Journal of Insect Conservation, 2, 167–178 (1998)

Moroccan locust *Dociostaurus maroccanus* (Thunberg, 1815): a faunistic rarity or an important economic pest?

Alexandre V. Latchininsky*

All-Russian Research Institute for Plant Protection (VIZR), 3, Podbelsky Street, 189620, St Petersburg-Pushkin, Russia

Received 10 February 1998; revised and accepted 23 April 1998

The Moroccan locust, *Dociostaurus maroccanus* (Thunberg), was traditionally considered as one of the most dangerous agricultural pests in the Mediterranean (*s.l.*) zone. Its broad polyphagy, extreme voracity, enormous fecundity and capability to migrate in swarms made it a major enemy of agriculturists from the Canary Islands to Afghanistan. However, outbreaks of the Moroccan locust seem to have been more frequent in the past and, in many regions, the species has become rare. Climatic factors, in particular the amount of spring rainfall, are critical for the developmental cycle of *D. maroccanus*. However, anthropogenic factors appear to have the most powerful effect on the locust's population dynamics. On the one hand, deforestation and overgrazing create the necessary prerequisites for colonization by the Moroccan locust. On the other hand, converting grasslands into croplands makes the habitat totally unsuitable for the insect because females can lay eggs into undisturbed soil. These two conflicting tendencies appear to govern the current evolution of Moroccan locust populations, their manifestations being different according to the geographical zone. Although in some regions (e.g. in many European countries) *D. maroccanus* has lost its formerly high economic importance, in others (North African and central Asian countries) the species continues to flourish and may even increase its pest status.

Keywords: habitat; anthropogenic factor; population dynamics; outbreaks; Mediterranean zone.

Introduction

> 'At his command came locusts, hoppers past all number, they consumed every green thing in the land, consumed all the produce of the soil.'
>
> Psalms 105: 34–5

This quote is one of nearly 100 references to insects and other arthropods in the Bible (Kritsky, 1997). Among them, the 40 references to locusts and grasshoppers far outnumber all other related quotes. Though we can only speculate which locust species is referred to in each case, at least some of the spectacular biblical descriptions of the locust plagues are likely related to the Moroccan locust, *Dociostaurus maroccanus* (Thunberg) one of the principal pests in the 'biblical' Mediterranean area. The notoriety of locusts as eternal enemies of humans shades the fact that, currently, some locust species are under severe anthropogenic pressure. This is true for the Moroccan locust, which has probably lost a portion of its genetic diversity because of possible local extirpations in some peripheral zones of its range. As with the more familiar case of wolves in Yellowstone, the situation with this locust presents an example of psychological and cultural prejudice against 'dangerous pests' which can be endangered themselves and need (at least locally!) a conservation status.

The common name 'Moroccan locust' of *D. maroccanus*, though technically correct, is misleading. The species was described by Thunberg in 1815 from the foothills of the Atlas Mountains in Morocco – the extreme west of its continental distribution. The actual distribution range of the 'Moroccan' locust spreads from the Atlantic islands (Madeira and Canary Islands) in the west, through the Mediterranean zone (*s.l.*), to Afghanistan and South Kazakhstan in the east (Uvarov, 1977; Latchininsky and Launois-Luong, 1992). Because it is Mediterranean by origin and distribution (Sergeev, 1986), some specialists even proposed to change its common name from 'Moroccan' to 'Mediterranean' (Pasquier, 1934; Skaf, 1972). However, the newly coined name has never succeeded in overcoming the traditional one. Therefore and reluctantly, I will adhere to tradition and use the adjective 'Moroccan', while bearing in mind that Morocco is not the centre of the species' distribution. Efforts to consider this locust's

* Present address: Entomology Section, Department of Plant, Soil and Insect Sciences, PO Box 3354, University of Wyoming, Laramie, WY 82071, USA.

ecology and conservation must be based on sound biogeography and not on misleading common names.

Geographic range: implications of discontinuity

A picture of the geographic range of the Moroccan locust (Fig. 1) reveals its extreme longitudinal stretch – approximately 10 000 km, while it is restricted to 2000 km in latitude. If the Mediterranean Sea itself were excluded, the north–south spread of the Moroccan locust's range would be even smaller, with a maximum of approximately 1000 km only in the easternrnost part in Iran, Afghanistan and the adjacent countries of the former Soviet Union. In the widest parts of its range, the distribution of *D. maroccanus* is discontinuous, consisting of isolated foci (permanent breeding areas), separated from one another by mountain ranges or water bodies. During periods when densities of the species are very low, this isolation is absolute. During the outbreaks, however, some exchange of individual insects between adjacent populations is possible because swarms of the Moroccan locust can fly over distances of 70–100 km, rarely up to 200 km during their entire lifetime (Tokgaev, 1973). These characteristics make *D. maroccanus* a very unusual pest. Its population fluctuations are intermittent, with usually short (1–3 years) but devastating outbreak periods, occurring at very irregular intervals. During such periods, the swarms of the Moroccan locust expand from the permanent breeding zones in the foothills down into the valleys, ravaging croplands. In periods between outbreaks, areas occupied by the species shrink dramatically. Populations retreat into remote and less-inhabited montane refugia, often for many consecutive years. As a result, a ruthless pest becomes no more than an obscure member of the local acridofauna.

The isolation of numerous local populations of the Moroccan locust suggests a possibility of genetic and phenetic differentiation throughout the species' range (Uvarov, 1977). This most interesting phenomenon remains largely unexplored except for an early work of Tarbinsky (1932) who found some distinctions in the structure of the epiphalli of males from different geographical zones. Morphological expression of differences between solitary and gregarious phases (e.g. the ratio between the length of tegmen and hind femur) in individuals belonging to the separated populations also seems to vary geographically (Latchininsky and Launois-Luong, 1992). Therefore, extirpations of genetically unique local populations, presumably occurring during the declines that follow the locust outbreaks, may result in a loss of the species' biodiversity.

Economic importance

The *Locust and Grasshopper Agricultural Manual* (Anonymous, 1982), published by London's Centre for Overseas Pest Research (formerly the Anti-Locust Research Centre), assigns the Moroccan locust the highest rank

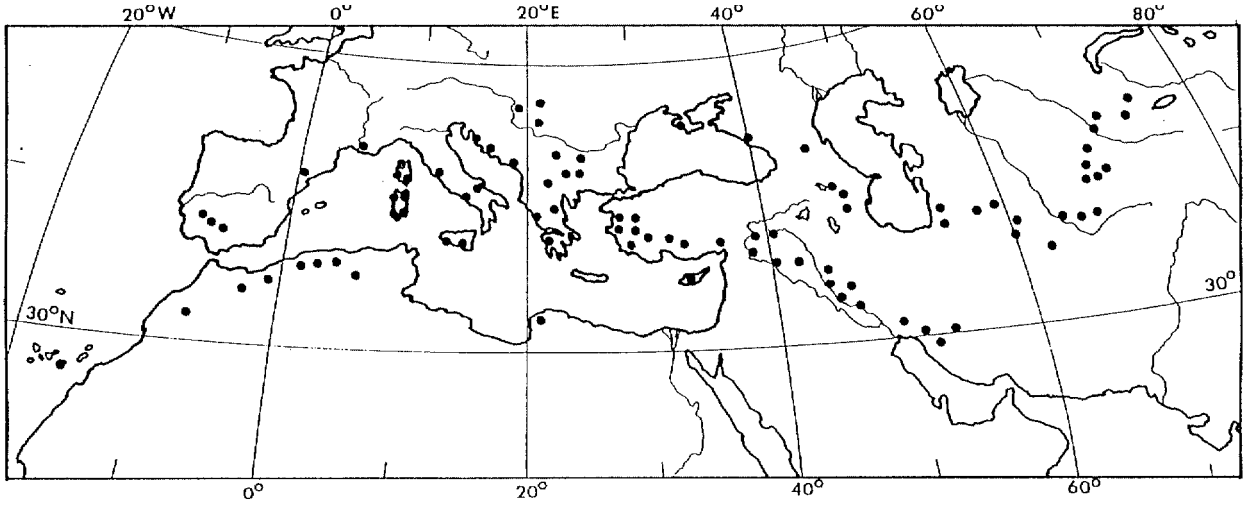

Figure 1. Geographic range of the Moroccan locust. Modified from Uvarov (1977) and Latchininsky and Launois-Luong (1992). Although Soltani (1976) found specimens of the Moroccan locust in the British Museum (Natural History) collections from Somalia, the presence of the species in this region has not been confirmed or rejected since. This paper has not included Somalia in the distribution range of *D. maroccanus*.

of economic importance as a 'major pest of many crops'. Indeed, the list of food plants used by *D. maroccanus* compiled from Russian sources alone consists of more than 150 species belonging to 33 families, including approximately 50 different crops (Latchininsky and Launois-Luong, 1992). In two regions of Algeria, the diet of the Moroccan locust includes 46–59 plant species belonging to 17 families (Ben Halima, 1983; Doumandji-Mitich *et al*., 1993). Being highly polyphagous, the locust attacks all principal cereals (wheat, barley, millet, sorghum, rye, oats and corn), fabaceous plants (beans, peas and lentils), vegetables (cabbage, onions, lettuce, carrots, beets, potatoes, tomatoes, pepper and cucumber), forage, oil and industrial crops (alfalfa, clover, vetch, sesame, cotton, olives, sugar beets, rape and tobacco). Many tree species, including fruit trees (cherry, apple, pear, peach, apricot, plum, fig and mulberry), date palms and even the conifers (pine and juniper) are also ravaged. Frequently, a swarm landing in cropland results in the clipping of plant stems almost at the soil level, as the thirsty insects seek to replenish water lost during flight. After such raids, the crop fields look like they were beaten by a hailstorm (Bei-Bienko, 1936). Crop damage from *D. maroccanus* has been reported in more than 25 countries. Some of these data are summarized in Table 1.

Control of the Moroccan locust during its outbreaks requires a massive campaign because vast infested territories need to be treated in a very short window of time dictated by the insect's brief developmental period. That is why military forces are often engaged in the operations against the Moroccan locust, as was seen in France in 1921 (Vayssière, 1923), in Azerbaijan in 1923 (Filipyev, 1926) and currently in Morocco (Anonymous, 1996a). The areas treated annually against the Moroccan locust can be enormous, exceeding 650 000 ha (Table 2). Data on the economic importance of *D. maroccanus* unreservedly confirm the status of the species as a primary agricultural pest in many regions. However, the periodicity of the Moroccan locust outbreaks calls this assertion into question.

Periodicity of outbreaks

In analysing the upsurges and declines of the Moroccan locust in the first half of the twentieth century, Uvarov (1977) came to the conclusion that its outbreaks occurred more frequently in the past. The decline of the economic importance of the pest over the last few decades was also stated in the *Locust and Grasshopper Agricultural Manual* (Anonymous, 1982). Indeed, in Europe, most of the recent important outbreaks of the Moroccan locust took place during the 1920s–1940s (Table 3), with one notable exception – Spain – which will be addressed later.

These records seem to suggest that *D. maroccanus* is losing or may have already lost its extreme economic importance. However, these data concern only the European part of the pest's range - the countries with highly developed 'industrialized' agriculture. Historical records from other countries show that Moroccan locust outbreaks occurred in the 1980s and 1990s (Table 4).

In order to understand better the nature of the spatiotemporal fluctuations in the transcontinental metapopulation of the Moroccan locust, it is necessary to

Table 1. Crop and forage losses due to the Moroccan locus

Year	Locality	Crop damage	Source
1901	South Kazakhstan	41 000 ha of different crops, mostly cotton	Tsyplenkov (1970)
1901	Turkmenistan	30 000 ha of different crops (cereals, vegetables and cotton)	Sïiazov (1912)
1921	South France	35 000 ha of native grasslands	Vayssière (1923)
1923	Azerbaijan	13 200 ha of cotton (80% of country's cottonfield)	Filipyev (1926)
1925	Iraq	In 17 000 ha of wheat and barley, 70% of yield destroyed	Rooke (1930)
1930	South Russia (Northern Caucasus)	2000 ha of cereals and 3000 ha of cotton	Predtetchensky *et al.* (1935)
1931	Syria	2346 ha of different crops	Skaf (1972)
1958	Afghanistan	100 000 tons of cereals and vegetables destroyed, 25% of country's crop area ravaged	Shumakov (1963) and Shamonin (1964)
1983	Uzbekistan	2500 ha of cotton	Gapparov (1988)
1993	Uzbekistan	2000 ha of cotton	Anonymous (1994)

consider the principal processes governing the species' population dynamics.

Factors favouring population increase

The habitats of *D. maroccanus* are restricted to the dry foothill zones receiving a mean of 300–500 mm of precipitation annually. Early spring rainfall is critical for the species to flourish, with the optimum being approximately 100 mm (Uvarov, 1957). Thus, a shortage in spring rainfall usually results in the increase of locust numbers (Zhdanov, 1934; Bei-Bienko, 1936; del Cañizo, 1942; Safarov, 1965). If this spring precipitation deficit continues for two or more consecutive years, a dramatic population upsurge, leading to an outbreak, takes place. According to Uvarov (1957), three major Moroccan locust plagues in the twentieth century in Spain were each preceded by 3–5 years of below average spring rainfall. Spring drought induces profound changes in vegetation cover, creating a characteristic mosaic pattern with patches of bare soil and short, tufty grasses (mostly *Poa bulbosa*), making the habitat very favourable for the Moroccan locust. Such a mosaic provides excellent conditions for oviposition (bare spots) and feeding (vegetation patches) assuring both survival and reproduction of the species (Uvarov, 1957, 1977).

Table 2. Maximum areas of annual Moroccan locust control in different countries (compiled from Latchininsky and Launois-Luong (1992)

Country	Year	Area treated (ha)
Uzbekistan	1984	651 600
Tajikistan	1933	330 692
Turkmenistan	1984	219 700
Azerbaijan	1964	199 800
Morocco[a]	1996	124 738
Kyrghyzstan	1980	100 000
Kazakhstan[b]	1993	290 000
Afghanistan	1960	52 456
Georgia	1965	11 774
Russia	1932	10 009

[a]Source: Anonymous (1996[b]).

[b]Source: Garkushenko and Evdokimov (1994).

The favourable 'ecometeorological background' is a necessary, but often insufficient, prerequisite for the process of outbreak formation of *D. maroccanus* (Latchininsky, 1992). A striking characteristic of the Moroccan locust is its close association with human agricultural activities, which have different, sometimes antithetical, implications for the species' population dynamics. It appears that, in various geographical zones, humans have created suitable habitats for the Moroccan locust. For example, deforestation and scrub destruction are held responsible for the species' spread in Algeria, Spain, Italy, the Balkans, Turkey and the Mediterranean islands (Uvarov, 1957). In Hungary, the drainage of the reed beds in the Pannonian Plain has created vast, dry grassland areas which were inhabited by swarms of the Moroccan locust starting from 1889 (Jablonowski, 1926). Similarly, the drainage of flood plains in 1927 resulted in the mass colonization of *D. maroccanus* in the Northern Caucasus (Zakharov, 1930).

Another type of human practice that increases Moroccan locust numbers is excessive grazing by domestic animals. The reduction of available grasslands due to expansion of croplands inevitably leads to a higher

Table 3. Dates of the most recent major outbreaks of *D. maroccanus* in some European countries

Country	Year	Reference
Russia (Crimea)	1923	Filipyev (1926)
Russia (Northern Caucasus)	1929–1931	Zhdanov (1934)
France (continental)	1917–1921	Vayssière (1921, 1923)
France (Corsica)	1943–1947	Blanck (1959)
Ex-Yugoslavia	1930–1933	Gradojević (1937, 1938)
Hungary	1948–1949	Nagy (1964)
Italy (continental)	1933–1937	Jannone (1934) and Paoli (1937)
Italy (Sardinia)	1932–1934	Melis (1934)
Bulgaria	1939–1940	Tchorbadjiev (1941)

degree of utilization in the remaining pastures, resulting in heavy overgrazing and trampling by cattle. Consequently, the once uniform and dense vegetation cover becomes fragmented, and the upper soil horizon compact and often bare, creating the ideal milieu for the Moroccan locust. The severely grazed grasslands become mosaic and provide the necessary conditions for locust concentration and gregarization. This is the initial link in a chain of events leading to an outbreak (Latchininsky, 1991). Such situations of overgrazing are very common throughout the entire distribution area of *D. maroccanus* (Uvarov, 1977). Moreover, in the southern parts of its range (North Africa and the Middle East), the Moroccan locust seems to be even more closely associated with humans, colonizing only the areas where the natural vegetation has been disturbed and become patchy. Such areas in the semi-desert are concentrated around human settlements and that is why *D. maroccanus* earned the name of *djerad-el-adami* ('man's locust') in Algeria (Pasquier, 1934). Similarly, the penetration of the Moroccan locust into the previously uninhabited arid areas of the Middle East usually follows the paths of the nomadic herders of cattle and sheep (Skaf, 1972). The infested areas can be very large, approximately 300 000 ha in Syria (1947) and 400 000 ha in Iraq (1948) (*l.c.*).

Table 4. Frequency and duration of outbreaks of *D. maroccanus* in some former Soviet Union countries in the twentieth century

Country	Outbreaks: start and duration (years)	References
Azerbaijan	1922 (3)	Filipyev (1926)
	1929 (4)	Predtetchensky *et al.* (1935)
	1960 (3)	Latchininsky and Launois-Luong (1992)
	1964 (3)	Latchininsky and Launois-Luong (1992)
	1975 (2)	Latchininsky and Launois-Luong (1992)
	1981 (3)	Latchininsky and Launois-Luong (1992)
Kazakhstan	1932 (2)	Predtetchensky *et al.* (1935)
	1956 (1)	Latchininsky and Launois-Luong (1992)
	1961 (2)	Latchininsky and Launois-Luong (1992)
	1979 (4)	Latchininsky and Launois-Luong (1992)
	1992 (2,	Garkushenko and Evdokimov (1994)
Uzbekistan	1901 (2)	Sïïazov (1912)
	1916 (1)	Plotnikov (1917)
	1931 (3)	Predtetchensky *et al.* (1935)
	1956 (5)	Latchininsky and Launois-Luong (1992)
	1967 (2)	Latchininsky and Launois-Luong (1992)
	1972 (3)	Latchininsky and Launois-Luong (1992)
	1982 (4)	Gapparov (1988)
	1992 (3)	F.A. Gapparov (personal communication)
Tajikistan	1916 (1)	Safarov (1965)
	1931 (3)	Predtetchensky *et al.* (1935)
	1956 (3)	Latchininsky and Launois-Luong (1992)
	1982 (4)	Latchininsky and Launois-Luong (1992)
Turkmenistan	1901 (3)	Tokgaev (1966)
	1915 (2)	Tokgaev (1966)
	1935 (2)	Predtetchensky (1936, 1937)
	1958 (4)	Tokgaev (1966)
	1983 (2)	Latchininsky and Launois-Luong (1992)

Finally, one more type of human activity can have a favourable impact on the Moroccan locust: wars. To be more precise, the consequences of war on the state of agriculture in the affected countries have been associated with locust outbreaks. According to Baranov (1925), the *D. maroccanus* plague in Montenegro (Yugoslavia) in the late 1910s was a direct result of the devastating effects of the First World War on the Balkans: fields abandoned and turned to fallow, agricultural equipment destroyed, etc. A similar situation was observed in the south of France which suffered an unprecedented Moroccan locust outbreak during approximately the same period (Vayssière, 1919, 1921, 1923). During and after the Second World War, severe Moroccan locust plagues ravaged Spain (Mendizábal, 1943; Moreno Márquez, 1944; del Cañizo and Moreno, 1949) and Corsica (Pasquier, 1947; Blanck, 1959; Bonflls, 1974). At the beginning of the 1990s, Tajikistan, a country undergoing military conflicts, experienced a major outbreak of *D. maroccanus*. Two main factors, the general collapse of agricultural activities and inability to conduct efficient phytosanitary measures, were responsible for the upsurges of pests in general and the Moroccan locust in particular, during and immediately after the war periods. To sum up, human impacts contribute greatly to the creation of the conditions leading to Moroccan locust plagues.

Factors limiting the Moroccan locust

The patchiness of the distribution of *D. maroccanus* suggests the locust's rather narrow ecological requirements. Indeed, this species is associated with one particular type of environment: an ecotonal zone between foothills and valleys, at a range of altitudes of 400–800 m above sea level. This zone is covered by a dry-steppe vegetation consisting of tufty, short grasses (*P. bulbosa*, *Cynodon dactylon*, *Hordeum murinum* and *Festuca* spp.), sedges (*Carex* spp.) and ephemeral spring forbs (*Alyssum desertorum*, *Medicago minima* etc.). Practically all descriptions of Moroccan locust habitats, no matter how far apart from one another, include the presence of *P. bulbosa*, the plant which provides food and shelter for the species (Zhdanov, 1934; Uvarov, 1957, 1977). This type of vegetation cover has only a limited distribution in the Mediterranean zone, restricting the Moroccan locust's habitats.

However, the soil type constitutes the most powerful limiting factor for the colonization of *D. maroccanus*. The females are known only to lay eggs into compact and undisturbed soil with a high clay content (Plotnikov, 1926; Moreno Márquez, 1943; Basu Choudhuri, 1956; Merton, 1959; Arias *et al.*, 1994, 1995). Ploughing appears to be catastrophic for the Moroccan locust (Latchininsky, 1993). As a side issue, this aspect of soil quality for oviposition makes laboratory rearing of the Moroccan locust extremely difficult. Turning formerly virgin land into a crop area makes it unsuitable for the insect's colonization. In many regions, intensive agricultural expansion (crop production) has caused the complete disappearance of the Moroccan locust. Thus, the formerly 'permanent' breeding areas in southern Russia, Ferghana Valley (Uzbekistan), continental Italy and many other regions have ceased to exist (Latchininsky and Launois-Luong, 1992). The impact of these local extirpations, particularly the possible loss of the genetic diversity within the species, remains uninvestigated.

Among the abiotic factors affecting the population dynamics of the Moroccan locust, the important role of weather (in particular spring rainfall) was discussed above. In general, deficient spring rainfall, modifying the vegetation cover, serves as a catalyst for the development of locust outbreaks. However, an excess of spring rainfall can be detrimental to the insect, provoking fungal epizootics which often cause wholesale mortality of eggs in the egg pods (Bei-Bienko, 1936). On the other hand, extreme drought in the spring can also be responsible for egg mortality from desiccation and nymphal mortality via food shortage (Plotnikov, 1917; Dempster, 1957). This was the case in 1917 when a major outbreak collapsed in Uzbekistan due to a severe spring drought and the Moroccan locust 'disappeared' from the region for several years (Plotnikov, 1926).

The regulatory role of biotic factors (natural enemies) in the population dynamics of *D. maroccanus* is difficult to estimate unambiguously. As this univoltine species spends up to 85% of its life cycle period in the embryonic stage (Fig. 2), some authors argue that egg predators (e.g. meloid or bombyliid larvae) and pathogens (e.g. *Fusarium* fungi) are the principal causes of dramatic reductions in locust numbers from one year to the next (Zakhvatkin, 1931; Bei-Bienko, 1936; Merton, 1959). However, in most parts of the Moroccan locust's range, the fungal pathogens are active only in wet years. During a population increase, which is usually associated with hot and dry weather, cases of fungal infections of the locust eggs are extremely rare. The nymphs and adults are prey for dozens of species of insects, birds, mammals and reptiles, but their activity seems to yield perceptible results only towards the end of an outbreak, accelerating its crash. During the pop-

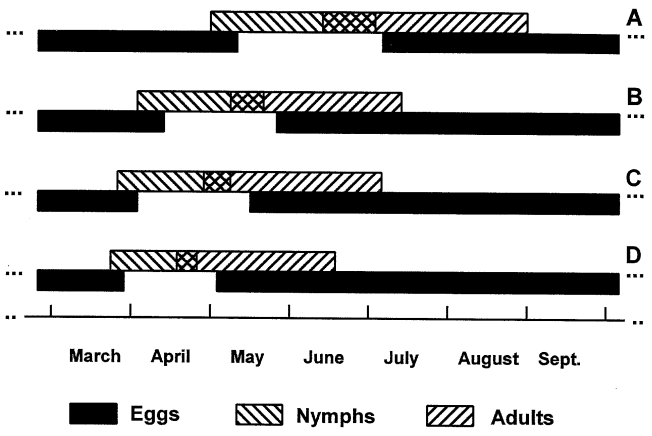

Figure 2. Annual developmental cycle of the Moroccan locust at different latitudes. (A) Northern Caucasus (45°N), (B) Azerbaijan (40°N), (C) Turkmenistan (38°N) and (D) Afghanistan (36°N).

ulation upsurge, the role of natural enemies is ordinarily recognized as negligible (Uvarov, 1977). However, Léonide (1969, 1983) argued that the action of parasitic flies (Nemestrinidae, Tachinidae and Sarcophagidae) might have been responsible for maintaining the Moroccan locust densities at low levels in the region of the La Crau steppe in southern France in the 1940s, while a severe outbreak was taking place in the adjacent continental zones and in Corsica (Delmas and Rambier, 1951, 1952; Pasquier *et al.* 1952). Attempts to introduce an egg predator native to continental Europe, the blister beetle *Mylabris variabilis* Pall., to control the Moroccan locust were undertaken in the late 1940s in Sardinia (Paoli and Boselli, 1947) and Corsica (Bonfils *et al.*, 1979). In as far as there have been no significant upsurges of *D. maroccanus* since these introductions, some authors contend that the programme was successful (Boselli, 1954; Crovetti, 1967), while others prefer to remain much more reserved in their conclusions (Bonfils *et al.*, 1979). If we accept the former, 'optimistic' point of view, the release and consequent acclimatization of *M. variabilis* in Sardinia (and probably in Corsica) constitutes the only case of the successful use of an insect biocontrol agent against the Moroccan locust.

As was previously pointed out, the impact of human agricultural practices can be both favourable (overgrazing) and disastrous (ploughing) for the species. It is necessary to add that according to my observations in central Asia, overgrazing is beneficial for the Moroccan locust only to a certain degree. Excessive grazing and trampling by cattle result in almost complete destruction of the locust's food plants and cause mechanical damage to the egg pods. In fact, *D. maroccanus* can serve as a bioindicator of the degree of grazing. If the locust disappears, the pasture is severely overgrazed and special measures to reverse the situation should be applied immediately (Latchininsky and Launois-Luong, 1992).

Finally, broad chemical control operations may also have an adverse impact on Moroccan locust populations. It is difficult to judge whether the treatments have been directly responsible for outbreak collapses, but, in many cases, they have helped to stop the spread of the plague and, probably, accelerated its end (Gapparov, 1988). Besides the necessity to act quickly, the challenge when controlling *D. maroccanus* can be illustrated by the fact that it possesses a high reproductive potential: each female lays a mean of three or four egg pods containing more than 30 eggs (Latchininsky and Launois-Luong, 1992). During outbreaks, the females tend to aggregate during oviposition. The egg-pod density is frequently 300–500 m^{-2}, with the maximum reaching 8000 (Siïazov, 1912). This is the second highest density among locusts after the Italian locust *Calliptamus italicus* (L.), which can lay up to 10 000 egg pods m^{-2} (Vasilyev, 1962). According to Plotnikov (1931), who based his calculations on a very moderate egg-pod density of 100 m^{-2} for the Moroccan locust, even 98% mortality during insecticidal control appears to be insufficient because the surviving 2% are capable of producing the same number of individuals in the following year! It is important to note that, frequently, the maximum areas are not treated in the year of an outbreak peak but rather in the next year, when the plague has already begun to collapse. This was the case in southern Russia and Azerbaijan in 1930–1932, in Afghanistan in 1958–1960 and in Uzbekistan in 1983–1984 (Latchininsky and Launois-Luong, 1992). In this respect, the human impact (control) is comparable to the action of natural enemies which are usually in a lag phase relative to their host's dynamics.

To summarize thus far, human activity appears to be the single most powerful factor governing contemporary Moroccan locust population dynamics. On the one hand, humans create new habitats for the species. On the other hand, we make environmenta1 conditions unsuitable for it and conduct extensive control operations. These conflicting sources represent the key elements in the evolution of the current situation of the Moroccan locust (Latchininsky, 1991, 1992, 1993). The question is, which tendency will prevail and what are the future prospects?

Moroccan locust at the threshold of the twenty-first century: contrasting scenarios

As climate plays an important role in the population dynamics of the Moroccan locust, it will be interesting to predict the influence of the global climatic trends (i.e. the predicted global warming) on the species' numbers and distribution. Although today it is difficult to predict in detail the possible effect of potential global warming on the Moroccan locust, I tend to agree with Nagy (1995) that its consequences are unlikely to be adverse for the species given its need for warm, dry conditions.

The current and future state of the Moroccan locust situation differs significantly depending on the geographical zone within its range. In southern France, although *D. maroccanus* constitutes a continued element of the acridid assemblages in the La Crau steppe near Marseille, it no longer produces the swarming phase (Foucart, 1997). The remaining habitats of the Moroccan locust are too fragmented and restricted for the species to gain the 'critical mass' of numbers and densities necessary to trigger an outbreak. Because of agricultural and industrial activities, the area that could be colonized by *D. maroccanus* and other acridids in the La Crau steppe has shrunk from 56 000 ha in the 1920s (Vayssière, 1923) to only 10 000 ha today (Foucart and Lecoq, 1996). Thus, habitat fragmentation and destruction, which, according to Samways (1997), constitute the two most powerful forces limiting the distribution of any Orthoptera species, are directly responsible for the current situation with the Moroccan locust in continental France. The probability of an outbreak caused by an indigenous population in this area is extremely low.

This situation is not the case for the Moroccan locust in Spain. Contrary to France where La Crau constitutes probably 'the last steppe in the country', in the south of Spain (Extremadura) there are still vast, continuous zones of native, dry grasslands available for colonization by the Moroccan locust. The outbreaks of the species persisted there through the 1980s and 1990s, demanding broad-scale chemical control interventions. For example, in 1983 the area treated to control *D. maroccanus* in Extremadura reached 130 657 ha (Arias *et al*., 1993), including approximately 60 000 ha in the Badajoz province alone, where the costs of its chemical control exceeded 90 million pesetas (US$600 000) (del Moral de la Vega, 1986). In 1992, of more than 373 000 ha surveyed in Extremadura, 113 600 ha were infested by the Moroccan locust. Chemical treatments were applied to 68 015 ha and the costs of the campaign exceeded 143 million pesetas (US$953 000) (Arias *et al*., 1993). The authors estimated forage losses to grassland at 836 million pesetas (US$5 573 000). Apparently, the Moroccan locust threat will persist in Spain in the near future.

This situation in turn is different from that of Hungary. In Hungary, after the appearance of *D. maroccannus* in the late 1880s, several outbreaks occurred in the Pannonian Plain, the last having taken place in 1948–1949 (Nagy, 1964). In the subsequent four decades, the Moroccan locust never produced swarms. In the course of extensive surveys, only one specimen was found between 1959 and 1988 (Nagy, 1988). According to Nagy (1990), two intertwined factors, the intensification of agriculture and the reduction of the available area of native pastures, were responsible for the situation in which a formerly important pest became a faunistic rarity. The further development of the Moroccan locust situation in Hungary seems to be particularly instructive. In 1991–1992, several scattered specimens were found and, in 1993, the species produced a restricted (several hundred hectares) but rather dense (up to 300 individuals m^{-2}) outbreak requiring the implementation of chemical control (Nagy, 1995). This 'unexpected' abrupt upsurge of the Moroccan locust is considered to be a consequence of anthropogenic and climatic factors. Current economic constraints in the country have resulted in an increase of fallow area and diminished pesticide use and recurrent droughts in the late 1980s and early 1990s combined to foster the locust build-up (Nagy, 1995).

Similar to Hungary, the Crimea and Northern Caucasus represent the northernmost periphery of the Moroccan locust's range. However, the situation in these regions differs from that in the Pannonian Plain. In the Crimea, the habitats of the Moroccan locust were restricted to a narrow steppe along the littoral zone in the southeastern part of the peninsula. The most severe outbreak took place in the 1920s, with a maximum of 3800 ha treated with poison baits in 1923 (Filipyev, 1926). The last chemical treatments in the region were applied in 1932 (311 ha). Afterwards, this 'permanent breeding area', which served as an important source for colonization of the Northern Caucasus by *D. maroccanus* (Zhdanov, 1934), virtually ceased to exist due to severe anthropogenic pressure (ploughing). Only very scattered specimens were captured there in the 1980s and early 1990s (Latchininsky and Launois-Luong, 1992). Some authors even paradoxically considered the Moroccan locust as a possible candidate for conservation in the Crimea (Woznessenskij, 1990). In the Northern Caucasus, the Moroccan locust tracked human

settlements approximately 200 years ago (Uvarov, 1957). The grazing of native *Stipa* steppe by domestic animals has caused its gradual substitution by a short grass plant association dominated by *P. bulbosa*. Consequently, a mosaic vegetation cover that is favourable for the locust has been established in a habitat previously uninhabited by the locust and from 1900 through to the 1930s, *D. maroccanus* produced several outbreaks (Zhdanov, 1934). Since then, according to Nikulin (1969, 1972), severe overgrazing of the remaining pasture areas has caused profound modifications in the vegetation (*Artemisia* spp. and other dicotyledonous weeds have replaced the grasses, including *P. bulbosa*). Consequently, *D. maroccanus* has given way to *Calliptamus barbarus* (Costa), a species that is much more ecologically plastic. Now the probability of a Moroccan locust outbreak in both the Crimea and Northern Caucasus is extremely low and the species is extremely scarce (Woznessenskij, 1990; Latchininsky, 1994; A.A. Nikulin, personal communication).

Nevertheless, the Moroccan locust still remains a pest in zones where continuous areas of arid grasslands are not subject to conversion into cropland or severely overgrazed. This is the case in Afghanistan, Iran, Algeria, Morocco, Uzbekistan and southern Kazakhstan where the pest infested more than 1 000 000 ha in 1993 (Latchininsky, 1994).

The dynamics of Moroccan locust populations provides some valuable insights into the role of anthropogenic factors in the bioecological conditioning of its pest status. In many regions, the necessary conditions for colonization of Moroccan locust have been created by various human activities: deforestation (southern Europe, Mediterranean islands), flood plain drainage (central Europe and the Northern Caucasus), expansion of sheep and cattle grazing zones into the desert (northern Africa and the Middle East) or overgrazing by domestic animals (central Asia and the Transcaucasus). On the other hand, human agricultural practices, including severe overgrazing and the increase of croplands through the reduction of grasslands, are responsible for the extirpation of the Moroccan locust via destruction of its habitats. At the periphery of the Moroccan locust's range, where the climatic conditions are at the limit of suitability (Hungary, the Crimea and the Northern Caucasus), the latter tendency prevails. The habitat changes are virtually irreversible and the insect has essentially lost its economic importance. However, I am far from predicting the fate of its North American 'brother-in-arms', the Rocky Mountain locust, *Melanoplus spretus* (Walsh), for the Moroccan locust. This one and only representative of the locust cohort in North America devastated agriculture in the second half of the nineteenth century, but then it became extinct at the beginning of the twentieth century, presumably under the pressure of increased human agricultural activities in its breeding zones (Lockwood and DeBrey, 1990). Because of its narrow ecological requirements, *D. maroccanus* may disappear from some regions losing unique local genotypes. At the same time, the locust may increase in outbreak frequency in habitats where its high biotic potential and flight capabilities serendipitously coincide with anthropogenic factors (recurrent droughts via global warming and weakening of anthropogenic pressure). The 'return' of the Moroccan locust in Hungary illustrates the lability of this dynamic situation: the period of the outbreak build-up took only three seasons (1991–1993) which is a remarkably short lapse of time for univoltine species. In regions such as North Africa and central Asia, the existing ecological and agricultural conditions assure the survival of large populations.

The parallel drawn earlier between the Moroccan locust and the North American wolves could be extended: neither of them are endangered on a continental basis, and their conservation is a matter of concern in satellite (versus core) areas, where high genetic diversity may still be important. At the same time in the core area, the Sword of Damocles, the menace of the Moroccan locust outbreaks, will apparently continue to jeopardize the fruits of agriculture: 'You will carry out seed for your fields in plenty, but you will harvest little; for the locusts will devour it' (Deuteronomy 28: 38). However, indeed, the land of humankind may necessitate modification of our biblical expectations.

Acknowledgements

This project was partially supported by the Société Entomologique de France through a Germaine Cousin Memorial Scholarship and the Orthopterists' Society (a grant from the research fund). I would like to thank the colleagues from the Entomology Section, University of Wyoming, Professors R. Pfadt, J. Lockwood, M. Brewer, D. Kazmer and D. Legg, as well as Dr W. Kemp, research leader of the USDA-ARS Laboratory in Logan, Utah for their critical comments and invaluable suggestions on the early draft of this paper. Special thanks is given to my wife Alla for the processing of the manuscript.

References

Anonymous (1982) *Locust and Grasshopper Agricultural Manual.* London: Centre for Overseas Pest Research.

Anonymous (1994) *Newsletter SAS* (Surveillance des Acridiens au Sahel). Montpellier: CIRAD-GERDAT-PRIFAS.

Anonymous (1996a) *Newsletter SAS* (Surveillance des Acridiens au Sahel). Montpellier: CIRAD-GERDAT-PRIFAS.

Anonymous (1996b) Newsletter SAS (Surveillance des Acridiens au Sahel). Montpellier: CIRAD-GERDAT-PRIFAS.

Arias, A., Alvez, C., García, F., Martinez de Velasco, D., Olivera, J., Prieto, A. and Santos, R. (1993) La lucha contra la langosta marroquí (*Dociostaurus maroccanus* Thunb.) en Extremadura durante el decenio 1983–1992. *Bol. San. Veg. Plagas* **19**, 425–53.

Arias, A., Sánchez, M., Jiménez, I., Santos, R. and Martínez de Velasco, D. (1994) Distribución en el suelo de las ootecas de *Dociostaurus maroccanus* (Thunb.) e importancia de su depredación en dos fincas de Extremadura. *Bol. San. Veg. Plagas* **20**, 3–22.

Arias, A., Jiménez, J., Santos, R. and Martínez de Velasco, D. (1995) Distribución de las ootecas de *Dociostaurus maroccanus* (Thunb.) en dos fincas langosteras de Extremadura (España). *Bol. San. Veg. Plagas* **21**, 261–76.

Baranov, N.I. (1925) Moroccan locust (*Dociostaurus maroccanus* Thunberg) in Montenegro. *Zastchita Rastenii* **1**(6), 217–218 (in Russian).

Basu Choudhuri, J.C. (1956) Observations on the oviposition behaviour of the Moroccan locust (*Dociostaurus maroccanus* Thnbg.) in Cyprus. *Saugar Univ. J.* **5**(2), 123–39.

Bei-Bienko, G.Ya. (1936) The distribution and zones of economic importance of the Moroccan locust (*Dociostaurus maroccanus* Thunb.) in USSR. *Itogi Nauchno-Issldovatelskih Rabot VIZR za 1935*, 16–20 (in Russian).

Ben Halima, T. (1983) Etude expérimentale de la niche trophique de *Dociostaurns maroccanus* (Thunberg, 1815) en phase solitaire au Maroc. Thèse de Docteur Ingénieur soutenue à l'Universite de Paris-Sud, Centre d'Orsay.

Blanck, A. (1959) Les invasions d'Orthoptères du Sud-Est de la France et de la Corse. *Phytiatrie-Phytopharmacie* **8**(14), 181–90.

Bonfils, J. (1974) Chroniques acridiennes – documents relatifs à un siècle de pullulations en Corse. *Bull. Sac. Hist. Nat. Corse* **612**, 46–64.

Bonfils, J., Brun, P. and Botella, L. (1979) Essai de lutte contre les acridiens nuisibles de la Corse par l'introduction de *Mylabris variabilis* Pall. (*Coleoptera, Meloidae*). *Bull. Sac. Sci. Hist. Nat. Corse* **632-3**, 93–102.

Boselli, F.B. (1954) Acclimatazione della *Mylabris variabilis* Pall., parassita del *Dociostaurus maroccanus* Thnb. introdotto in Sardegna nel 1946. *Boll. Sac. Entomol. Ital.* **LXXXIV**(7–8), 115–116.

Crovetti, A. (1967) L'acclimatazione della *Zonabris variabilis* Pall. (*Coleoptera, Meloidae) in* Sardegna 20 anni dopo la sua introduzione. *Redia* **50**, 121–131.

del Cañizo, J. (1942) La langosta y el clima. *Bol. Pat. Veg. Entomol. Agricul.* **II**, 179–200.

del Cañizo, J. and Moreno, V. (1949) Biología y ecología de la langosta mediterranea o marroquí (*Dociostaurus maroccanus* Thunb.). *Bol. Pat. Veg. Entomol. Agricult.* **17**, 209–42.

Delmas, R. and Rambier, A. (1951) Contribution à l'étude de la répartition du Criquet marocain (*Dociostaurus maroccanus* Thunb.) en France continentale. *CR Acad. Sci. Fr. Paris* **232**, 566–567.

Delmas, R. and Rambier, A (1952) Remarques sur l'activité grégaire du Criquet marocain en France, en 1951. *CR Acad. Agricult. Fr. Paris* **38**, 389–391.

Dempster, J.P. (1957) The population dynamics of the Moroccan locust (*Dociostaurus maroccanus* Thunb.) in Cyprus. *Anti-Locust Bull.* **27**, 1–4.

Doumandji-Mitiche, B., Doumandji, S. and Benfekih, L. (1993) Régime alimentaire du Criquet marocain *Dociostaurus maroccanus* (Thunberg, 1815), (Orthoptera, Acrididae) dans la région de Ain-Boucif (Médéa, Algérie). *Med. Fac. Landboouww. Univ. Gent* **58/2a**, 347–53.

Filipyev, I.N. (1926) Insects and other injurious animals in USSR in the years 1921–1924. The Acridids. *Trudy Po Prikladnoï Entomologii* **XIII**(2), 57–176 (in Russian with English summary).

Foucart, A. (1997) Inventaire et dynamique annuelle du peuplement acridien de la plaine de la Crau sèche (Bouches-du-Rhône, France) (Orthoptera, Acridoidea). *Bull. Soc. Entomol. Fr.* **102**(1), 77–87.

Foucart, A. and Lecoq, M. (1996) Biologie et dynamique des populations de *Prionotropis hystrix rhodanica* Uvarov, 1923 dans la plaine de la Crau (France) (Orthoptera, Pamphagidae). *Bull. Soc. Entomol. Fr.* **101**(1), 75–87.

Gapparov, F.A. (1988) *The biological and toxicological foundations of locust control in Uzbekistan.* PhD thesis (cand.), VIZR, Leningrad (in Russian).

Garkushenko, V.M. and Evdokimov, N.Y. (1994) The acridid pests in Kazakhistan. *Zastchita rastenii* **1**, 31 (in Russian).

Gradojević, M. (1937) Compte rendu sur la dernière lutte contre le Criquet marocain en Yougoslavie, 1933. In *CR de 1a JV Conférence Internationale pour les Recherches Antiacridiennes*, pp. 1–8. Bulaq: Government Press, Le Caire.

Gradojević, M. (1938) Rapport sur la situation acridienne et l'organisation antiacridienne en Yougoslavie. In *CR de la V Conférence Internationale pour les Recherches Antiacridiennes*, pp. 186–189. Bruxelles: Ministère des Colonies, Royaume de Belgique.

Jablonowski, J. (1926) Ungarns Heuschreckengefahr emst und jetzt. eine entomologisch-biologische Skizze. *III Internat. Entomol. Kongr. Zurich. 1925* **2**, 377–88.

Jannone, G. (1934) Osservazioni ecologiche e biologiche sul

Dociostaurus maroccanus Thunb., *Calliptamus italicus* L. e loro parassiti in Provincla di Napoli (Primo Contributo). *Boll. Lab. Zool. Portici.* **28**, 75–151.

Kritsky, (1997) The insects and other arthropods of the Bible, the New Revised Version. *Am. Entomol.* **44**(3), 183–188.

Latchininsky, A.V. (1991) Forecasting of the Moroccan locust *Dociostaurus maroccanus* (Thunb.) outbreaks in the USSR. In *XIIIth International Plant Protection Congress*. Rio de Janeiro.

Latchininsky, A.V. (1992) Ecology and forecast of the Moroccan locust *Dociostaurus maroccanus* (Thunb.) in the USSR. In *Proceedings of the XIXth International Congress of Entomology*, p. 167. Beijing.

Latchininsky, A.V. (1993) Survival strategies of Moroccan locust *Dociostaurus maroccanus* (Thunberg, 1815) in different parts of its range: an ecotonal aspect. *Metaleptea* **14**(3), 12–13.

Latchininsky, A.V. (1994) Moroccan locust *Dociostaurus maroccanus* (Thunberg, 1815) (Orthoptera: Acrididae): a faunistic rarity or an important pest? In *Fifth European Congress of Entomology*, p. 283. York.

Latchininsky, A.V. and Launois-Luong, M.H. (1992) Le Criquet marocain, *Dociostaurus maroceanus* (Thunberg, 1815), dans la partie orientale de son aire de distribution. Etude monographique relative à l'ex-URSS et aux pays proches. Montpellier: CIRAD-GERDAT-PRIFAS/Saint-Pétersbourg: VIZR.

Léonide, J.C. (1969) Recherches sur la biologie de divers Diptères endoparasites d'Orthoptères. *Mém. Mus. Nat. Hist. Nat., NS, Sér. A., Zool.* **53**, 1–246.

Léonide, J.C. (1983) Richesse et intérêt du foyer acridien grégarigene et du foyer parasitogène acridiophage de la Crau. *Biologie-Ecologie Méditerrnnéenne* **X**(1–2), 145–54.

Lockwood, J.A. and DeBrey, L.D. (1990) A solution for the sudden and unexplained extinction of the Rocky Mountain grasshopper (Orthoptera: Acrididae). *Env. Entomol.* **19**(5), 1194–205.

Melis, A. (1934) Il grillastro crociato (*Dociostaurus maroccanus* Thunb.) e le sue infestazioni in Sardegna. *Atti Accad. Georgof. Firenze* **30**, 399–504.

Mendizábal, M. (1943) Datas sobre la plaga da langosta en la provincia de Alméria. *Bol. Pat. Veg. Entomol. Agricult.* **12**, 285–93.

Merton, L.F.H. (1959) Studies in the ecology of the Moroccan locust (*Dociostaurus maroccanus* Thunberg) in Cyprus. *Anti-Locust Bull. 34*, 1–123.

del Moral de la Vega, J. (1986) Discusión sobre la situación actual de la plaga de langosta (*Dociostaurus maroccanus* Thunb.) en Badajoz y resultados de un ensayo de insecticidas para su control. *Bol San. Veg. Plagas* **12**, 221–35.

Moreno Márquez, V. (1943) Observaciones sobre la oviposición de *Dociostaurus maroccanus* (Thunb.). In *Servicio de lucha contra la langosta.*

Moreno Márquez, V. (1944) Zonas permanentes de langosta en España: Buceto ecologico de la Serena. *Bol. Pat. Veg. Ent. Agricult.* **13**, 335–76.

Nagy, B. (1964) Data on the occurrence and habitat of the Moroccan locust (*Dociostaurus maroccanus* Thunb.) in Hungary. *Ann. Inst. Prot. Plant. Hung.* **9**, 263–299.

Nagy, B. (1988) Hundred years of the Moroccan locust in Hungary. *Növényvédelem (Budapest)* **24**, 536–540.

Nagy, B. (1990) A hundred years of the Moroccan locust, *Dociostaurus maroccanus* Thunberg, in the Carpathian Basin. *Bol. San. Veg. Plagas* **20**, 67–74.

Nagy, B. (1995) Are locust outbreaks a real danger in the Carpathian Basin in the near future? *Orthop. Res.* **4**, 143–146.

Nikulin, A.A. (1969) A review of the orthopteroid insects (Orthopteroidea) of the Central and Eastern Caucasus. *Entomologicheskoe Obozrenie* **48**(4), 774–86 (in Russian).

Nikulin, A.A. (1972) The acridids and other orthopteroids of the Central and Eastern Caucasus. PhD thesis (cand.), VIZR: Leningrad (in Russian).

Paoli, G. (1937) Studi sulle Cavallette di Foggla (*Dociostaurus maroccanus* Thnb.) e sui loro oofagi (Ditteri Bombiliidi e Coleotteri Meloidi) ed Acari ectofagi (Entreidi e Trombidiidi). *Redia* **23**, 27–206.

Paoli, G. and Boselli, F. (1947) Introduzione di oofagi del *Dociostaurus maroccanus* Thunb. dalle peninsola italiana in Sardegna,. *Mem. Soc. Entomol. Ital.* **26** (Suppl.), 21–40.

Pasquier, R. (1934) Contribution à l'étude du Criquet marocain, *Dociostaurus maroccanus* Thunb., en Afrique mineure (Ire note). *Bull. Soc. Hist. Nat. Afrique du Nord* **XXV**(3), 167–200.

Pasquier, R. (1947) Les acridiens en 1947. *'Agria', Bull. Mens. Assoc. Anc. Éleves de l'Inst. Agron. Algérie* **124**, 161–73.

Pasquier, R., Colonna-Césari, X. and Bonfils, J. (1952) Sur la détermination des regions grégarigènes du Criquet marocain, *Dociostaurus maroccanus* Thunb., en Corse. *CR Hebd. Séanc. Acad. Sci.* **235**, 1157–9.

Plotnikov, V.I. (1917) *Report of the Technical Director of Locust Control in the Tashkent Region in 1917*. Tashkent: Turkestanskaya Entomologicheskaya Stantsiya (in Russian).

Plotnikov, V.I. (1926) *Insect Pests of Agriculture in Central Asia.* Tashkent: UZOSTAZRA (in Russian).

Plotnikov, V.I. (1931) The increase in the area occupied by a hopper band of the Moroccan locust, and the rate of its control. *Trudy Sredneaziatskogo Instituta Zastchity Rasteniï (SAIZR)* **25**, 1–11 (in Russian).

Predtetchensky, S.A. (1936) The injurious acridids in the zone of cotton production in the USSR in 1935. In *Principal Agricultural Pests in the USSR in 1935*, pp. 172–87. Leningrad: VIZR (in Russian).

Predtetchensky, S.A. (1937) Gregarious locusts. In *Review of the Development of the Principal Agricultural Pests in 1936*, pp. 28–39. Leningrad: VIZR (in Russian).

Predtetchensky, S A., Zhdanov, S.P. and Popova, A.A. (1935) The injurious acridids in USSR. Review of the years 1925–1933. *Trudy Po Zastchite Rasteniï Ser. I (Entomol.)* **18**, 1–167 (in Russian with English summary).

Rooke, H.G.D. (1930) Notes on locusts in Iraq and control measures adopted. *Mem. Dept. Agricult. Iraq* **13**, 1–13.

Safarov, A.A. (1965) Moroccan locust (*Dociostaums marocca-nus* Thunb.) in the republics of central Asia. Ecology, current state of the breeding areas, principles of control. PhD thesis ceand.), VIZR: Leningrad (in Russian).

Samways, M.J. (1997) Conservation biology of Orthoptera. In *The Bionomics of Grasshoppers, Katydids and their Kin* (S.K. Gangwere, M.C. Muralirangan and Meera Muralirangan, eds), pp. 481–96. Wallingford, New York: CAB International.

Sergeev, M.O. (1986) *Principles of the distribution of the Orthopteroid Insects in N. Asia.* Novosibirsk: Nauka (in Russian).

Shamonin, M.O. (1964) *Moroccan and desert locusts in Afghanistan.* PhD thesis (cand.), VIZR: Leningrad (in Russian).

Shumakov, E.M. (1963) The acridids of Iran and Afghanistan. *Trudy Vsesoyuznogo Entomologicheskogo Obstchestva* **49**, 1–248 (in Russian).

Sïïazov, M.M. (1912) *Control of Locusts in Turkestan.* Tashkent: Izdanie Departamenta Zemledeliya (in Russian).

Skaf, R. (1972) Le Criquet marocain au Proche-Orient et sa grégarisation sous l'influence de l'homme. *Bull. Soc. Ecol.* **III**(3), 247–325.

Soltani, A.A. (1976) A taxonomic revision of the genus *Dociostaurus* (Acrididae: Acridoidea, Gomphocerinae). *Entomol. Phytopathol. Appl.* **40**, 118.

Tarbinsky, S.P. (1932) On the question of phase variability among locusts. *Bull. Lenigradskogo Instituta Borby s Vrediteliami v Selskom i Lesnom Khozyaïstve* **3**, 303–20 (in Russian).

Tchorbadjiev, P. (1941) *Moroccan and Italian Locusts and their Control.* Sofia (in Bulgarian).

Thunberg, C.P. (1815) Hemipterorum maxillosorum genera illustrata, plurimisque novis speciebus ditata ac descripta. *Mémoires de l'Académie Impériale des Sciences de Saint-Pétersbourg* **V**, 211–301.

Tokgaev, T. (1966) *Moroccan Locust in Turkmenia.* Ashkhabad: Turkmenistan (in Russian).

Tokgaev, T. (1973) *Fauna and Ecology of Acridids in Turkmenia.* Ashkhabad: Ylym (in Russian).

Tsyplenkov, E.P. (1970) *Harmful Acridoidea of the USSR.* Leningrad: Kolos (in Russian, English translation in 1978 by Amerind Publishing Co.: New Delhi/Bombay).

Uvarov, B.P. (1957) The aridity factor in the ecology of locusts and grasshoppers of the Old World. In *Arid Zone Research VIII. Human and animal ecology. Reviews of research*, pp. 164–98. Paris: UNESCO.

Uvarov, B.P. (1977) *Grasshoppers and Locusts. A handbook of general acridology. Vol. II: Behaviour, ecology, biogeography population dynamics.* London: Centre for Overseas Pest Research.

Vasilyev, K.A. (1962) The Italian locust, *Calliptamus italicus*, in Central Kazakhstan. *Trudy Nauchno-Issled. Inst. Zastchity Rasteniï (Alma-Ata)* **7**, 123–90 (in Russian).

Vayssière, P. (1919) Observations biologiques sur *Dociostaurus maroccanus*, en Crau. *Bull. Soc. Zool. Fr.* **44**, 359–363.

Vayssière, P. (1921) La lutte contre le Criquet marocain (*Dociostaurus maroccanus* Thunb.) en Crau en 1920. *Ann. Epiphyties* **7**, 117–167.

Vayssière, P. (1923) Les Acridiens en France en 1921–1922. *Ann. Epiphyties* **9**, 73–83.

Woznessenskij, A.Yu. (1990) About the status of several acridids of the Crimea. In *CR Stud. and Young Res. Conf. Inst. Agric. of Leningrad*, pp. 62–63. Leningrad: LSKHI (in Russian).

Zakharov, L.Z. (1930) Draining of the Azov reed-beds and the locust problem in the Kuban region. *Izvestiya Sev.-Kavkaz. Kraevoï STAZR* **5**, 97–104 (in Russian).

Zakhvatkin, A.A. (1931) Parasites and hyperparasites of the egg-pods of injurious locusts (Acridoidea) of Turkestan. *Bull. Entomol. Res.* **22**, 385–91.

Zhdanov, S.P. (1934) Moroccan locust (*Dociostaurus maroccanus* Thunb.) in the Stavropol region. *Trudy po Zastchite Rasteniï. Ser. I (Entomol.)* **9**, 3–51 (in Russian with English summary).