerable increase in the frequency of scanning, jumping, and walking for both male and female locusts within the first two hours after sunset and a subsequent decline in the activity of the insects (Figures 2(a)–2(c), 3(a)–3(c)). In photophase, most of the insects remained static or executed very limited movement (Figures 2(a)–2(c), 3(a)–3(c)). This is also reflected by the distance traversed by the insects which was highly significant (Tukey's studentized range test, $P < .05$) after dusk than in photophase (Figure 4(a)).

However, there was a notable difference between male and female locusts with the males having significantly higher (Tukey's test, $P < .05$) activity than the females at night. Furthermore, *ca.* 74% of the locusts attempted to take off within the first 5 minutes of the 30 min observation period after dusk. This was significantly higher ($\chi^2 = 30.66$, $P < .0001$) than in photophase, during which only 30% of the insects made the attempts over a similar period (Figure 4(b)). Furthermore, some locusts did not attempt to take off at all during the observation period. Only 12.5% of the insects failed to take off during night observations while a
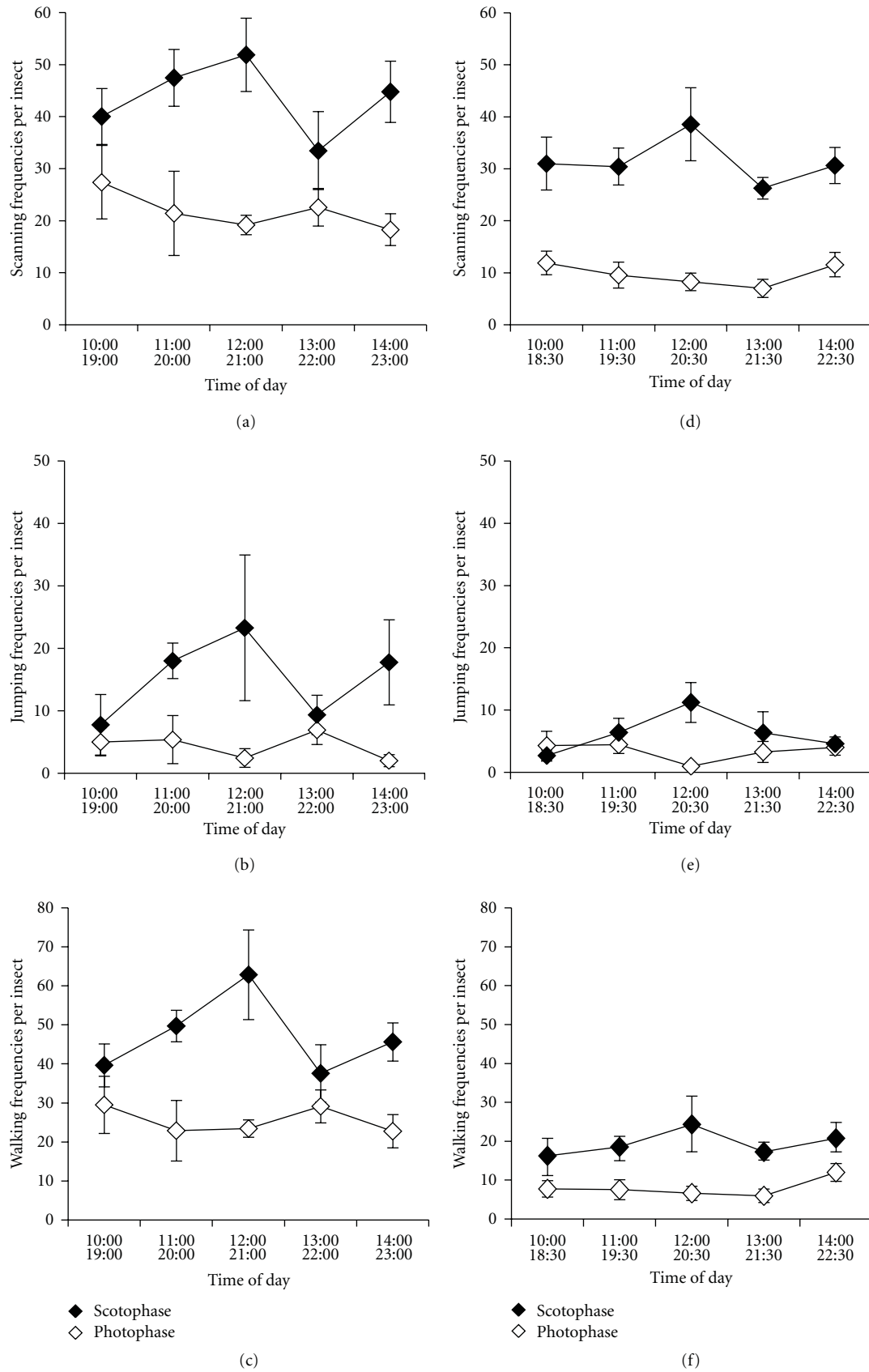
FIGURE 2: Activity of mature field-collected ((a)–(c)) and laboratory-reared ((d)–(f)) solitarious males. Bars represent standard errors (±SE); $N = 80$ insects used for each of the three behaviors.
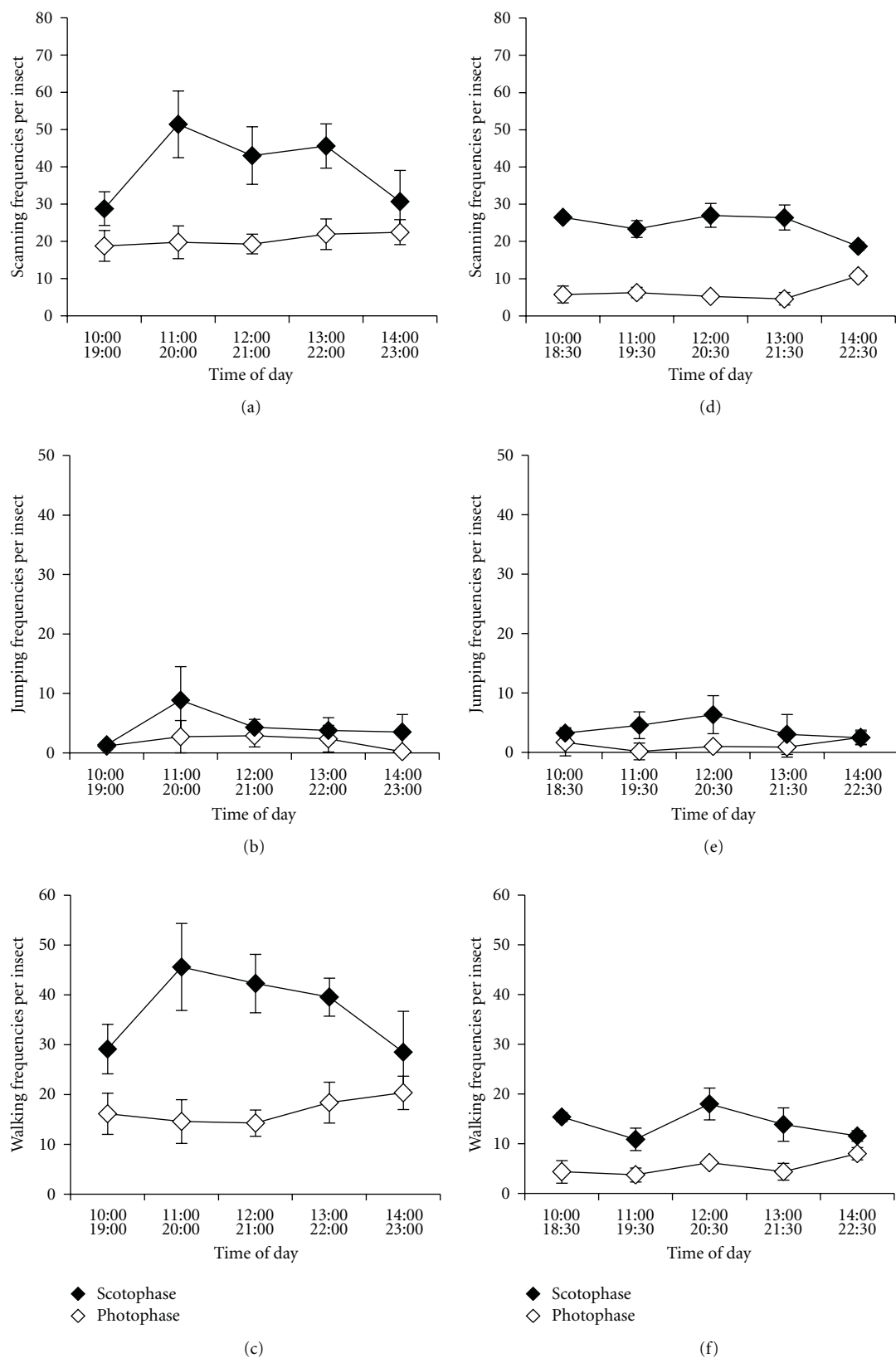
FIGURE 3: Activity of mature field-collected ((a)–(c)) and laboratory-reared ((d)–(f)) solitarious females. Bars represent standard errors (±SE); $N = 80$ insects used for each of the three behaviors.
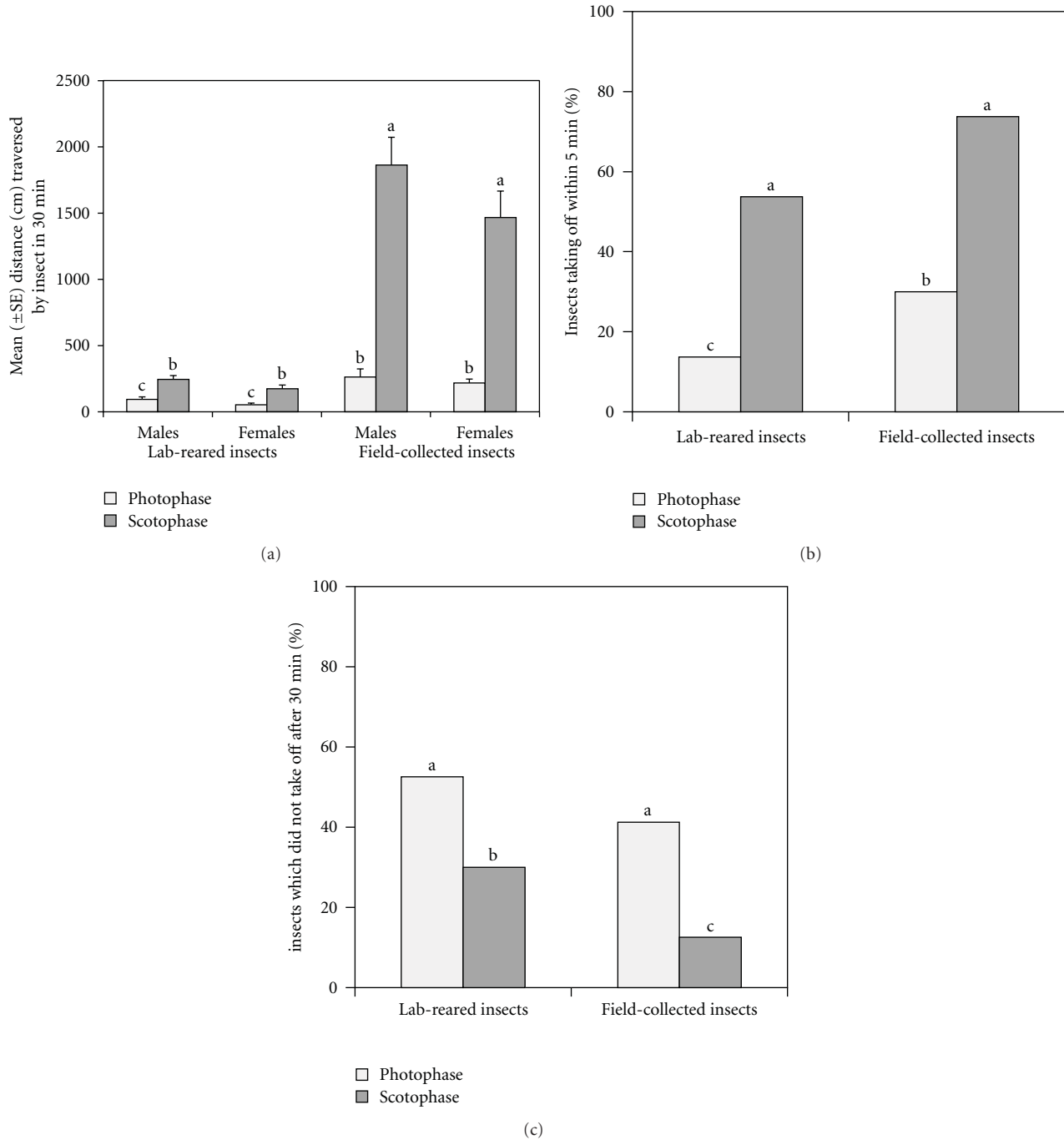
(a)

(b)

(c)

FIGURE 4: (a), Mean distance traversed by locusts during the 30 min observation period. Columns marked with different letters are significantly different ($P < .05$, Tukey's studentized range test). (b), proportion of insects that took off within the first 5 min of observation and (c), those that did not take off during the observation period.

TABLE 2: Comparison of the distance traversed and numbers that reached the host plant (*Heliotropium* sp.) stimulus in photophase and scotophase. $N = 80$ insects used for each of the three behaviors.

| | Mean distance traversed towards the host plant (cm)[x] | | Numbers reached the host plant source (%)[y] | |
Sex	Photophase	Scotophase	Photophase	Scotophase
Males	26.5 ± 3.2^{bc}	41.0 ± 2.3^{a}	35.0	60.0*
Females	24.8 ± 3.2^{c}	36.0 ± 3.3^{ab}	32.5	57.5*

[x]Means with the same superscript letter are not significantly different (LSD test, $P < .05$).
[y]Difference between photophase and scotophase activity for each sex in a group of locusts: *significant at $P < .05$ (*t*-test).
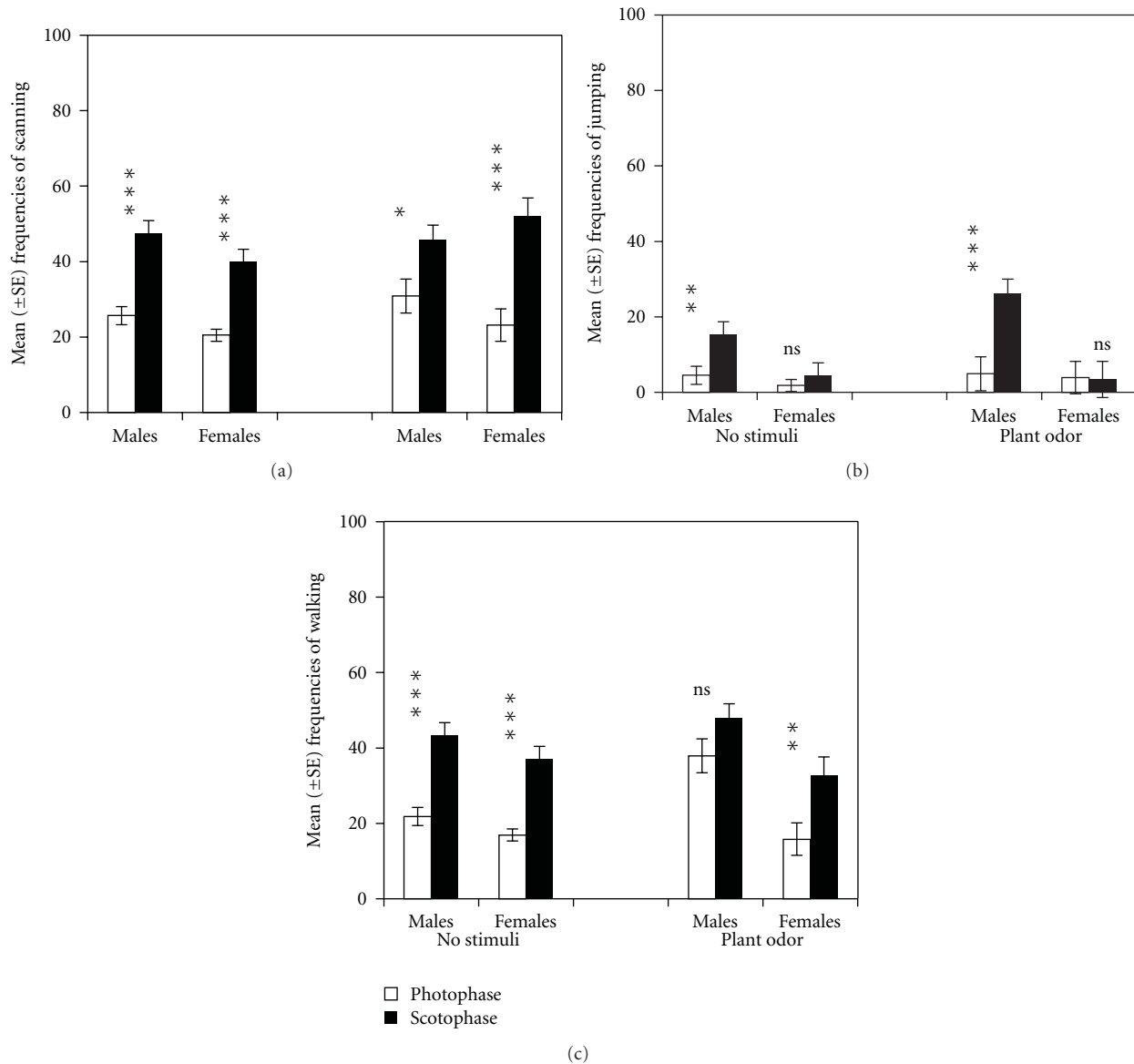
(a)

(b)

(c)

FIGURE 5: Difference between photophase and scotophase activities of mature field-collected solitarious locusts. Bars represent standard errors ($\pm$SE); $N = 80$ insects used for each of the three behaviors. Student's t test (*** = significant at $P < .001$; ** = significant at $P < .01$; * = significant at $P < .05$; ns = not significant $P > .05$).

significantly higher ($\chi^2 = 16.82$; $P < .0001$) proportion ($\approx 41\%$) was recorded during photophase (Figure 4(c)).

3.3. Comparative Behavior of Laboratory-Reared Locusts.
Solitarious locusts that had been kept in our laboratory's rearing unit for 20 generations had similar behavioral patterns to those of locusts collected from the field but the activity levels were much lower. In addition, the behavioral patterns of male and female laboratory locusts in photophase and after dusk were very similar (Figures 2(d)–2(f), 3(d)–3(f)). Frequencies of the behaviors monitored (scanning, jumping and walking) and the distance moved were significantly higher at the onset of dusk (especially the first two hours after sunset) than during daytime. The locusts

also traversed significantly longer (Tukey's studentized range test, $P < .05$) distance after dusk (Figure 4(a)). In addition, a significantly higher ($\chi^2 = 28.6$; $P < .001$) proportion ($\approx 54\%$) of the locusts attempted to take off in the first five minutes of the observation period compared to 14% in photophase (Figure 4(b)). Furthermore, throughout the observation period, 52% of the locusts did not take off during the day while only 20% ($\chi^2 = 8.35$; $P \leq .01$) failed to take off after dusk (Figure 4(c)). Thus, behavioral patterns of the two groups of solitarious insects were similar, although both male and female locusts caught from the field were significantly more active (Tukey's studentized range test, $P < .05$) and traversed about seven times the distance covered by the laboratory-reared insects after dusk (Figure 4(a)).

4. Discussion

In order to obtain a better understanding of the behavior and biology of *Schistocerca gregaria* populations, it is important to understand their interactions with host plants and their habitats. Kairomones are interspecific chemical cues, which may mediate host plant seeking and host acceptance behavior by locusts; they may also play a role in physiological predisposition of solitarious locusts to the gregarious phase [25]. Two groups of kairomones may influence the behavior of locusts; odors of host plants which play a role in the location of food [25, 26], and nonvolatile allelochemics involved in food selection [27]. Observations on field-collected solitarious locusts in the present study confirm that both sexes of this phase are attracted to volatiles emanating from *H. ovalifolium,* previously shown to be a preferred plant for oviposition and feeding by solitarious phase desert locusts in the field [19, 20]. However, the response of the insect was much more pronounced in the scotophase.

Diel periodicity in the behavior of some species of acridids has been observed in the field [4, 7, 11, 28, 29], but no detailed laboratory or field studies have been carried out. The present results from our laboratory observations show that solitarious desert locusts, *S. gregaria,* are more active after dusk than during daytime. The results also conform to the documented field observations that solitarious locusts are largely immobile throughout the day and only start flying after sunset [3]. The low frequencies of walking (and the distance traversed) and attempts to take off by both male and female locusts at daytime reflect the inactivity of solitarious locusts during the day. In the field, solitarious locusts start taking off 20–30 minutes after sunset. The flight activity reaches peak and then declines within the next 3 hrs [4, 7, 9, 11, 28, 29]. What triggers the onset of the high behavioral activity of the solitarious locusts after sunset? M.A. Volkonsky and M.T. Volkonsky [12] and Waloff [8] suggested that it may be induced by the sudden drop in light intensity. Roffey [9] observed that solitarious locusts apparently started taking off without any prior disturbance at evenings when the light intensity decreased from 400 to 3.5 lux. The compound eyes of solitarious locusts are structurally suitable for vision under subdued light and are sensitive to movements rather than sharp images [30]. Thus, solitarious adult locusts would be expected to be less active in bright sunlight during the daytime as opposed to their gregarious counterparts whose compound eyes are suited for diurnal vision. In daytime, solitarious locusts spend most of the time either resting on the ground or roosting within plant bushes [3]. Low behavioral activity during daytime may also aid crypsis which is adaptively used by solitarious desert locusts to minimize predatory pressure by birds, which are mainly daytime hunters [3]. Birds are the major predators of desert locusts, both the adults in swarms and nymphs in hopper bands.

In the wind tunnel observations carried out after sunset, locusts scanned their field of vision and walked at significantly higher frequencies than during the day. Take-off attempts were also more frequent, in particular during the first two hours of the night although this activity was significantly higher throughout the night observation period than in daytime. While the diel behavioral patterns in the two groups of locusts were similar, locusts collected from the field were overall more active than those maintained in the rearing facility. These differences may be due to a set of interacting internal factors such as muscle development and the levels of energy reserves in individual insects [31]. These may in turn be dependent on the rearing conditions and other external factors that the locusts are exposed to. For example, in the laboratory, confinement in small cages used for rearing isolated locusts limits their walking movements and makes them unable to execute any flights. This might stress the insects and may lead to underdevelopment of flight muscles in the insects as opposed to their field counterparts that undertake short distance and migratory flights [5–9]. In addition, environmental factors such as temperature and relative humidity under which the locusts are reared and kept may also play a role. In the laboratory, locusts are generally reared under constant controlled temperatures while in the field they are exposed to fluctuating temperatures and humidity [32]. In the field, large-scale night flights have been observed to occur when air temperatures are equal to or greater than 24°C [5, 10]. Another external factor which may influence the level of behavioral activity of the locusts is food quality which largely determines their energy reserves necessary for flight and other behaviors [31].

In conclusion, the results of this study confirm previous field observations that solitarious desert locusts are more behaviorally active after onset of dusk than during day. This is manifested as short distance and migratory flights in the field after sunset. While the diel behavioral patterns are preserved in the laboratory-reared solitarious locusts, it was evident that there is a significant decline in the levels of behavioral activities after several generations. We suggest that, where possible, insects freshly caught from the field are most suitable for use in bioassays aimed at evaluating and understanding various behaviors of the solitarious desert locust.

Acknowledgments

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Research Article

Immune Response of Mormon Crickets That Survived Infection by *Beauveria bassiana*

Robert B. Srygley and Stefan T. Jaronski

Northern Plains Agricultural Research Laboratory, USDA-Agricultural Research Service, 1500 N. Central Avenue, Sidney, MT 59270, USA

Correspondence should be addressed to Robert B. Srygley, robert.srygley@ars.usda.gov

Beauveria bassiana (Fungi: Ascomycota) is an entomopathogenic fungus that serves as a biological control agent of Mormon crickets *Anabrus simplex* Haldeman (Orthoptera: Tettigoniidae) and other grasshopper pests. To measure the dose-dependent response of Mormon crickets to fungal attack, we applied *B. bassiana* strain GHA topically to adults using doses of 5.13×10^4 to 1.75×10^6 conidia in sunflower oil, with oil only as a control. After three weeks, we assessed the survivors' hemolymph for fungal cells, active phenoloxidase (PO), and lysozyme. Mortality increased and body mass of survivors decreased with conidial dose. survivors' PO activity was elevated to the same level independent of dose. Those with fungal cells visible in their hemolymph did not differ in PO activity from those with clear hemolymph. We conclude that circulating PO may be an important enzymatic defense against *Beauveria* infection and that it is associated with attempted clearing of *Beauveria* blastospores and hyphae from Mormon cricket hemolymph.

1. Introduction

Nomadic insects risk contact with fungal pathogens [1]. Mormon crickets, a long-horned grasshopper or katydid, form bands and march across western United States grasslands seeking food, salt, and oviposition sites (Figure 1, [2, 3]). Wingless, they must walk, which increases the risk of contacting insect-pathogenic ascomycetous fungi, such as *Beauveria spp.* and *Metarhizium spp.*, on plants or soil [4]. These fungal pathogens occur naturally, but some strains, such as the commercial *Beauveria bassiana* GHA, may be applied artificially as control agents.

The ability of the fungus to infect an insect depends on its ability to adhere and penetrate the exoskeleton, resist the insect's hemolymph-borne defenses, and grow rapidly [5]. The conidium adheres to the cuticle and germinates to penetrate the exoskeleton with a combination of mechanical pressure and a cocktail of lytic enzymes. The insect may respond to the wounding with local induction of the phenoloxidase (PO) cascade, resulting in production of toxic quinones and cuticular melanization. Following penetration into the hemolymph, the fungus grows as a yeast-like blastospore or as short lengths of vegetative hyphae. Insect defenses include encapsulation of the fungus by granulocytes and plasmatocytes (both circulating hemocytes) and formation of a nodule that may be melanized [6]. Grasshoppers may also respond with behavioral fevers, elevating body temperature to inhibit fungal growth [7, 8]. Mormon crickets do not demonstrate behavioral fever per se; their preferred body temperatures are 34–37°C [9], above the upper thermal limit for most entomopathogenic Ascomycetes. Death of the host may result from competition with the pathogen for nutrients, mechanical damage resulting from hyphal growth, and fungal toxins [5].

The humoral defenses of insects to pathogenic fungi have only been investigated in a handful of species. *Metarhizium* infection may result in declining hemolymph protein and PO titres over the course of the infection until death (*Schistocerca gregaria* [10], *Locusta migratoria* [6]) whereas *Beauveria* infection increases active PO levels (*Melanoplus sanguinipes* [11], *Spodoptera exigua* [12]). Lysozyme activity may decline (*Schistocerca gregaria* [10]) or remain unchanged

(*Spodoptera exigua* [13]). In this paper, we investigate circulating PO and lysozyme titres in adult Mormon crickets that have successfully defended themselves against invasion from topically applied *Beauveria bassiana* strain GHA. On rangeland and crops, control agents are frequently not applied until Mormon crickets have reached the adult stage because the public demand for control is greatest when Mormon crickets have banded together and migrated from natal sites into habitats where they interfere with human activities.

2. Materials and Methods

2.1. Fungal Conidia. The *B. bassiana* conidia were obtained from Laverlam International (Butte, Montana, USA.) as a dry technical grade conidial powder. Conidial viability was determined by plating aqueous conidial suspensions onto quarter-strength potato dextrose agar, incubating the fungi at 28°C for 18–20 hr, then examining with 400x phase-contrast microscopy for germination. A conidium was considered germinated and thus viable if a germination peg was visible. A concentrated stock suspension in sunflower oil was prepared from the dry conidia, and the concentration was determined by hemocytometer counts of kerosene-diluted samples and adjusted for conidial viability. Working dilutions were prepared from the two concentrates using positive displacement pipettes, and the exact concentrations were determined by hemocytometer counts of kerosene-diluted samples. All conidia concentrations are viable conidia per unit volume.

2.2. B. Bassiana Dose Response. Adult Mormon crickets were collected at Lodge Grass, Montana on July 17, 2007, and fungal treatments were topically applied on July 24 (1st replicate) and July 25 (2nd replicate) to the base of the first leg, including the following fungal doses suspended in $1 \mu l$ sunflower oil: $1.75 * 10^6$, $1.07 * 10^6$, $3.54 * 10^5$, $1.13 * 10^5$, or $5.13 * 10^4$ conidia/μl *B. bassiana* strain GHA or a control treatment of only sunflower oil. Survivorship was measured over 21 days at 28°C.

2.3. Immunity Assays and Total Protein. After three weeks, we drew hemolymph from the surviving adults (five males and five females for each treatment, fewer if there were not enough survivors) to assess spontaneously active PO, lysozyme-like activity, and total hemolymph protein. We measured the body mass of each cricket to the nearest mg with an Ohaus microbalance (model AV53) and then punctured the arthrodial membrane at the base of the hind leg of each insect with a 26 gauge hypodermic needle so that it exuded hemolymph. A total of $14 \mu L$ of hemolymph was collected into a capillary tube, with a second puncture performed when necessary. For assays of PO activity and total hemolymph protein, the hemolymph was diluted 1 : 50 with phosphate buffered saline (PBS) solution and frozen at $-20°C$. An additional $10 \mu L$ hemolymph diluted 1 : 10 with PBS was stored at $-20°C$ for subsequent measuring of lysozyme activity. For ten insects, we did not collect sufficient blood for all of the tests.

FIGURE 1: Migrating Mormon crickets basking near Jarbidge, Nevada in July 2009.

To measure PO activity, we followed the protocol of Wilson et al. [8]. Samples of thawed hemolymph diluted in PBS were centrifuged (4°C, 10,300 rpm for 10 minutes) and activated with 10 mM dopamine solution. The plate was loaded into a temperature-controlled BioTek microplate reader (25°C), and absorbance at 492 nm was read between 5 and 15 minutes. If sample absorbance was linearly related with time, we calculated mean V (change in absorbance min^{-1}). One unit PO activity per ml hemolymph is defined as the amount of enzyme resulting in a 0.001 increase in absorbance.

To measure lysozyme-like antibacterial activity, a turbidimetric method was used, following the protocol of de Azambuja et al. [14]. Thawed and PBS-diluted hemolymph was added to a well with suspended gram-positive bacteria cells *Micrococcus lysodeikticus* (Worthington). Clearing of the well was compared to a serial dilution of egg-white lysozyme (Sigma) added to the bacteria suspension. The plate was loaded into a temperature-controlled Biotek microplate reader (25°C), and absorbance at 450 nm was read between 10 and 30 minutes. If the sample absorbance was linearly related with time, we would calculate mean V. When sample activity fell below $6.5 \mu\text{g ml}^{-1}$, the sample was excluded because the standards showed that the data were unreliable when samples were this weak.

We measured total hemolymph protein in mg protein ml^{-1} hemolymph with a Total Protein Kit, Micro (Sigma) compared to a serial dilution of the human albumin standard.

2.4. Verifying Infection. An additional $10 \mu L$ of hemolymph collected as described above was smeared on a slide and stained with a drop of lactofuchsin. Hemolymph samples were scanned at 400x, using dark-field, phase-contrast microscopy, for hyphae and blastospores.

2.5. Statistical Analyses. To analyze the *B. bassiana* dose response data, we combined the data from both replicates because Fisher's Exact Tests indicated no significant differences between the replicates at each dose. The combined data

Table 1: Pathogenicity of *Beauveria bassiana* strain GHA for adult *Anabrus simplex* based on mortalities 21 days after topical application.

LD50 (conidia/insect)	95% Confidence Limits (conidia/insect)	Slope (S.E)	Chi-Square $(P)^*$	g^{**}
6.46×10^5	$3.97 \times 10^5 - 1.275 \times 10^6$	0.885 (0.171)	6.745 (.08)	0.144

*Chi-square of heterogeneity: measures goodness of fit to the weighted regression line with $P > .05$ indicating a good fit of the data to the line. D.F. = 5
$^{**}g$ is the index of regression significance.

were then subjected to probit analysis using LDP Line (LdP Line, 2000 by Ehab Mostofa Bakr, Cairo, Egypt). Lysozyme and $\log_{10}$-transformed PO were normally distributed. Applying ANCOVA, we covaried the dependent variables with body mass and tested them for effects of replicate, sex and fungal dose (sample sizes in order of dosage from highest to lowest: $n = 2, 8, 9, 10, 10,$ and 10 for the 1st replicate and $n = 3, 5, 8, 6, 9,$ and 10 for the 2nd). Body mass was not a significant covariate, and so here we report the results from the three-way ANOVA's. Only for the males did the total protein meet the assumptions for parametric statistical analyses, and so we applied nonparametric statistics to data for the females.

Data for PO and total protein were normally distributed after $\log_{10}$ transformations. Lysozyme activity was normally distributed after squaring the data. Applying ANCOVA, we covaried the dependent variables with body mass and tested them for effects of sex and fungal treatment. However, body mass was not a significant covariate, and so we simplified the analysis and reported the two-way ANOVA's.

3. Results

Mortality at 21 days ranged from 22% to 80% and increased with the dose of *B. bassiana* applied to the cuticle (Table 1) with an LD50 estimate of 6.46×10^5 conidia per insect.

For survivors, mean body masses of replicates were significantly different ($P = .038$), and those for all treatments except one were significantly less than that for controls, but there was no difference in body mass among *B. bassiana* doses (Figure 2(a)). Log PO differed significantly between replicates and dose ($P = .0015$ and $P = .0048$, resp.) whereas it did not differ between the sexes ($P = .80$). In a post hoc comparison among the means, Mormon crickets treated with *B. bassiana* had greater PO activity than uninfected controls, but none of the fungal treatments differed from one another (Figure 2(b)). The second replicate also had significantly greater lysozyme activity than the first ($P = .030$) whereas sex and dose did not have significant effects ($P = .81$ and $P = .57$, resp.). Within males, total protein was proportional to body mass ($P < .0001$), and insects in the second replicate had significantly greater total protein than those in the first ($P = .0025$, resp.), but fungal treatment was not a significant factor affecting total protein ($P = .635$). Females in the second replicate also had significantly greater total protein
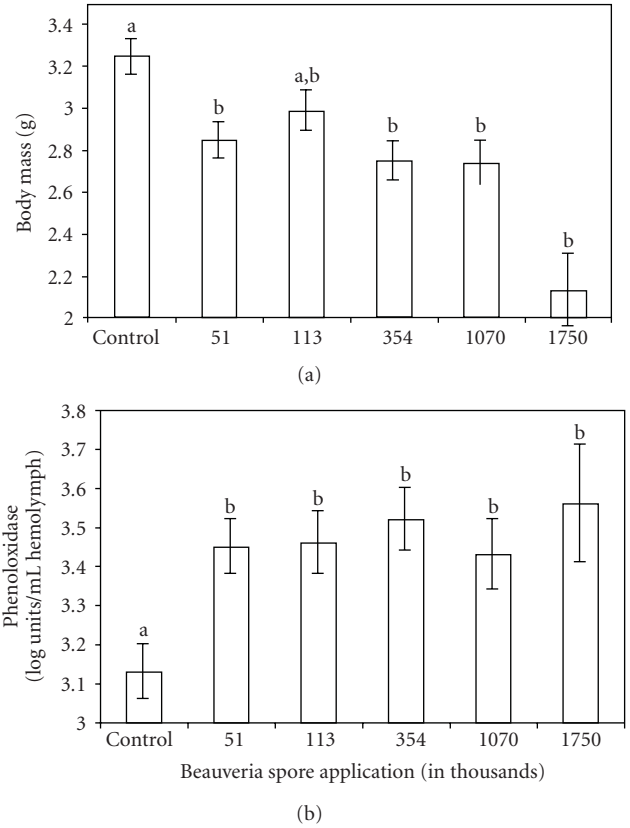
(a)

(b)

Figure 2: (a) Body mass and (b) phenoloxidase (PO) activity of adult Mormon crickets relative to the dose of *Beauveria bassiana* applied. Means and standard errors of the two replicates are shown with significantly different means in post hoc comparisons indicated by different letters.

than those in the first replicate (Wilcoxon test, $S = 423$, $z = 2.02$, $P = .043$), but fungal treatment was not a significant factor affecting total protein within replicates ($P > .60$).

4. Discussion

Mormon crickets responded to *B. bassiana* infection with an increase in PO. *Beauveria* infection also increased active PO levels in the grasshopper *Melanoplus sanguinipes* and the army cutworm *Spodoptera exigua* [12]. Gillespie and Khachatourians [11] found that after topical application of 10^8 conidia to *M. sanguinipes*, PO levels increased 3.8 times in males peaking at 3 days postinfection and 8.3 times in females peaking on the first day postinfection. In *M. sanguinipes* after 5 days, PO levels had returned to near control levels in males, but in females remained more than twice that of controls. Our applied doses were lower, and more of the Mormon crickets survived the application. At 21 days, PO levels remained higher in *Beauveria*-treated Mormon crickets relative to controls. We did not observe a difference in PO levels between the sexes for either controls or those that survived fungal application. Surprisingly, PO titres of *Beauveria*-treated survivors were independent of the dose applied.
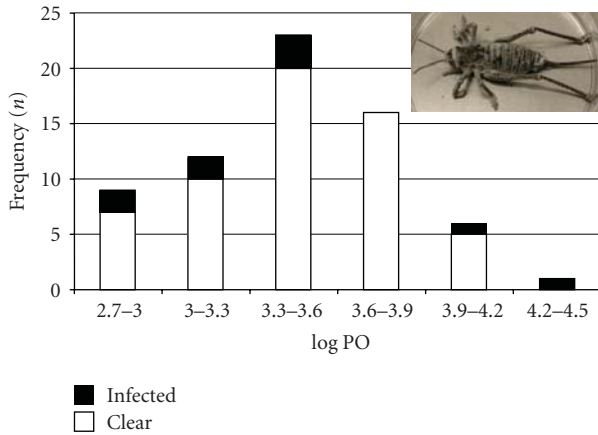
Figure 3: Phenoloxidase (PO) activity of survivors with fungal cells visible in their hemolymph (infected) and that of survivors with clear hemolymph. Inset: dark brown adult female Mormon cricket with white *Beauveria* sporulating on its cuticle.

Total circulating protein concentrations did not differ between treatments in males or females. In *Melanoplus sanguinipes*, protein concentrations of males and females peaked 30% above that of controls within three days of infection, but returned to the same level as controls by day five post infection [11].

The second replicate had higher PO, lysozyme, and total protein titers than the first. Adults were collected from the same location on the same day and treated only a day apart to make replicates as similar as possible, and thus the reason for these differences is not known. Body mass of individuals did not differ significantly between control groups ($n = 20$, $P = .38$), and so individuals in the second replicate were probably in no better overall condition to defend against the fungus than the first. Indeed, the average mass of the first replicate was 6% greater than that of the second replicate—the opposite of what one would expect if condition were a factor.

Beauveria-treated individuals lost on average 17% of their mass relative to controls. Reduced food consumption is the most likely cause. *Schistocerca gregaria* eats less when infected with *Metarhizium* [15], and *Manduca sexta* stops feeding altogether [16]. However, an increase in metabolism with infection could also increase mass loss. Metabolic rate might increase because the Mormon cricket is fending off the infection or as a result of the contribution of the growing fungus. Reduced nutrient absorption from the gut or greater water loss might also contribute to mass loss and warrant further study.

PO activity of survivors with fungal cells visible in their hemolymph did not differ significantly from those with clear hemolymph ($n = 57$ fungus absent, $n = 9$ fungus present, Welch ANOVA $F = 0.06$, d.f. $= 1, 9$, $P = .81$, Figure 3). We conclude that circulating PO may be an important enzymatic defense against *Beauveria* infection and that it is associated with attempted clearing of *Beauveria* blastospores and hyphae from the hemolymph of Mormon crickets.

Beauveria bassiana infection did not affect lysozyme activity in the Mormon crickets. Hence, elevation of PO did not result in an elevation of antibacterial activity in an all-or-none manner. Lysozyme activity declined with *Beauveria* infection in the desert locust *Schistocerca gregaria* [10] but remained unchanged in the army cutworm *Spodoptera exigua* [13].

In some Mormon cricket bands, migrating individuals seek protein [3], and protein ingestion is associated with an increase in PO activity [17]. Thus, protein deficiency evident in migratory bands is also likely to result in greater susceptibility to and more efficacious application of *B. bassiana* GHA.

Acknowledgments

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