CLIMATIC DETERMINATION OF SYNANTHROPIC PEST ARTHROPOD PERFORMANCE: SPECIES RICHNESS, PESTICIDE RESISTANCE, AND CONTROL STRATEGIES

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Abstract - This review concerns aspects of climatic and microclimatic effects on biology and pest status of synanthropic pest species. The number of medical and synanthropic pest species in an area parallels overall species richness and the pest faunas of tropics and subtropics are more abundant than the fauna of temperate regions. The richer is the fauna of pest species the greater is probability of appearance of a "key pest". The increased species richness is not necessarily correlated with overall pest damage, however, it requires greater complexity of control measures. The length of season favorable for performance of pest species increases as one moves from temperate zone to tropics. As a consequence, generation time of pest species decreases and the importance (pest status) of key species increases. Global increase of temperature may spread the area of high pest importance towards the North/South. Microclimatic changes associated with human activity already influence pest status and distribution of many species and proceeding urbanization spread convenient conditions nearly worldwide. Climatization of buildings may even change the timing of pest activity making winter period more convenient for pest breeding than the summer and set out of phase the dynamics of indoor and outdoor pests. Decreasing efficiency of chemical control increases the importance biological methods and baits. The frequency of insecticide resistant populations of medical and stored product pests is greatest in tropical and subtropical regions. The zone of highest frequency of origin of resistant strains of medical pests is between 20 - 40° latitude. This is the area of maximum conflict between temperature-driven speed of pest population growth and human effort to protect the resources from animal competitors. Climatic change may shift the boundary of this zone northwards.

Key words - Temperature, seasonality, microclimate, voltinism, overwintering

INTRODUCTION

Climatic conditions, particularly temperature, have a prominent effect on distribution and performance of exotherm populations. In this paper we review the importance of climatic factors for populations of synanthropic pests some of which live in artificial "environments" where temperature may largely differ from outside. We consider four aspects of pest biology: 1) species distribution, 2) development rate and seasonality, 3) factors of the magnitude of inflicted damage, and 4) selection of pesticide resistant strains.

Is species richness in the tropics correlated with numbers of synanthropic pest species?

The overall species richness is greatest in the tropics and decreases as one moves towards the poles. Although this general trend cannot be explained by any generally accepted theory (Begon *et al.*, 1980; Clarke, 1998) it may be established in many taxonomic groups of terrestrial and marine animals. The numbers of ant species provide a good example as they decrease from equator towards 70° N or 50° S (Kusnetzov, 1958). South-north gradient of species richness was observed also in structure-infesting synanthropic ants in the USA (Hedges, 1992); about 40% of the species is limited to southern regions, and about 44% occurs nationwide and only about 15% is typical for northern regions. The number and importance of serious ant pests also increases towards the South. Above 40° N about 5 species of ants are considered as serious pests. Interestingly, *Monomorium pharaonis*, a key pest of buildings at similar latitudes in Europe is not important in the USA. Southern regions are plagued by total 16 serious pest ant, including biting ants (e.g. *Solenopsis* spp.). The discomfort from ant presence is maximum in Florida and California (Josof, 1998).

The total number of mosquito species increases as one moves from temperate regions toward the tropics and the greater richness correlates with the number of plague species (Fig. 1). Similar geograph-

ic trend could be established also for other important medical pests (Fig. 1). A different trend could be established in Simuliidae with mainly temperate distribution, and in human body parasites (e.g. Cimicidae and Anoplura) which are relatively independent of climate and evenly distributed in tropical and temperate regions. Difference in numbers of tropical species and cosmopolitan species with largely tropical origin vs. species typical for temperate zone is conspicuous also in stored product pests (Fig. 2). Moreover, a large proportion of cosmopolitan eusynanthropic house pests (*Musca domestica, Drosophila* spp.*, Blattella germanica, Supella longipalpa, Monomorium pharaonis, Tapinoma melanocephalum, Linepithema humile, Coptotermes* spp.*)* and primary stored product pests (e.g. *Plodia* sp.*, Tribolium* sp.*, Rhyzopertha* sp.*, Prostephanus* sp.) is, certainly or probably, of tropical or subtropical origin (Klausnitzer, 1988; Robinson, 1996). Synanthropy of some species probably originated in ancient centers of human civilization, the Mediterranean and Near East regions (*Sitophilus granarius, Lepisma saccharina, Acheta domestica*).
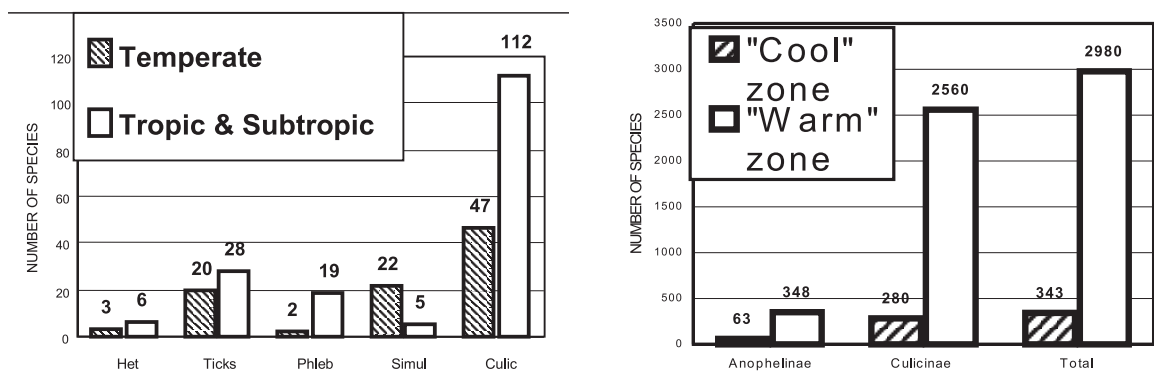

Figure 1. Species richness in selected groups of important synanthropic pests in "cold" and "warm" climatic areas of the World. Above: Numbers of Culicidae mosquito species in Holarctic Region ("cool zone") and Afrotropic, Australian, Neotropic and Oriental Regions ("warm zone"). Below: Numbers of bugs *Heteroptera* (Het), ticks *Ixodidae* and *Argasidae* (Ticks), *Phlebotomidae* (Phleb), *Simuliidae* (Simul) and mosquitoes *Culicidae* (Culic) with medical importance in tropical and subtropical (below 40o N or S) vs. temperate zone. Data recalculated from Rosický and Daniel (1989) and Kettle (1984).

These lists, although incomplete, demonstrate the increase of species richness of synanthropic pest species when approaching warm, particularly tropical regions. This difference is in concert with theoretical expectations. The rich tropical communities provide greater pool of species convenient for "synanthropization", i.e. species with convenient pre-adaptation. The theory (Lawton and Strong, 1981) will predict that a suddenly emerged "scene" (synanthropic habitats in this case) provides a rich palette of "parts" but is short of "actors". In most cases, rich tropical communities may offer more "actors", potentially pre-adapted species, than relatively poor communities of temperate regions.

An important component of the synanthrohpic pre-adaptation may be a convenient developmental response to temperature. Tropical species have generally higher "development threshold" and a lower "sum of effective temperatures" required to complete the development of a particular stage. At a high temperature the combination of these characteristics enables a species to develop faster than a cold-adapted species with contrary characteristics, low "development threshold" and high "sum of effective temperatures" (Honěk and Kocourek, 1990; Honěk, 1996a). Many eusynanthropic pests, particularly stored product pests, have development requirements similar to other species of the tropics from where they originate (Honěk, 1996b) (Fig.3.).

Key species, socioeconomic factors and pest status

Samways (1996) pointed out that "warm climates present more formidable pest control challenges than temperate ones, partly because there are more opportunistic species in the tropics and also because
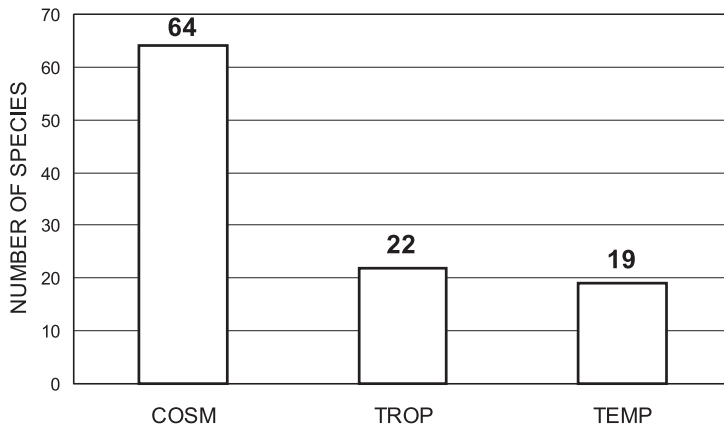
Figure 2. Geographic distribution of pest stored product beetles. The species limited to temperate zone (TEMP) are less numerous than species with exclusively tropical distribution (TROP) and cosmopolitan species (COSM) also largely of tropical origin. Data from Sinha and Walters (1981)

buildings are leakier to the outside environment. It then follows from the last points that there is relatively rich fauna in tropical buildings, in stark contrast to the situation in temperate lands." Of course, the magnitude of problems cannot be measured only by pest species richness. Climate itself may affect the magnitude of pest problems. The damage caused by stored product pests in tropics are much greater (5-30%) than in temperate regions (1-3%) although numbers of pest species that contribute to the total damage are similar. However, the extent of inflicted harm may be determined by one or a few key species with particular population dynamics (e.g. temporary mass appearance of mosquitoes or ticks) or particular economic or epidemiological significance. According to the review of Rosický and Daniel (1989), the number of epidemiologically important species of mosquito born arboviruses is only slightly
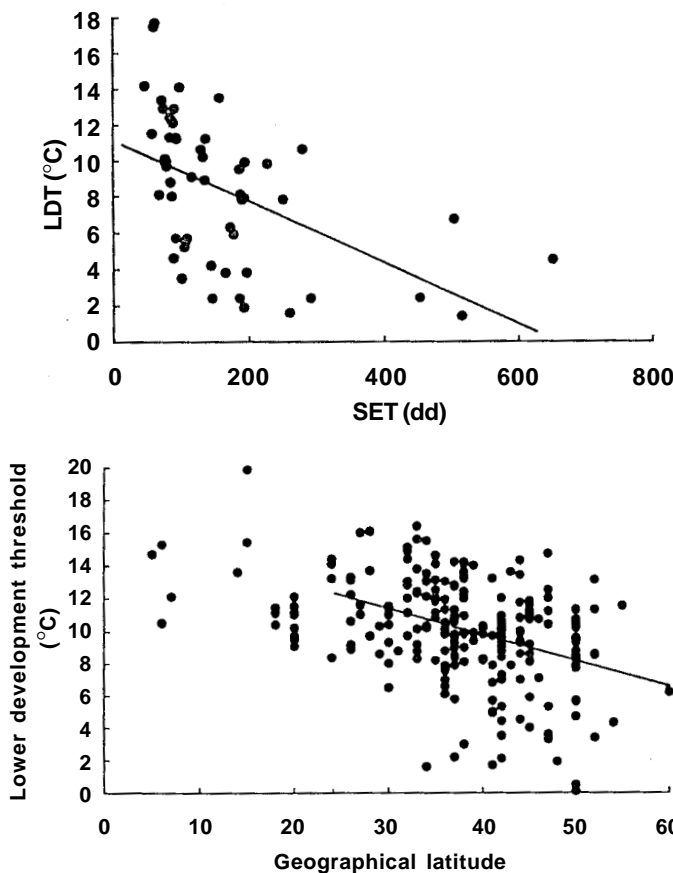

Figure 3. Above: The negative relationship between sum of effective temperatures (SET, day degrees dd) and lower development threshold (LDT, degrees C) for total pre adult development of Diptera species. Each point stands for one population for which temperature requirements were established and some species are represented by several points. Below: The relationship between development threshold (LDT) for egg development of popula-tions of insect species (all taxonomic groups pooled) and geographic origin (degree N or S latitude) of the population for which temperature requirements were established. No trend could be established in the tropics, the trend for subtropic and temperate regions (above 23°N or S) is indicated by regression line. From Honěk (1996a, b).

higher in tropics than in temperate regions although the total number of mosquito species is much greater in the tropics. However, the importance of diseases spread by the mosquitoes and resulting human mortality are greater in tropics than temperate regions considerably (Gratz, 1988). In 1989, malaria killed about 1 million children victims, only in Africa. And about 2.1 billion people of the tropic regions are permanently endangered by this plague (Šerý, 1993). Poisonous arthropod species whose importance is negligible in temperate zone have a considerable importance in the tropics. Scorpion stings are followed by 10-60% mortality, spider stings by 0.5-5% mortality (Šerý, 1993). Forty people die every year in consequence of hymenopteran stings in the USA (Chipps *et al.*, 1980), the figures from tropics are not known but certainly higher. A "key pest effect", socioeconomic conditions and geographic region where the species appear are also of importance. An example may be the disproportion between a total annual damage of ca. 1 billion USD caused by 5 termite species in the USA, and annual damage of only about 100 million USD inflicted by nearly 20 termite species in Australia (Robinson, 1996).

Pest control complexity

Although greater species richness should not be inevitably followed by greater pest problems it presents a strong challenge for pest control. The complexity of protection increases, particularly when "species-specific" advanced strategies like integrated pest management, target or site-specific pest control are used. With increasing species richness increases the difficulty and price of decision making (pest identification and monitoring, planning specific control strategies), needs for qualified staff and risks of pest misidentification resulting in improper control measures. With decreasing latitude "pest control complexity" increases. Under current economic situation of developing countries of tropics and subtropics the increase of pest control complexity is inversely proportionate to availability of means and qualified personage (Youdowei, 1983). This disproportion is aggravated by massive use of cheap and non-selective pesticides which are thought to compensate for pest species determination and monitoring. Combined effect of several factors contribute to often problematic results of pest control in poor countries of the Third World (Gratz, 1988).

The consequences of increasing pest control complexity may be demonstrated also in developed countries. In central and northern Europe, buildings are usually populated, besides stored product pests and Diptera, by only 5-10 species of synanthropic arthropods. Decision making in professional pest control does not require special erudition as distinguishing the key pest species and adopting convenient control is relatively simple. The situation changes already in warm temperate or subtropic conditions, e.g. at the south of the USA where there are 20-50 regularly occurring synanthropic species, ants, cockroaches, fleas, termites etc. (Bennet *et al.* 1988; Hedges, 1992; Robinson, 1998). Structure infesting ants are a rich taxonomic group uneasy to determine into the species. At the same time ants are the most important structure-inhabiting insects (Josof, 1998). "Ant like ant" control strategy is often inefficient (Katz, 1998) since the ant species have different feeding and nesting behaviour and require different control technology. In developed countries, wrong determination and related failures of control do not result from general poverty or lack of specialized education, but from pressure on decreasing control costs. The one way of decreasing risks issuing from increased PCC and pest species richness is using "ecological" and target multi-species strategy, e.g. multi-species attractive baits which were already developed for ants (Williams *et al.*, 1998). Most advanced "multi target and ecological strategy" represent bait box constructed to contain baits for several species of pests (ants, cockroaches, termites), e.g. Perimeter Patrol System (B & G Equipment) (Smith, 1998).

Change of global climate and pest status

Pest status means a complex evaluation of the risks of presence of a given species. Pest status of a species varies with climatic conditions. This was already demonstrated for ants of northern and southern USA. Termites (Mampe, 1990) and stored product pests of North America (Cuperus *et al.*, 1993) provide another example of changing PS exhibiting strong north- south gradient. In stored product pests

pest status is related to the number of generations completed by a species in a particular area. In temperate regions this figure may vary annually (Wood *et al.*, 1997).

The point we would like to stress here is that pest status not only may be slightly affected by annual climatic variation. Dramatic consequences may follow the long-term global climatic change. The Intergovernmental Panel on Climatic Change (IPCC) presented several scenarios of global warming according to which air temperatures will increase by 1 °C (emission scenario IS92c), 2 °C (e.s. IS92a) or 3.5 °C (e.s. IS92e), by 2100. Since development time of multivoltine pest species is determined by temperature we may predict the spread of pest importance following global warming. The increase of importance of a pest species consist in increasing the number of generations which the species is able to complete annually. This process was simulated by Yamamura and Kiritani (1998), other programs (GISS, CLIMEX) are available for agriculture (Sutherst and Maywald, 1991). Climatic change may influence also medical pests and facilitate spread of diseases into territories where they were not known previously. Thus Reeves *et al.* (1994) predicted that 3 - 5 °C temperature increase will cause, in the USA, a significant northwards spread in two arboviral encephalitis transmitted by *Culex* spp. (Western Equine Encephalitis, St. Louis Encephalitis). However, the spread of areas of vector distribution should not always have dramatic consequences. Takkenn *et al.* (1994) presented a model of climatic limitation of geographic distribution of *Anopheles maculipennis*. He concluded that even if geographic distribution will extend considerably the risk of renewed malaria transmission in Europe is low, due to high standard of living and easy access to medical care. Further evidence and examples may be found in an excellent review on consequences of climatic change on emerging diseases by Patz *et al.* (1996). Horizontal (competition) and vertical factors (hosts, predators, pathogens) affect the outcome of climatic change whose effect thus cannot be predicted only from studies of temperature relationship of a species (Yamamura and Kiritani, 1998).

Important may be also the consequences of increasing climatic instability which might accompany climatic change. The catastrophic events may facilitate temporal outbreak of pests. An example may be a mosquito calamity in central Europe which followed local floods (Rettich and Ryba, 1998). Extreme rainfalls were correlated also with outbreaks of arthropod born diseases, Murray Valley Encephalitis and Ross River Virus in Australia, Eastern equine encephalitis in the USA, West Nile fewer in southeastern Africa, cyclical malaria epidemics in Argentina and Pakistan (Patz *et al.*, 1996). These changes have corresponded with El Nino Southern Oscillation (ENSO).

Anthropogenous microclimates facilitate the spreadof arthropods and change their pest status

It is well known that microclimate (e.g. climatic conditions near the ground level) may dramatically differ from climatic data measured by standard meteorological procedures. Due to solar radiation and radiation of Earth surface temperatures of solid surfaces may differ from standard meteorological records (taken at 2 m above ground surface) by several degrees. The microclimate is varied by human activities and may affect distribution and abundance of pest species is less appreciated. The large cities represent "microclimatic islands" where average temperatures are higher, by several degrees, than in the surrounding landscape (Klausnitzer, 1998). The main reason of the temperature increase is reduced evaporative cooling caused by drainage of water and covering of large proportion of ground surface with water impermeable pavements (L. Nemec, pers. comm.). A number of thermophilic pests colonized these man-made thermal "islands" scattered in the cold temperate zones (Frankie, 1978; Klausnitzer, 1988).

The arthropods use also other localized sources of heat. Several species including *Blattella germanica* (Stein and Haschemi, 1987) and *Monomorium pharaonis* (Kohn and Vlèek, 1986) make use of increased temperature of waste dumps for survival of winter period "in the open". In stocks of stored small-grain cereals primary beetle pests aggregate in response to pheromones. This often results in local increase of temperature by 20-40 °C, as a consequence of accumulation of insect metabolic heat and growth of saprophytic microorganisms (Sinha and Wallace, 1966). Stored product pests make

full use of these thermal sources. This behaviour may cause a significant increase the area where tropical pest species, e.g. *Rhyzopertha dominica* (Stejskal *et al.*, 1999), may overwinter.

The heated structures are classical places of survival of thermophilic species. Synanthropic flies become increasingly dependent on buildings as one proceeds towards the North (Nuorteva , 1963). In the 19th century, pioneer populations of several pest species now generally associated with human dwellings (*Monomorium* spp*., Linepithema* spp*., Periplaneta* spp.), started their spread over European cities from glasshouses, which were, at that time, the only structures with warm and stable annual environment. The most revolutionary factor of their further spread was constructing of large complexes of buildings with central heating and especially use of climatization, during the last 60 years. Central heating has dramatically supported the spread of *Monomorium pharaonis* (Rupeš, 1998) and *Blattella germanica* (Stejskal and Verner, 1996) in Europe observed since the mid 20th century. Also a mosquito, *Culex pipiens molestus*, was able colonize the distributions of warm water and breed there continuosly all-year round. Now this species plagues the inhabitants of centrally heated buildings, not only in central Europe (Rettich, 1983) but also in cool Ural mountains (Nikolaeva, 1994).

Climatised buildings represent an extreme case of isolated microclimatic environment where, in cold temperate zone, ambient temperature may be higher during the winter than in the summer. This may result in a "reversed population dynamics" of pest species, a seasonal annual fluctuation of abundance which is out of phase with seasonal fluctuation of the weather in the open, schematically outlined in Fig. 4. In cold areas of Europe, population growth, swarming, foraging activity and pest problems with invading species of "garden" ants (*Lasius* spp*., Tetramorium* spp*.)* are strictly associated with the vegetation season. By contrast, structure-inhabiting pharaoh ant , *Monomorium pharaonis,* has usually its major population peak during the winter (Boase, 1992; Rupeš *et al.*, 1997). Only in warm years a small peak occurs during the summer when, however, the pharaoh ant's populations do not aggregate in the insides of buildings (V. Rupeš, pers. comm.). Also annual variation of abundance of *Blattella germanica* may be reverted by climatization. In Virginia, USA (Robinson, 1996), the period of its peak occurrence are summer months. In a cooler climate of the Czech Republic, however, the population peak in a climatised building could be shifted to December - February (Stejskal, unpubl.), as a consequence of summer cooling and winter heating.

Some species, usually not considered "pests" use buildings and non-heated shelters for overwintering. Providing the hibernacula may spread northwards the geographic area of the species of hemipteran genera *Rhyparochromus, Gastrodes* and *Lygeus* in Europe (Štys, 1996). Conspicuous synanthropic overwintering of hemipteran bugs was described also from USA (*Boisea trivittata*) and Japan (*Menida scoti, Hylamorpha mista*) where aggregations of the latter species may be as large as 30,000 individuals per building (Robinson, 1996). Conspicuous aggregations of lady-beetles (Coleoptera, Coccinellidae*)* are also sometimes associated with man-made structures or occur at places of human recreation
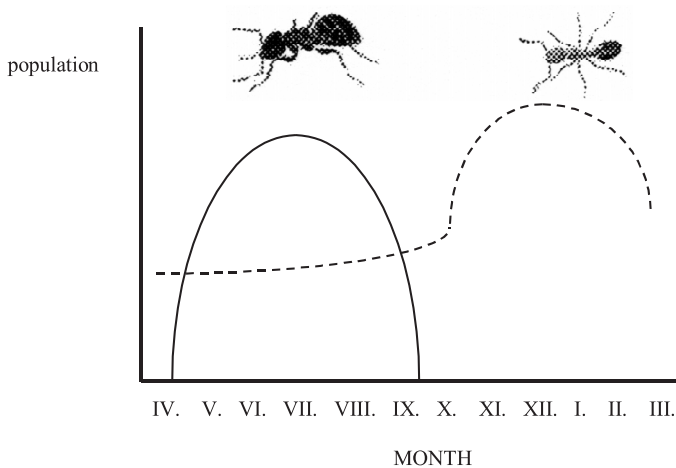

Figure 4. Schematic representation of seasonal population size and activity of outdoor pests (solid line) and indoor pests inhabiting climatized buildings (dotted line). The phase of maximum occurrence and pest effect are shifted by 1/2 year.

(Hodek and Honěk, 1996). Occasionally all these aggregations may inflict discomfort to some persons. They are perceived as problems since the insects are encountered in massive quantities at unusual place or time. However, the aggregations are not a true reversed population dynamics since the insects do not reproduce.

Seasonality and its implications for strategies of pest control

Considering the role of seasonality is increasingly important component of planing protection measures against synanthropic arthropod pests. The cause of this interest is the pressure on decreasing costs of protection and decreasing use of chemicals in urban and agricultural environments which resulted in development of "target pest control". This type of control means application of pesticides and baits at places wher the pest insects prefer to aggregate (e.g. cracks, crevices), and at the part of the year/day in which pests are most sensitive to particular control means. Baits, formerly used only against rodents, were later employed against synanthropic insects: cockroaches, crickets, ants, and most recently termites. The efficiency of baits and bioagents depends far more than traditional chemical sprays on temporal environmental conditions. Therefore, the importance of the study of seasonality for bait efficiency increases, and this trend is particular also for this conference. Very important are the studies of foraging and feeding behaviour of termites (Getty *et al.*, 1998) and ants. For example, in central Europe the baits for *Monomorium pharaonis* are efficient only during the cool period (Rupeš, 1987, 1988). One of the early examples of using seasonally specific approach to traditional chemical pest control was differentiation between spring and autumn strategy of control of *Periplaneta americana* (Bao and Robinson, 1988). Much attention was paid also to timing of application of biological pesticides (e.g. *Bacillus thuringiensis*) against mosquitoes, which should be applied during a narrow phase of insect development.

The presence of seasonality is an important difference between indoor and outdoor pests. These categories of pests are well manifest in temperate zone. **Outdoor pests** live in the open and only in periods of their activity enter human settlements. The length of this period generally increases as one moves from temperate regions towards the tropics. By contrast, **indoor pests** complete their life cycle within man-made structures and their occurrence is largely a seasonal, although the abundance may oscillate considerably. In temperate zone the populations are "isolated", confined to the microclimatic "islands" of buildings, with a limited possibility of migration. This isolation enabled a temporary local eradication of pest populations, e.g. *Monomorium pharaonis* (Rupeš, 1998) in central Europe. At subtropic and tropic conditions the difference between indoor and outdoor pests largely disappears. Considering both kinds of pests with respect geographic position of the locality has practical consequence. For example, *M. pharaonis* is generally considered an indoor pest. However, in Florida Oi *et al.* (1994) observed that workers of this species foraged more at outdoor places (51.7%) than within the buildings (11.6%). Thus commercial baits placed only outside the buildings provided a 94% control of the population within one week.

Length of the season for which the control is desirable is of crucial importance for performance of the control of outdoor pests, especially in mosquitoes. Nearly continuous appearance of mosquitoes in tropical and subtropical regions is accompanied by an extended application of pesticides. Hainze (1993) reported that total price of mosquito coils sold each year, largely in tropical countries, is approximately one billion US dollars, this being the world largest sale of household insecticides. Generally, a long period of pest appearance combined with a massive use of pesticides is the very best pre-condition for selecting resistant pest populations.

CLIMATE AND ORIGINS OF PESTICIDE RESISTANCE (ZORRO)

Factors that promote the selection of insecticide resistant pest strains include repeated application of nearly sub-lethal doses of insecticide with residual effects on a population with short generation time. We may therefore expect the origin of resistant populations in tropics where several conditions are often

fulfilled. Although the statistics may be biased (Kay and Collins, 1987), the data indicate increased risks of the origin of pesticide resistance in the tropics.

To detect the effect of residual pesticides we used the data of WHO (Brown and Pal 1971) from before 1970 which might be little influenced by effects of cross-resistance and migration. Geographic distribution of first records of resistant strains of medical insect pests established during two decades
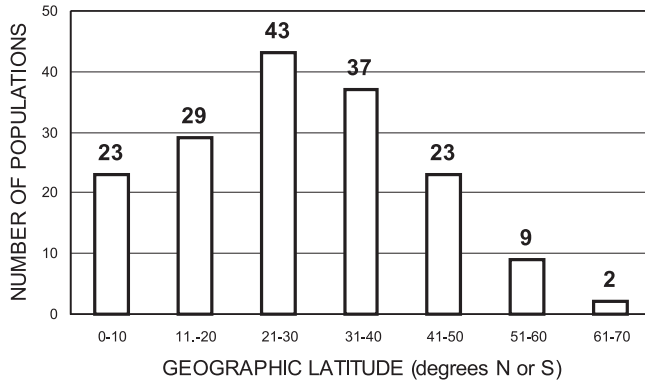

Figure 5. Geographic distribution of first records of populations resistant against DDT, chlordane and organophosphorus insecticides in medical pest species. Each species considered in this figure is represented by maximum three records each of which means a first record of resistance against one of the above categories of pesticides. Data recalculated from Brown and Pale (1971).
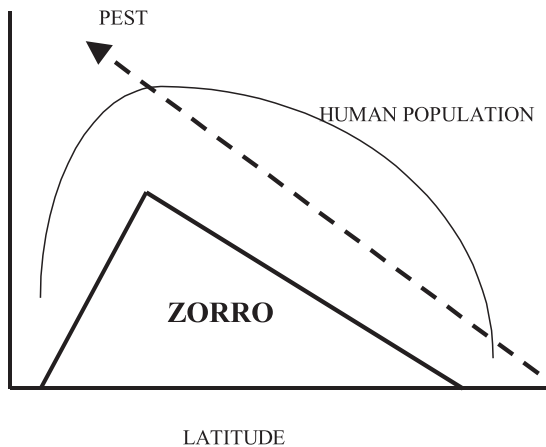

Figure 6. Schematic representation of factors determining the "zone of risk of resistance origin" ZORRO. The influence of PEST species decrease in parallel with geographic latitude - due to decreasing pest species richness, decreasing lenght of breeding season and number of generations and temperature-dependent pest activity. The HUMAN POPULATION concern with pest species effects increase and decrease with geographic latitude due to demographic distribution of human population, its wealth and decision to defend the resources by chemical means. Both factors determine the intensity of chemical control of synanthropic pest species (the area below both curves). The peak indicates the level and position of ZORRO.

following the first use of organic pesticides indicates Fig. 5. The classical example are mosquitoes whose resistance was an important problem in the tropics (Brown and Pale, 1971). In his recent review Zeman (1998) demonstrated increased occurrence of resistant strains and a high incidence of multi-resistance in ticks of Africa, Central and South America and Australia. But even in the eusynanthropic *Blattella germanica* the first resistant population was recorded in warm temperate southern Texas (Brown and Pal, 1971) and the highest level of resistance ever recorded to chlordane was reported from subtropical Hawaii in this species (Cornwell, 1968). Intuitively we would suppose that the origin of resistance will be more influenced by climatic conditions in outdoor than indoor pests. In fact, the first resistant population of *Musca domestica* was reported from Italy and Sweden (Brown and Pal, 1971) where pesticides were used for indoor housefly populations living in warm conditions, e.g. stables. However, in stored product pests the resistance was also more frequent in tropical and subtropical strains. This may be documented (Table 1) from comparison of the proportion of populations resistant against lindane and malathion, based on data of FAO from before 1977 (Champ and Dyte, 1977). The proportion of resistant strains was in the average 2.5 times greater among tropical than temperate populations of 8 beetle species.

Table 1. The frequency of pesticide resistant populations of 8 stored pest beetle species in temperate, subtropical, and tropical zones. The table indicates proportions of populations resistant to malathion and lindane in the total populations tested. Recalculated from FAO data (Champ and Dyte, 1977).

PEST SPECIES	PESTICIDE	ZONE	
		TEMPERATE	SUBTROPICAL & TROPICAL
		Percent of resistant populations and (total tested)	Percent of resistant populations and (total tested)
Sitophilus oryzae	MALATHION	1.7 (19)	16.1 (66)
	LINDANE	78.2 (55)	73.9 (180)
Sitophilus zeamays	MALATHION	0.0 (35)	3.6 (168)
	LINDANE	62.8 (35)	82.1 (151)
Sitophilus granarius	MALATHION	4.2 (119)	20.5 (44)
	LINDANE	13.7 (117)	47.5 (40)
Rhyzopertha dominica	MALATHION	24.0 (25)	33.1 (133)
	LINDANE	55.0 (27)	69.1 (110)
Tribolium castaneum	MALATHION	71.7 (99)	90.6 (406)
	LINDANE	87.8 (86)	94.5 (377)
Tribolium confusum	MALATHION	58.2 (55)	68.7 (67)
	LINDANE	28.3 (53)	56.1 (41)
Oryzaephilus surinamensis	MALATHION	2.8 (107)	14.5 (76)
	LINDANE	70.2 (94)	79.3 (58)
Oryzaephilus mercator	MALATHION	8.3 (12)	8.4 (24)
	LINDANE	41.7 (12)	54.6 (22)

   Interesting results were obtained from analysis of geographic distribution of resistance against non-residual pesticides. Fumigants do not leave any residua and the probability of the origin of resistance against these non-residual pesticides is considered much smaller than for residua leaving pesticides. The selection of resistant strains depends on the frequency of fumigant application and doses of the pesticide. The resistance most frequently originated in the tropics and subtropics. However, the correlation with climate is apparently indirect. In fact, the resistance appears in developing countries where the fumigants are applied most frequently and technology of their application is likely to be below the high standard. The first failures of pest control due to resistance to phosphine were reported from India (Borah and Chahal, 1979), Bangladesh (Tyler *et al.*, 1983). Few years later, Taylor and Halliday (1986) established phosphine resistance in seven countries: Bangladesh, Bhutan, Brazil, Mali, Nepal, Pakistan and Sri Lanka and as late as in 1989 phosphine resistance was reported from USA (Zettler *et al.*, 1989).

   We suppose that increased frequency of the origin of resistance in tropical and subtropical areas is due to three factors. 1) Greater development rate and number of generations (due to longer vegetation and breeding season) in pest populations which result in frequent pesticide application. The risk of resistance origin increases also in climatised buildings. 2) Poor application technology and lack of the qualified staff. Warm climate increases the demand for pesticide application in tropical countries many of which are poor. 3) Increased richness of tropical pest fauna may contribute since the species may differ in their sensitivity to pesticide treatments and probability of resistance origin.

Finally, we should consider whether there exist areas and conditions where the risk of resistance selection is at maximum as showed in the graphical model at Fig. 6 . We suppose that the "zones of risk of resistance origin" (ZORRO) are the areas or conditions where factors 1-3 of the above list match each other in their maximum intensity: pest populations find there biological optima and, at the same time, in these areas there are the most intensively chemically defended large resources (objects of human interest) for which human population compete with pest populations. Resources are not only buildings or food stocks but also health and other qualities of life. For outdoor pests, ZORRO are areas which may be well geographically delimited. For synanthropic and medical pests, ZORRO are the areas of warm climate and high human population density (Fig. 5), while Northern/Southern areas where biological conditions for pest species are far from optimum, season of pest activity is short and their populations and small do not belong to ZORRO. For indoor eusynanthropic pests, ZORRO are fragmented into small isolated "islands" - climatised and heated buildings and glasshouses.

From these ZORRO sources pesticide resistant strains spread into "sink" areas where the origin of resistance is improbable. Globalization of the world market increases the risks of transport of resistant strains. This was demonstrated by Dyte and Holliday (1985) who find a highly resitant phosphine-strain of *Cryptolestes ferrugineus* on commodities imported to United Kingdom from India. Since in outdoor pests, ZORRO is limited climatically, and with possible global warming we may expect the shift of its edge towards the North/South.

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