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"Physiological Phase Transition in Non-Migratory Grasshoppers"

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Executive Summary

This report documents reciprocal meetings of the participating investigators, and data collected in the field in Kazakhstan and in laboratory studies in Israel. An initial visit of Professor Kambulin to Israel when this project was first launched was followed by a reciprocal visit of Professor Applebaum together with Dr. Popov of the Natural History Museum in London (an advisor to this project) to Almaty. Whilst in Israel, Professor Kambulin met with the participants of the Israeli team, and discussed administrative issues with Ms. Elinor Slater of the Authority for R&D of the Hebrew University.

Field studies were performed on *Locusta migratoria migratoria* and *Calliptamus italicus* in Kazakhstan and laboratory studies on *Locusta migratoria migratorioides* and *Aiolopus thalassinus* performed in Israel.

Success in the control of locusts depends on the accuracy of predicting population dynamics. This requires monitoring the location of infestation, the duration of egg-development and the time of hopper emergence. In these current studies, we have found that summing stored heat of temperatures higher than 0°C in the air is accurate for calculating the time of egg-hatch in the Spring. It has been established over many years that the most effective time for chemical control is in the second instar, after all nymphs have already hatched, with control commencing 10 days after the first nymphs hatch. Even when populations of *L. m. migratoria* are in a period of relative recession, as has been the case over the last few years (although with some local fluctuations), gregarization and the potential for damage exists.

Distribution in different habitats indicates that *C. italicus* generally prefers dry-weed plant associations with *Artemisia* or alternatively, *Artemisia* half-deserts, on sandy soil. In the north of Kazakhstan, the area of such habitats increased during the years of 1996-97. Fallow fields are preferred to arable fields. It has been previously recorded that during periods of wet and cold years or in the year afterwards,

populations of *C. italicus* decrease, whereas hot and dry years correspond to increasing density. Population outbreak of *C. italicus* occurs sequentially from the east towards the west of Kazakhstan.

Groups of *L. migratoria* nymphs shift the average phase index of individual *A. thalassinus* nymphs (4L1A) over the threshold of discrimination towards gregarious behaviour, but the majority of *A. thalassinus* individuals still remain behaviorally solitarious. Individual *L. migratoria* nymphs are themselves unaffected by close proximity to grouped *A. thalassinus.* Gregarious behavior of crowded nymphs of *A. thalassinus*, grouped for two instars with equal numbers of *L. migratoria* nymphs (5A5L), was depressed as a consequence of the presence of the latter, but the reciprocal behaviour of the *L. migratoria* nymphs, in the presence of the *A. thalassinus* nymphs, was not. From these studies of interspecific crowding, we tentatively conclude that *L. migratoria* nymphs are themselves indifferent to the presence of *A. thalassinus* nymphs, but affect phase behavior of the latter.

Section I.A. Research Objectives

In the original project proposal these were formulated as follows:

(1) To determine the behavioral response, food consumption and associated physiological characteristics of three representative grasshopper species of Kazakstan and Israel, to **intra**-specific (homogenous) population density. One of these will be the Migratory Locust (*Locusta migratoria* L.), the second - one of the species of *Calliptamus*, which does not exhibit a gregarious form, but does migrate to a limited extent, the third - *Aiolopus thalassinus*, a typical non-migratory grasshopper.

(2) To determine the comparative behavioral response, food consumption and associated physiological characteristics of these three grasshopper species to **inter**-specific (mixed) population density.

(3) To compare the behavioral phase transformation of the Israeli solitariform population of *L. migratoria* to the phase transformation of *L. migratoria* from Kazakhstan, which exhibits classical gregariform locust morphology and coloration.

Of these three objectives, the first part of this research project has been devoted to several aspects of the first two items:

(a) To study the effect of environmental factors on population dynamics of *Locusta migratoria migratoria* and *Calliptamus italicus* in Kazahkstan;

(b) To compare, in controlled laboratory experiments in Israel, the response of *Locusta migratoria migratorioides* to the presence *of Aiolopus thalassinus thalassinus*, and vice versa, at equal and unequal densities.

To date, significant steps have been made in dealing with these objectives. We have also accumulated background information on the effect of population density on feeding of single species, in controlled laboratory experiments, and we have preliminary data of damage to various host plants in different habitats in Kazakhstan.

Section I.B. Research Accomplishments:

General Introduction:

In addition to transition from the solitary to the migratory phase in locusts, partial phase transition is evident to varying degrees in "permanently solitarious" populations of known locust species (Heifetz et al., 1994), and even in non-migratory grasshoppers (Heifetz and Applebaum, 1995). For example, crowding induced chromatic, morphometric and behavioral characteristics in *Chorthippus albomarginatus*, but to less of an extent than occurs in locusts. At the other extreme, the non-migratory grasshopper *Aiolopus thalassinus thalassinus* responds behaviorally to population density, but no overt chromatic or morphometric characteristics are apparent (Heifetz and Applebaum, 1995). Phase polymorphism in grasshoppers may occur to varying degrees in species of the same genus. Thus, the genus *Gastrimargis* comprises more than forty species, many of them responding to population density to some extent as observed by changes in coloration, morphometrics and various descriptors of behavior. However, only one of them, *G. musicus*, has been observed to swarm, whereas *G. africanus* apparently does not respond to density by any of the measured parameters (Uvarov, 1996).

Orthopteroid insects within a specific habitat are frequently found in mixed populations, comprising several species. Their specific response to siblings or to individuals of other species may depend on a variety of factors. Behavioural response to population density is partly dependent on the biological characteristics of the species in question, on intraspecific competition, on availability of resources and on environmental conditions (Uvarov, 1966; 1977; Roffey and Popov, 1968; Rainey, 1989). Mixed dense populations of the Desert Locust (*Schistocerca gregaria*) and the African Migratory Locust (*Locusta migratoria migratorioides*) have been observed in the subsaharan Sahel, although their preferred habitats are dissimilar. The former - prefer a drier environment, the latter - a more humid one. *L. migratoria* is also more strictly graminivorous. *S. gregaria* may be found in conjunction with the Sudan Plague Locust (*Aiolopus simulatrix simulatrix*) (SAS Newsletter, 1955) and mixed populations of *L. migratoria* and of the Brown Locust (*Locustana pardalina*), with the latter dominant, have been observed in Southern Africa (Brown, personal comm.).

However, other than such incidental observations, no detailed studies of interspecific interactions amongst locust and grasshopper nymphs have been reported.

I.B.1. In Kazakhstan:

Following is a summary of field ecology studies performed in 1996-97 on two major locust species:

I.B.1.1. *Locusta migratoria migratoria* L.

1. The migratory locust in central Asia

Locusta migratoria migratoria (Orthoptera, Acrididae) is the most wide-spread sub-species of the migratory locust. It breeds in the delta of rivers, from the Danube to West China. Nowadays, the delta of many rivers (Dnepr, Don, Kuban, Kuma, Kura and Ural) are no longer primary breeding sites of the *Locusta*. However, nuclei of breeding sites still exist in Central Asia in the Caspian lowland, in reedbeds along the rivers Sir-daria and Amu-daria, reedbeds around the Balhash, Sasikkol, Alakol, Zaisan lakes and in the Kashgar and Dgungar lakes in China (Tziplenkov, 1959; 1970; Shamuratov, 1975).

Density of the *Locusta* population changes in cycles over a period of several year (Starostin, Shumakov, 1967; Popov, 1987). Until 1956 there were four periods of high density: 1921-1927, 1931-1937, 1944-1947 and 1953-1956. The years of 1967-1970 were also characterized by high population densities in spite of extensive use of insecticide sprays. In 1970-80 the locations fragmented, because the area of the reedbeds were reduced. During 1980-87 the density of *Locusta* populations increased in the river-deltas of Sir-daria and Amu-daria. In the Ballhash-Alakol site the *Locusta* populations formed aggregations of gregaria nymphs and increased their populated area to several dozens of thousands of hectares. In 1988 the density of *Locusta* declined as a result of floods.

2. The present situation of the migratory locust in Kazakhstan - general

Nymphs of *L. m. migratoria,* surviving in 1995 after control treatment, formed new aggregations of about 10,000 nymphs per hectare. The following year, progeny of this surviving population formed numerous groups of gregarious phase nymphs. The degree of gregarization was determined by morphometrical measurements (Nikulin, 1968). Even when only 50-100 nymphs survived per hectare, groups of the gregarious phase evolved in 1996 (observations from the breeding site at "Babakas" in 1996). Even when populations of *L. m. migratoria* are in a period of relative recession, as has been the case over the last few years (although with some local fluctuations), gregarization and the potential for damage exists.

3. Prediction of population structure - current studies

Success in the control of *Locusta* depends on the accuracy of predicting the population dynamics (Nikolskiy, 1925; Volkov, 1947). This requires monitoring the location of infestation, the duration of egg-development and the time of hopper emergence (Tziplenkov, 1979). It has been established over many years that the most effective time for chemical control is in the second instar, after all nymphs have already hatched (Nikolskiy, 1925; Dukov, 1936; Pilenkov, 1970). In current field operations, control commences 10 days after the first nymphs hatch.

In this present study, sites in the western, central and eastern parts of lake Balhash were examined. Sampling of nymphs from different groupings showed high instar variability within the groups. Average weighted age of the nymphs (B) was determined with the help of the following formula:

$$B = \frac{L_1x1 + L_2x2 + L_3x3 + L_4x4 + L_5x5 + Ax6}{K}$$

Where:

$L_1 \ldots L_5$ = the number of nymphs of the respective instar in the population sample,

A = the number of adults in the population sample,

K = total number of nymphs in the sample.

Following are representative results from one of the sites studied. The general pattern is similar in other sites as well.

Table 1: Instar composition of *Locusta* in the Kziltan site*

	Date of Hatching						
Instar	30.05	5.06	12.06	18.06	24.06	30.06	5.07
I	100.0	90.5	7.2	1.8			
II		19.5	85.1	15.5	1.5		
III			8.0	72.2	30.2	2.2	
IV				10.5	59.2	22.8	10.2
V					9.1	71.1	33.6
Adult						3.9	56.2
Average instar	1.0	1,2	2.0	2.9	3.8	4.8	5.5

*First instar nymphs started emerging on May 30.

It is possible to predict the approximate time of egg hatch by boiling the eggs and examining their color afterwards. The nearer the eggs are to hatching, the redder they become after boiling (Veltishev, 1941). In these current studies, we use environmental measurements to calculate the time of egg-hatch in the Spring. The influence of precipitation on egg-hatch is probably negligible, because the reedbeds, wherein egg pods of the migratory locust are deposited, are constantly fed by ground-water (Fedoseev, 1964).Our calculations are based on either summing **daily ambient temperatures** higher than 0°C (Vinokurov, 1949; Kemp and Sanches, 1978; Safarova, 1987; Kemp and Dennis, 1989), or on summing **stored heat** (Alexandrov, 1971) in the air at temperatures higher than 0°C.

Stored heat takes into account the relative humidity (RH) at different temperatures: 1 kg of air contains 6.1 kilo-calories at 20°C and 20% RH, compared to

9.5 kilo-calories when the RH is 50% and 13.5 kilo-calories when the RH is 100%. This index has been successfully applied for prognosis of rape weevils (Gar and Melnikova, 1986), and to predict the time of sexual activity of insects (Balkov, Danilov and Balkova, 1987). Eggs of *L. m. migratoria* undergo embryonic diapause. Therefore, the time of egg-hatch in the Spring is independent of the time of oviposition (Shumakov and Jahimovith, 1987) and it is possible to apply stored-heat values to predict egg-hatch. Meteorological data collected during several years from various stations located in Uch-Aral (1993-97) and south Balhash (1978-87) were used.

Table 2: Environmental data collected in Uch-Aral, in relation to nymphal stages of *L. m. migratoria*

		Temp > 0 °C		Stored heat in air*	
Year	**1st Dates with Temp. > °C**	**L1**	**L3**	**L1**	**L3**
1993	03.04	715	880	353	498
1994	04.04	891	1041	345	506
1995	01.04	799	1113	393	463
1996	25.03	747	1128	385	570
1997	23.03	800	1255	383	584
average±SE		790.4±83.1	1083.4±76.4	371.8±26.5	524.2±63.5

*Kilo-calories/kg

Daily averages of the two temperature-related indices were calculated with the help of the following formulas:

(1) Sum of positive temperatures: $\Sigma = T_c \times n$

Where T_c = Average daily temperature (°C);

N = duration (number of days).

(2) Daily amount of heat in air: $\mathbf{J} = 0.24t + 0.001d\,(595 + 0.46t)$

Where J = amount of heat in air (kilo-calories/kg);

t = temperature (^{o}C);

d = amount of water in air (gr/kg) = $622\,\dfrac{P^{o}vap}{P - Pvap}$

Where P = atmospheric pressure including water vapor

Pvap = partial pressure of water vapor

$P^{o}vap$ = partial pressure of water vapor at saturation

φ = RH ($Pvap/P^{o}vap$)

The average duration of egg development was 61 day at air temperatures above 0°C. This corresponds to 371.8 kilo-calorie/kg stored heat and to the sum of positive temperatures - 790.4 °C. Both of the indexes are significant ($p < 0.05$) (Table 2).

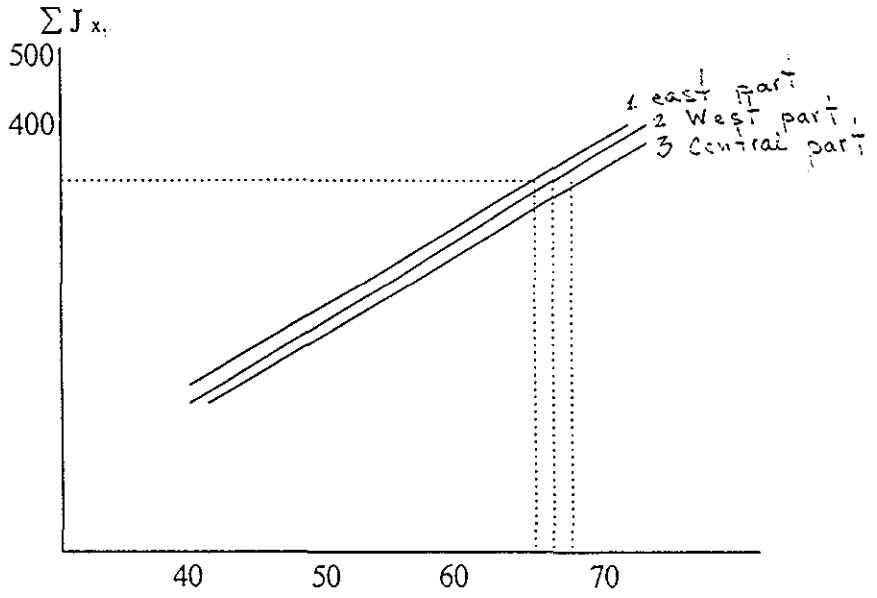
$\sum_{x=1}^{100} J\,X$ = stored heat per X days of temperatures above 0°C

The following are representative regression equations from data collected at Uch-Aral:

$$\sum_{x=1}^{100} J\,X = 2.46X-3.36 \quad \text{when } 0<X<10$$
$$= 4.72X-34.5 \quad \text{when } 11<X<40$$
$$= 7.52X-150.78 \quad \text{when } 41<X<70$$
$$= 9.67X-300.34 \quad \text{when } 71<X<100$$

Similar, but not identical equations were calculated from data collected at stations in the South Balhash and in Aidarli.

The relation between stored heat and days from when temperatures are above 0°C is not identical at different sites in Balhash-Alakol (Fig.1).



Days with temperatures > °C

Fig. 1 Amount of stored heat calculated at different locations of Balhash-Alakol in Kazakhstan.

I.B.1.2. *Calliptamus italicus* L.

1. Spatial Distribution and habitats of *C. italicus*

In central Kazahstan there are areas of continual development of *C. italicus* (these are the primary breeding sites) and temporary development - subzones of frequent or occasional development (Vasiliev, 1962). Distribution maps have been drafted, which describe the extent of damage (damage zones) (Fedosimov and Telepa, 1982).

Patterns of spatial distribution and damage zones in Kazakhstan do not correspond to each other well, because they are conceptually different.

Zones of potential damage by *C. italicus* are:

(1) zone of extensive damage (dry steppe of north-east and north-west regions),

(2) zone of medium damage (dry steppe of north, west and central regions),

(3) zone of minor damage (medium-dry steppe of mountains).

Table 3: Population density of *C. italicus* in different habitats (1996-1997) in Kazakhstan

Habitat	Plants	% ground-cover	*C. italicus* Density (Individuals/sq.m)
Fallow land			
3 years	Cereal weeds	50	0.5-1.0
3-5 years	Cereal weeds + *Artemisia*	60	1.0-4.0
5-7 years	Weed complex	60	2.0-6.0
Many years, near forests	Cereal weeds +*Artemisia*	50	3.0-8.0
forest glade	*Stipa* and *Artemisia*	60-80	0.5-1.0
> 5 years	Weeds, mainly *Artemisia*	70	2.0-8.0
Forest glades	Weed complex	40-60	3.0-10.0
Steppe	*Stipa*	40	0.01-0.1
Steppe	*Stipa*	60	0.03-0.3
Steppe	*Stipa*+cereal weeds	70	0.01-0.4
Virgin land	Weed complex	60	1.0-5.0
Steppe adjacent to forest	Weeds + *Artemisia*	50	1.0-10.0
Virgin land near forest	Weed complex	40	2.0-12.0
Bush	Weed complex	70	0.4-0.5
Shoulders of forest roads		40	0.5-0.7
Vistas in forests	Cereal weeds	40	2.0-5.0
Shoulders of field roads		60	3.0-8.0
Lands near Irtysh River	Weeds, mainly cereals	85	0.02-0.1
Tree-fences around fields	Weeds, mainly cereals	60	0.5-1.5
Arable land			
Fodder-grass		60	0.03-0.5
Wheat			0.01-0.03
Barley			0.01-0.03
Buckwheat			0.01-0.02
Wheat with weeds			0.5-3.0
Barley with weeds			0.5-4.0

Within these different broad categories of habitats, *C. italicus* nymphs encounter an even broader variety of plant composition. The percentage of damage imposed by the different instars of *C. italicus* on the different plant species was assessed in preliminary field observations. To some extent, damage to the plant biomass represents host-plant preference, but does not necessarily imply suitability for development of *C. italicus.*

Distribution in different habitats indicates that *C. italicus* generally prefers dry-weed plant associations with *Artemisia* or alternatively, *Artemisia* half-deserts, on sandy soil. In the north of Kazakhstan, the area of such habitats increased during the years of 1996-97. Fallow fields are preferred to arable fields. Within the preferred habitats, and in addition to the dominant *Artemisia* sp., several other plant species are attractive to *C. italicus.* The plant species bearing most consistent damage during the nymphal stages were: *Artemisia frigida, Galium verum, Trinia muricata, Chenopodium album, Medicago falcata.*

2. Long-Term Temporal Distribution

Population outbreak of different grasshopper species does not occur synchronously within the same damage-zone. On a broad time-scale, aggregations of solitarious phase Acrididae have been observed to occur sequentially from the east towards the west of Kazakhstan (Kopaneva, 1991). Similar information is available for Kirgizia (Pavluchenko and Naumovich, 1986). We too have observed these same trends in the past and more recently, as part of this project (1996-97) (Fig. 2)

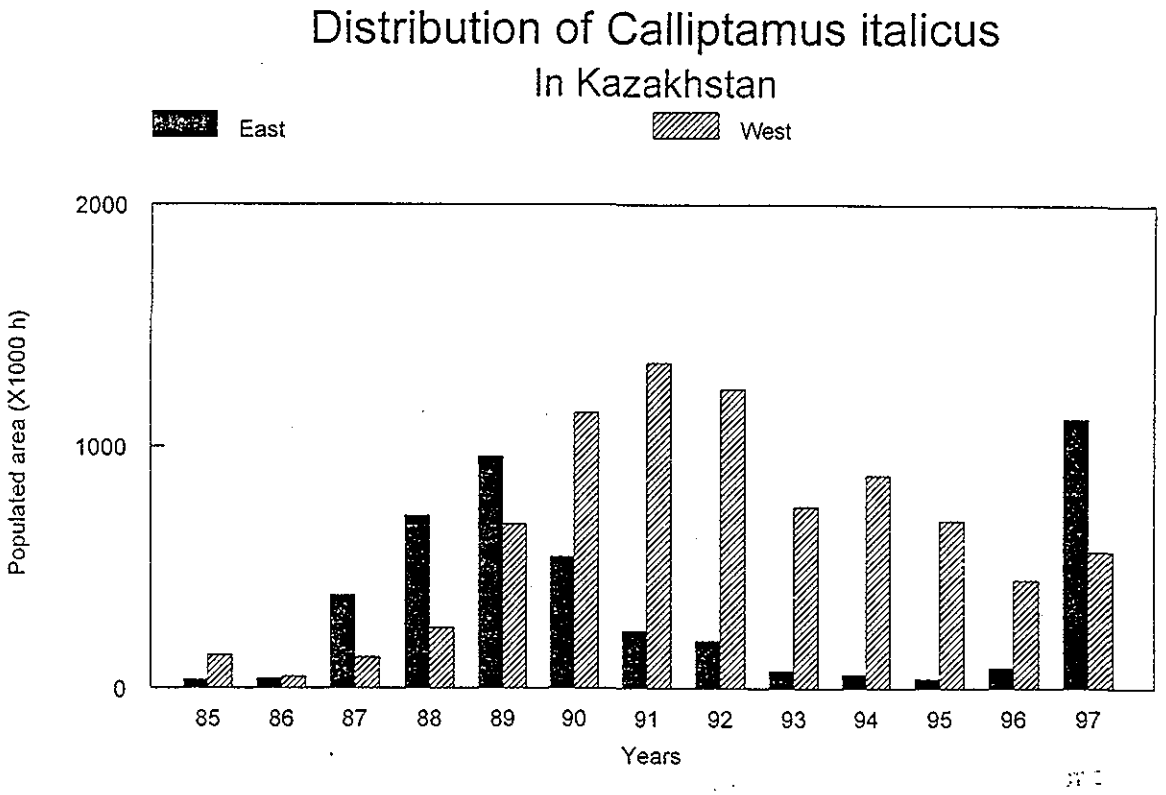


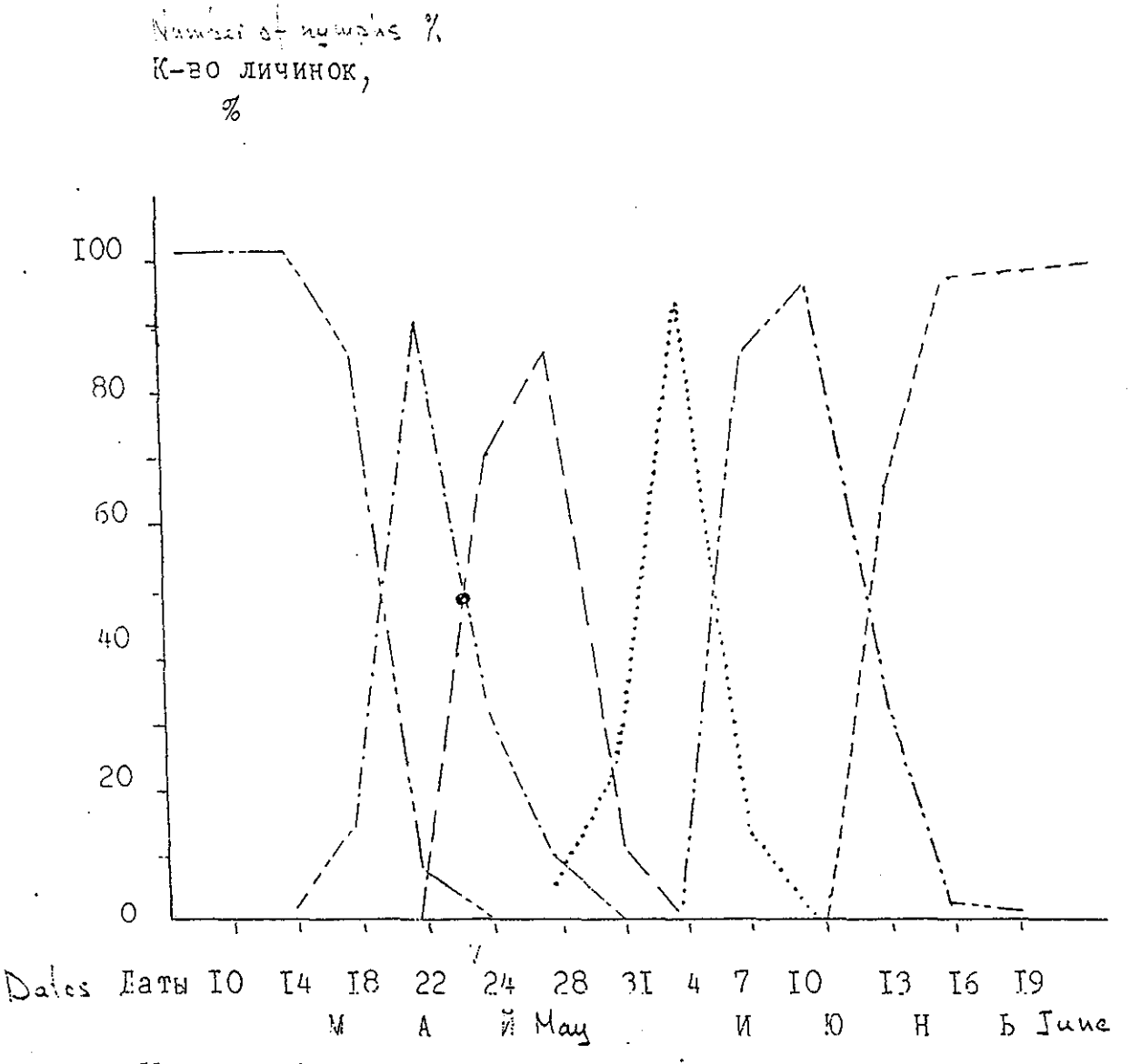
Fig. 2 Long-term fluctuations of *Calliptamus italicus* populations in Kazakhstan

3. Long-term forecast of *Calliptamus italicus*

No model of *C. italicus* population dynamics in Kazakhstan exists, and it is therefore not yet possible to predict outbreak years. Our purpose - based on retrospective analysis of dynamic and spatial distribution is to design a model of its population development.

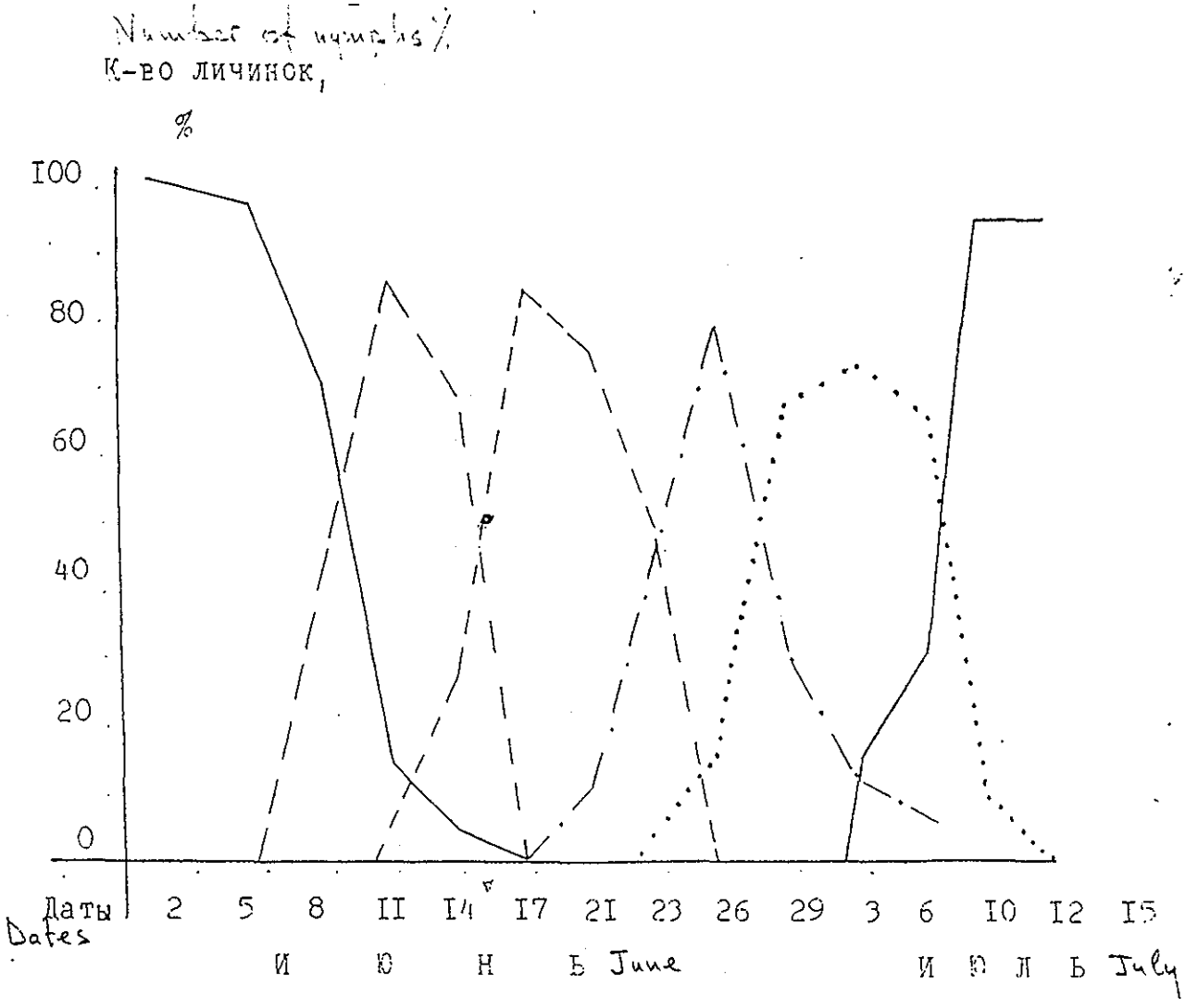
Field data concerning *C. italicus* has been collected in Kazahstan from 1900 and thereafter. During periods of wet and cold years (Stoliarov, 1967) or in the year afterwards (Vasiliev, 1962), populations of C. italicus decrease, whereas hot and dry years correspond with increasing density. We have seen that atmospheric precipitation is related to solar activity: The highest amount of atmospheric precipitation take place in years preceding maximal solar activity. In years of maximal activity, precipitation is reduced.

The duration of nymphal development depends on ambient temperature and RH, although within a certain habitat it is possible for nymphs to find preferential microclimatic conditions. According to data from west Kazakhstan, the duration of nymphal development in the summer is 35 days, with an average temperature of 19.7°C. The same duration of development was observed for north-east Kazakhstan, with an average temperature of 18.1°C. Th atmospheric precipitation during the period of maximal development was 12.0 - 15.6 mm. Duration of nymphal development in 1996 and 1997 is shown in the following two graphs:



Условные обозначения:
Личинки 1 возраста ___ 1 instar
Личинки 2 возраста _._._ 2 instar
Личинки 3 возраста _ _ _ _ 3 instar
Личинки 4 возраста ..... 4 instar
Личинки 5 возраста _.._.. 5 instar
Имаго ____ Imago
Дата начала обработок • Begining of insecticide treatment.

Fig. 3 Development of *C. italicus* in the Dgangal Region, West Kazakhstan (1996)



Условные обозначения:
Личинки 1 возраста ___ 1 instar
Личинки 2 возраста _._._ 2 —"—
Личинки 3 возраста __.._ 3 —"—
Личинки 4 возраста ..... 4 —"—
Личинки 5 возраста _.._.. 5 instar
Имаго ____ Imago
Дата начала обработок • Begining of insecticide treatment

Fig. 4 Development of *C. italicus* in the Lebiage Region, Pavlodar, Kazkhstan (1997)

Field behavior of *C. italicus*

Observations were performed in the Kaik-kanar site in 1996. Hatching started from 8-10 May. Young nymphs aggregated into small but dense groups. During the day the nymphs climbed on the stems of plants (in case air temperature was > 15°C and soil temperature > 20°C). Nymphs remained on plant stems as long as air temperature was less than 42-45°C. At 55°C, the aggregations were destroyed. During the day, in case of even short periods of clouding, the nymphs descended to and moved on the soil. In the evening and throughout the night, nymphs of youngest instars concentrated on the plant stems, while nymphs of older instars descended and remained stationary on the soil surface where temperatures were 2-5°C higher.

During the night adults stayed on the soil surface. During the morning hours they orientated perpendicularly to sun rays, and commenced flight at 10-11 am to a distance of 10 - 100 meters. On some days, most of the flying adults were females. They formed aggregations at oviposition sites. Oviposition occurred from 1 to 4 PM, while temperature on the soil surface was 40-47°C and was 34-40°C at a depth of 5 cm, where eggs were deposited. In case of cloudy weather - duration of egg-laying was just 1.5-2 hours, in case of rain - there were no egg-laying. Preferable places for egg-laying were condensed sandy soil, with *Artemisia* covering 40-50% of the surface.

Damage to plant biomass by *L.m. migratoria* and *Calliptamus italicus*

In general, damage is proportional to the area and density of nymphs (Popov, 1987). In *C. italicus* it is estimated as the difference in plant biomass before and after aggregation (Kambulin, 1975; Kambulin, Bugaev, 1982).

L. m. migratoria nymphs may destroy up to 100% of young reed-plants, although they do not feed on shoots of the previous year. The estimated damage to reed plants by *Locusta* is presented in the following table:

Table 4: Reduction in biomass of reed-plants due to feeding of *L. m. migratoria* nymphs in Balhash-alakol (1996, 97).

	Biomass decrease tons/hectare±SE	Affected hectares	Total loss (tons)
Ahmadsu, 1996			
05 June	0.87±0.13	5.9	5.13
10 June	0.99±0.14	10.8	10.69
15 June	1.18±0.14	21.2	25.02
20 June	1.40±0.13	37.9	53.06
25 June	1.52±0.13	38.5	58.52
30 June	1.57±0.20	57.2	89.80
5 July	1.68±0.20	60.8	102.14
Kziltan, 1997			
30 May	0.40±0.07	0.3	0.12
5 June	0.64±0.07	1.5	0.96
12 June	0.83±0.10	4.6	3.82
18 June	1.00±0.10	7.6	7.6
24 June	1.10±0.10	9.3	10.23
30 June	1.21±0.10	12.9	15.61
5 July	1.45±0.10	13.0	18.85
Bakabas, 1996			
3 June	1.78±0.21	0.4	0.72
9 June	1.96±0.23	1.3	2.55
15 June	2.27±0.25	2.6	5.90
21 June	2.68±0.27	8.7	23.32
28 June	2.94±0.21	13.0	38.22
5 July	3.40±0.24	12.0	40.80
Ertu, 1997			
2 June	1.05±0.12	0.1	0.11
8 June	1.25±0.09	0.2	0.26
14 June	1.60±0.15	0.4	0.64
20 June	1.70±0.15	0.8	1.36
26 June	1.99±0.16	0.9	1.79
2 July	2.23±0.16	1.5	3.34
8 July	2.43±0.18	2.0	4.86

Loss of host biomass is seen to be related to the average weight of nymphs, their activity and coefficient of food assimilation (Hemmingsen, 1960; Vinberg, 1962; Zubkov, 1971;; 1979; Hewitt and Osnager, 1982). It is known that the rate of metabolism in active nymphs is 2-3 times higher than in passive ones (Hemmingsen, 1960; Zubkova, 1971). The coefficient of food assimilation is about 30% (Stoliarov, 1975) to 50% (Popov, 1987). In 1 gr of dry reed-plants there are 430 calorie.

Food consumption tests were performed in cages of 1 m^2 floor area with fresh-cut shoots of reed-plants and nymphs of *Locusta* The shoots were weighed before and after 24 hours feeding of nymphs. (Four replicates were performed). The amount of consumed food was calculated as its dry weight (Dospehov, 1985). The coefficient of Results of the experiments are seen in the following table:

Table 5: Daily consumption of reed biomass by individual nymphs of different instars and from different densities

Instar	Nymphal density m^2	Avg weight (gr)	Food consumed Dry wt (gr/day)	Coefficient (Y)
I	1000	0.026	0.032	0.49
II	500	0.064	0.064	0.50
II	250	0.176	0.114	0.42
IV	100	0.348	0.213	0.47
V	60	0.920	0.413	0.44
Adult	25	1.452	0.582	0.44
Avg				0.46

I.B.2. (In Israel)

Following is a summary of laboratory studies on density-dependent intraspecific phase transition performed in 1996-97 with the African migratory locust, *L.m. migratorioides*) and the non-migratory grasshopper species, *Aiolopus thalassinus thalassinus*).

These present experiments were designed to focus on simple experimental protocols from which comparisons could be drawn between possible asymmetrical interactions of two different grasshopper species, at two densities (a total of 5 nymphs or 10) and numerical dominance (equal numbers or in the ration of 1:5). The possible effects of competition for a common food resource was overcome by a supply of fresh wheat sprouts and dried flaked oats in excess. Mutual avoidance of the nymphs one from another was precluded by the small size of the chambers in which they were reared. We do not regard these experimental procedures as mimicking conditions in the field. Firstly, field habitats are more diverse in plant composition and in total resources abundance and secondly, more than two species usually co-exist. In fact, co-existing grasshoppers and locusts in the same habitat may exploit different plant resources, whereby no real competition occurs, and avoid one another. Even in cases where the exact same resource is exploited (e.g., a preference for graminaceous plants), non-symmetrical interactions may occur.

Stock cultures of the two species were maintained in separate culture rooms under crowded conditions (density of >200 locust per cage of 50×50×50 cm) at a temperature-controlled regimen of 28±2°C within the cages and under constant illumination. They were fed fresh wheat supplemented with flaked oats.

Solitarious nymphs were reared from the beginning of the second instar and used in experiments at mid-fourth instar (in the case of the migratory locust) or from the third instar until mid-fifth instar (in the case of *A. thalassinus*). Rearing was performed in small aluminum rearing cages partitioned into 4 chambers of 10x10x15 cm each. These cages were placed in temperature controlled rooms separate from the stock cultures and kept at 28±°C. Nymphs were fed on wheat sprouts and flaked oats.

Behavioral phase

Assays were performed with developmentally synchronized mid-fourth instar nymphs of *L. migratoria* or mid-fifth instar nymphs of *A. thalassinus*. Fifth instar nymphs of *A. thalassinus* are in the same size range as fourth instar nymphs of the two locust species. The nymphal density response of each species to population density

was first established at the densities used for reference in this present work. Bioassays were performed with groups of 10 nymphs in a 45cm diameter circular arena. Activity Levels and Associative Indices were calculated as previously described (Heifetz et al., 1996). Discriminant analysis (SAS, 6.04) of these two behavioral parameters was performed and the phase affiliation of the nymphs determined, comparative to the discriminant function calculated from the distinctive behavior of solitarious and crowded control nymphs of the same species kept at the same density. Nymphal behavior is graphically presented as a phase index on a sliding scale, calculated from the discriminant function. Negative values are classified as solitarious and positive values - as gregarious. Percentage phase prediction indicates the degree to which the replicate bioassays conform to the predicted phase category: The average phase index may position the behavior on the solitarious side of the threshold of discrimination, while a certain percentage of the replicates are individually categorized by the discriminant function as gregarious, and vice versa).

1. Behavior of single nymphs of one species grouped with four nymphs of a second species

Mixed groups of the two species were examined and analyzed. Each mixed group was composed of five nymphs, the one termed "minor" species, was represented by one nymph and the one termed "major" species - by four. Mixed groups were kept together in chambers of 10x10x15 cm for two instars. Phase classification of the minor species was determined by performing standard behavioural assays. Discriminant functions for each species were derived from values of the chosen behavioural responses – activity levels and associative indices - of nymphs reared individually (termed solitarious), or in homogenous groups of 5 per chamber (termed gregarious) (Table 6)

Table 6. Activity levels and associative indices of fourth instar nymphs of *L. migratoria* and fifth instar nymphs of *A. thalassinus*, kept at two densities during two instars

Insect	Density	Activity Level	Associative Index
L. migratoria	1	1.69±0.46	0.07±0.02
	5	38.36±3.9	0.24±0.08
A. thalassinus	1	0.70±0.44	0.17±0.06
	5	12.63±5.02	0.1±0.06

Individual *L. migratoria* nymphs are unaffected by close proximity to grouped *A. thalassinus* (4A1L) (Fig. 5).

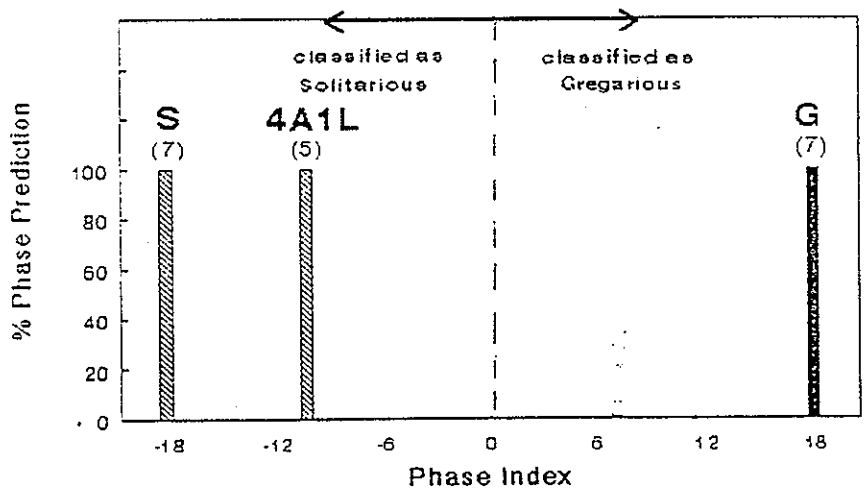


Fig. 5 Phase index of *L. m. migratoria* reared for two generations as single larvae in the presence of four *A. thalassinus* larvae (4A1L)

While groups of *L. migratoria* nymphs shift the average phase index of individual *A. thalassinus* nymphs (4L1A) over the threshold of discrimination towards gregarious behaviour, the majority of *A. thalassinus* individuals still remain behaviorally solitarious (Fig. 6).

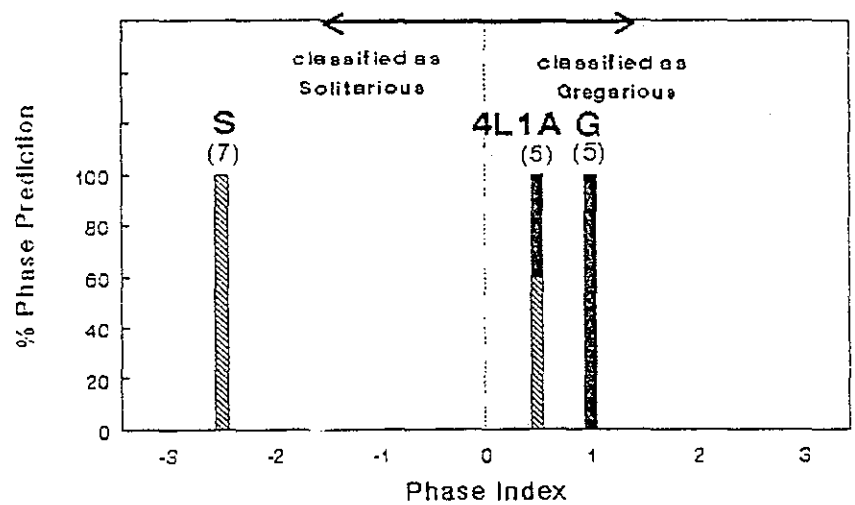


Fig. 6 Phase index of *A. thalassinus* reared for two generations as single larvae in the presence of four *L. m. migratoria* larvae (4L1A)

Interaction of mixed populations of equal density

Mixed groups of equal density (5 nymphs of each species) were reared together in individual chambers (10x10x15 cm) for two instars. The behavior of the nymphs of each species was examined separately by the standard behavioural assay procedure. The typical gregarious behavior of crowded nymphs of *A. thalassinus*, grouped for two instars with equal numbers of *L. migratoria* nymphs (5A5L), was depressed as a consequence of the presence of the *L. migratoria* nymphs (Fig. 7) , but the reciprocal behaviour of the *L. migratoria* nymphs, in the presence of the *A. thalassinus* nymphs, was not (Fig. 8).

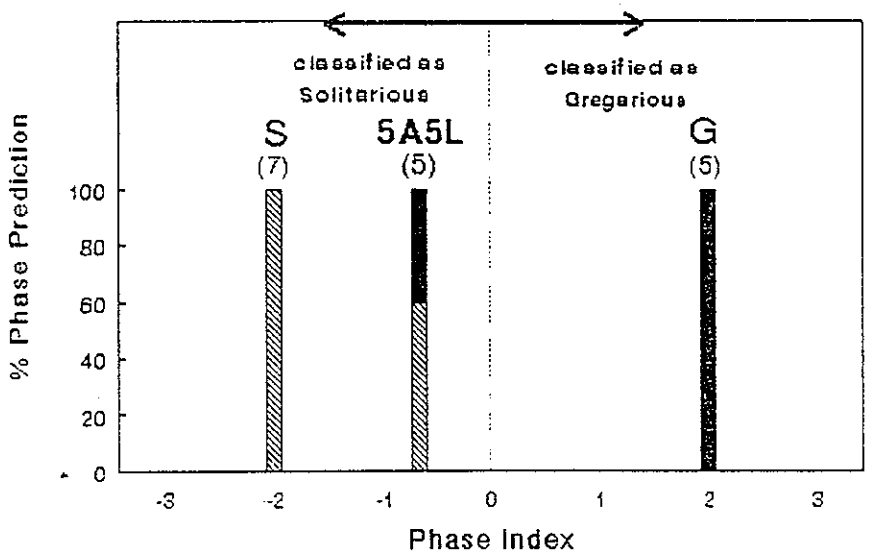


Fig. 7 Phase index of *A. thalassinus* reared for two generations at equal density with *L. m. migratoria* larvae (5A5L)

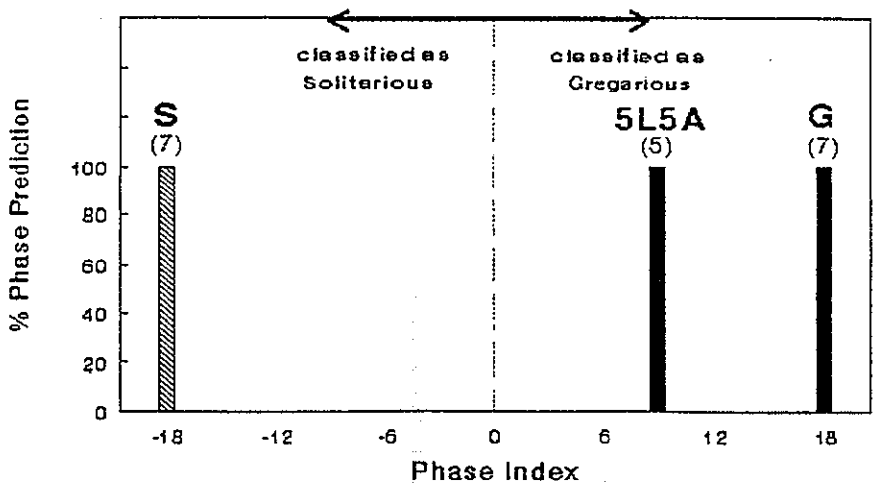


Fig. 8 Phase index of *L. m. migratoria* reared for two generations at equal density with *A. thalassinus* larvae (5L5A)

Interactions among insect species co-existing in the same habitat are complex. Some of the observed effects on population dynamics of the individual species may be simple responses to competition for resources on the same hosts plants. Additional cross-response to allelochemicals of closely-related or distant species may induce positive, negative or neutral responses in different instances. We have now examined behavioural responses of developmental stages between two orthopteroid species. The migratory locust *L. migratoria* and the non-migratory grasshopper *A. thalassinus* represent species of different genera belonging to the same sub-family (Acrididae: Oedipodinae). These present experiments were designed to focus on simple experimental protocols from which comparisons could be drawn between possible asymmetrical interactions of two different grasshopper species, at two densities (a total of 5 nymphs or 10) and numerical dominance (equal numbers or in the ration of 1:5). The possible effects of competition for a common food resource was overcome by a supply of fresh wheat sprouts and dried flaked oats in excess. Mutual avoidance of the nymphs one from another was precluded by the small size of the chambers in which they were reared. We do not regard these experimental procedures as mimicking conditions in the field. Firstly, field habitats are more diverse in plant composition and in total resources abundance and secondly, more than two species usually co-exist. In fact, co-existing grasshoppers and locusts in the same habitat may exploit different plant resources, whereby no real competition occurs, and avoid one another. Even in cases where the exact same resource is exploited (e.g., a preference for graminaceous plants), non-symmetrical interactions may occur.

Gregarious behaviour implies enhanced activity and greater food consumption. A dominant species might well benefit by depressing behavioural phase transition in competing minor species, whereas that same minor species would clearly improve its performance by exploiting the abundance of the dominant species in order to initiate enhanced activity and metabolism. Alternatively, a dominant species might disregard other species if they do not interfere with its performance. In the particular case examined here, A. *thalassinus* responds to the presence of the related *L. migratoria*, but the latter is indifferent to the presence the presence of the former.

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Section I.C. Scientific Impact of Collaboration: none as yet.

Section I.D. Description of Project Impact: none as yet.

Section I.E. Strengthening of Developing Countries Institutions:
None as yet.

Section I.F: Future Work:

In Kazakstan:
The third objective of the project entails a comparison of the behavioral phase transformation of the Israeli solitariform population of *L. migratoria* to the phase transformation of *L. migratoria* from Kazakhstan, which exhibits classical gregariform locust morphology and coloration. This comparison requires the performance of laboratory experiments in Kazakhstan, under controlled conditions,. Such experiments are dependent on the release of the incubators impounded in the airport in Almaty. Experiments on this objective will be performed when this release is realized. Field studies on the population dynamics and damage to biomass by *L. migratoria* will continue, in order to refine prediction models.

No model of *C. italicus* population dynamics in Kazakhstan exists, and it is therefore not yet possible to predict outbreak years. Our purpose - based on retrospective analysis of dynamic and spatial distribution is to design a model of its population development, alone and in the presence of other grasshopper species.

In Israel:
A major part of the laboratory research has been completed. It should be noted that although this report is for research conducted over a two-year period, we expended funds from this research grant only during the first year, and refrained from using funds thereafter, pending clarification of the status of this project in light of the managerial difficulties encountered. We have now overcome the major part of these difficulties, and propose to continue. During the duration, we intend to complete and publish the studies performed hitherto in Israel, and send an experienced field

ecologist to join in the studies performed by Professor Kambulin in Kazakhstan for part of the 1999 field season.

Section II.A. Managerial Issues:

This project was approved by USAID to start in mid-November 1995. The contract was sent to Kazakhstan to be officially approved in April 1996. Work started when Professor Kambulin visited Rehovot in the first half of June, 1996 followed by the site visit of Professor Applebaum and Dr. Popov to Kazakhstan in the second half of June 1996.

We must explain the very long delay in submitting this report. From the beginning, and until the last half-year, there have been numerous technical difficulties of communication between the principal investigators, which hindered the initial coordination of this project, and are now resolved. The main reason for this was that during this period, the capital of the government of Kazakhstan was relocated to Akmola, as was the Agricultural University. Concurrently, Professor Kambulin was transferred to the new capitol. Meanwhile, Dr. Popov, to whom a draft of the first annual research report was sent for evaluation by Professor Kambulin, fell seriously ill. Professor Kambulin thereafter sent his report covering the last 1.5 years (from the summer of 1996 to the end of 1997) directly to Rehovot. His studies are incorporated into this present first joint report.

This is officially a three-year project. The laboratory studies in Israel, independent of seasonal restraints, started in November 1995. Field studies in Khazakhstan are proscribed by seasonal conditions, and started later. It would clearly be to the benefit of the progress and final conclusion of this study to extend the duration of the project until the end of 1999. **No additional financial support** beyond that allocated in the grant contract is requested for this extension.

Section II.B. Budget:

No major changes in the budget are anticipated.

Section II.C. Special Concerns:

No special concerns were relevant to the project when approved and no changes in this item have occurred since.

Section II.D Travel.:

Professor Kambulin visited Professor Applebaum at the Faculty of Agriculture in Rehovot during in early June, 1996, met with associates and students participating in this project and observed the behavioral methodology used in the laboratory experiments. Details of the work plan and of protocols to be used in the experiments were discussed.

Professor Applebaum and Dr. Popov of the Museum of Natural History in London (a consultant in this project) afterwards traveled to Almaty in Kazakhstan in late June, 1996 and visited field locations where the field studies were to be conducted. During this visit, a computer and peripheral equipment were chosen and ordered for the use of Professor Kambulin.

Section II.E. Request for USAID or Office of International Affairs Actions:

A major issue concerns the impoundment of two incubators purchased for the use of Professor Kambulin in his studies, which is particularly troubling. The incubators were paid for from the grant, shipped from the supplier in the U.S. via Lufthansa to Almaty, and from that point on, the versions of what happened, diverge. The agent in Kazakhstan claims that he was unable to contact Professor Kambulin, but this does not sound reasonable, as Professor Kambulin's address and local telephone numbers were on record. Professor Kambulin was not informed at any stage of the arrival of this consignment, and the local officials in charge of storage have been demanding from the start, what was from the first an excessive, and is now an exorbitant payment for its release. We kindly request the intervention of USAID to resolve this issue.