

Climatic changes and shifting species boundaries of *Drosophilids* in the Western Himalaya

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Abstract : Population dynamics studies under shifting environmental conditions over a longer time scale can help to determine how different species react to new biotic and abiotic conditions. Two different field surveys with similar collection methods as well as sites in the western Himalayas (1961 – 1962 and 2003 – 2004) were compared on the basis of relative abundance and dominance indices of different *Drosophila* species. Climatic data for the last fifty years involves a significant change in average temperature (Tave) of western Himalayas , which has affected the distribution and boundaries of various *Drosophilids* in this region. Current study reports a significant decline in the number of *Drosophila nepalensis* and other cold adapted species from lower ranges ; and introduction of *Drosophila ananassae* and other warm adapted species to lower and mid mountainous ranges. For *D. nepalensis* , species abundance is negatively correlated ($r = -0.93 \pm 0.03$) with Tave of the localities of origin and while reverse trend was observed for *Drosophila ananassae* ($r = 0.90 \pm 0.05$). Thus , climatic changes over long periods (42 years) have affected invasive ability of different *Drosophila* species in the western Himalayas.

Key words : *Drosophilids* ; Western Himalayas ; temperature profile ; shifting species boundaries ; cold and warm adapted species

INTRODUCTION

Population ecology is a major issue among environmental sciences for understanding the function of ecological communities , protecting endangered species and controlling noxious species. Demography is referred to as population dynamics and such investigations at the level of wild populations are limited. Indian subcontinent represents species richness and seasonal climatic changes along latitude , longitude and altitude. During the evolutionary process , the ecological niches exhibit a huge diversification and introduction of species to new territories corresponds to ecological experiments. For this we require ecological data concerning localization , abundance and population dynamics of each species as well as meteorological data for each locality. Such studies can help in analyzing adaptive capacities and functioning of ecological communities (Parsons , 1991 ; Vitousek , 1992 ; Parmesan , 1996). Unfortunately , opportunities for such investigations on the Indian subcontinent remain untapped.

The family *Drosophilidae* originated presumably in the Oriental biogeographic region more than 100 MYA. The *melanogaster* group comprises only Oriental , African and Australian species and is subdivided into ten subgroups. Several of these subgroups such as

ananassae , *montium* , *takahashii* and *melanogaster* are widespread in India with endemic species. Also these subgroups harbor cosmopolitan species such as *D. melanogaster* , *D. ananassae* , *D. malerkotliana* and *D. kikkawai*. With respect to climate , India is basically a warm , tropical and subtropical country. It offers quite different conditions with respect to average temperature , seasons and humidity *etc.* However , northern parts including the western Himalayas offer cooler and less humid places.

Global warming has affected the distribution pattern of species across different continents (Parmesan , 1996 ; Kumar , 2006). Currently , worldwide temperature is undergoing a rapid increase as compared with prehistoric climatic changes (Vitousek , 1992). According to Inter-governmental Panel on Climate Change (IPCC) , a global increase in temperature of 0.6°C since mid-nineteenth century is an alarming sign for all biological systems (Hughes 2000 ; McCarthy *et al.* , 2001).

A considerable rise in tropospheric temperature is reflecting in the changes in mass balance of glaciers and size reduction of ice caps in Andes (South America) , African highlands , European Alps , Asian highlands , Indonesia and New Zealand (Kaser and Noggler , 1991 ; Hastenrath and Kruss 1992 ; Thompson *et al.* , 1993 ; Haeberli , 1995 ; Santer *et al.* , 1996). Under such

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Received : 2007-06-08 ; Accepted : 2008-03-06

situations, species are expected to move upwards (higher latitudes and/or altitudes) in response to shifting temperature zones. It has been suggested that changes in worldwide climate will lead to shifts in species geographic boundaries (Schneider, 1993). Range shifts can also impose serious problems for human health, *e. g.* in Asia, Africa and Latin America mosquito borne diseases have increased significantly in the highlands (Epstein *et al.*, 1998). A growing number of investigators propose that vector-borne diseases (VBDs), involving insects or snails as carriers could shift their range in response to climate change (Leaf, 1989; Shope, 1991; Patz *et al.*, 1996; McMichael *et al.*, 1996; Carcavallo and de Casas, 1996). There are certain other investigations as well which indicate the potential for spread of the geographic areas that could sustain VBD (Vector Borne Diseases) transmission to higher elevations and higher latitudes under global warming scenario (Maskell *et al.*, 1993; Martens *et al.*, 1997; Focks *et al.*, 1995).

Species differ in their rate of migration; demographic and evolutionary adaptive characteristics (Trelles *et al.*, 1998). A major question is to determine which key ecological factors limit species distribution and how they limit. Temperature, a key factor of the environment has affected geographical distribution of many ectothermic species (Andrewartha and Birch, 1954; Brneie *et al.*, 1981; Leather *et al.*, 1993; Cossins and Bowler, 1987). *Drosophila* species are generalists in exploiting tropical resources and can tolerate changes in climatic conditions. Therefore, *Drosophilids* are good candidates for invasion of novel territories; often far from their centers of origin *e. g.* *Zaprionus indianus* (an afro-tropical *Drosophilid*) in recent times has invaded into South America and quickly extended its distribution to various Brazilian states (Vilela, 1999; Tidon *et al.*, 2003) and Uruguay (Goni *et al.*, 2001). Over the last 20 years, a shift has been observed in the latitudinal cline of alcohol dehydrogenase of *Drosophila melanogaster* in eastern coastal Australia. It has been suggested that these genetic changes are likely to reflect increasing warmer and drier conditions and may serve as sensitive biomarkers for climatic change (Umina *et al.*, 2005). Several *Drosophila* species demonstrate latitudinal clines on the Indian subcontinent and genetic variations are strongly correlated with local climatic conditions especially seasonal thermal amplitude or Tcv (Parkash *et al.*, 1998; Parkash and Munjal, 1999a, 1999b). Thus it would be interesting to monitor changes in Indian *Drosophilids* in context of global warming effects.

Some cases of invasion due to climate change examples include warm-water species that have recently appeared in the Mediterranean and North seas (Nehring, 1996; Nieder *et al.*, 2000). Even in some remote places as some sub-Antarctic islands, it is estimated that introductions by humans over the last two centuries account for a considerable proportion of the insect and mite fauna (Pugh, 1994). Monitoring in other parts of the world has identified a large number of ecological and biological changes due to recent climate change (Hughes, 2000; McCarty, 2001; Walther *et al.*, 2002). These include both latitudinal and altitudinal shifts in species ranges (Zalakevicius and Zalakeviciute, 2001) as well as changes in abundance and local extinctions.

In the present study, two different field collections (1961 – 1962 and 2003 – 2004) were compared on the basis of percent distribution, relative abundance and dominance indices of different *Drosophila* species. A significant change in average temperature in western Himalayas has affected the distribution of various *Drosophilids* in this region. Due to climatic changes, cold adapted species (*D. nepalensis*, *D. takahashii*, *D. rufa* and *D. bifasciata*) have shifted their boundaries to mid and high elevational localities while lower to mid altitudinal sites have been invaded by warm adapted species (*D. ananassae* and *D. repleta*).

MATERIALS AND METHODS

In order to compare the species distribution pattern across a span of 45 years (1961 – 1962 vs 2003 – 2004 and 2005 – 2006), collections of *Drosophila* species were made from seven geographical sites of western Himalayas (Fig. 1) in accordance with earlier survey conducted by Parshad and Paika (1963). Data on the altitudinal as well as latitudinal locations of all the seven sites (which include low, mid and high altitudes) are given in Table 1. Methods of collections (net sweeping and bait trap methods) were similar to that of Parshad and Paika (1963). For random sampling of *Drosophila* species, collections were made from gardens, houses, nurseries, fruit shops, fruit godowns and dustbins, in accordance with the earlier collections made by Parshad and Paika (1963). Earlier data were based on nearly 5 000 *Drosophilids* while the current data include 7 108 and 6 317 individuals for 2003 – 2004 and 2005 – 2006 collections, respectively. For the two species (*D. nepalensis* and *D. ananassae*) which showed highly significant changes in their percent distribution across a span of 42 years (1962 vs 2004), monthly collection data were analyzed for pre-winter,

winter and post-winter periods as a function of the average temperature (T_{ave}) of the sites of origin.

Relative abundance (R) of the species refers to the number of individual of the species i divided by the total number of individuals in the sample. **Species richness (S)** was considered equal to the number of different species found in the sample. **Dominance index (D)** of each species was calculated as: $D = n_i / (n_i - 1) N(N - 1)$; where n_i is number of individuals of the species i and N is the total number of the samples (Simpson, 1949). The above indexes were calculated using the frequencies of species individuals collected from all the collection sites.

Temperature data for western Himalayan region were obtained from Indian Institute of Tropical Meteorology (IITM; www.tropmet.res.in). Temperature averages (T_{ave}) were calculated using temperature maximum and temperature minimum values and are shown in Fig 2. All the seven localities of origin of populations in the western Himalayas have undergone extensive changes due to population growth and deforestation. Furthermore, the low altitude locations have shown extensive industrialization during the last 3–4 decades.



Fig. 1 Geographical map of Indian sub-continent. Sites of collection in the western Himalayan region are indicated as a polygon.

Table 1 Data on common collection sites used for two different collections (1961–1962; 2003–2004) of *Drosophila* species from western Himalayas

SITES	Chandigarh & Pinjore	Kalka	Dharamshala	Kullu	Solan	Kasauli	Manali
Altitude (m)	400–450	600	1 210	1 310	1 440	1 960	2 040
Latitude (°N)	30.44	30.51	32.16	32.00	30.80	30.64	32.16

All collections were made through net sweeping and bait trap methods.

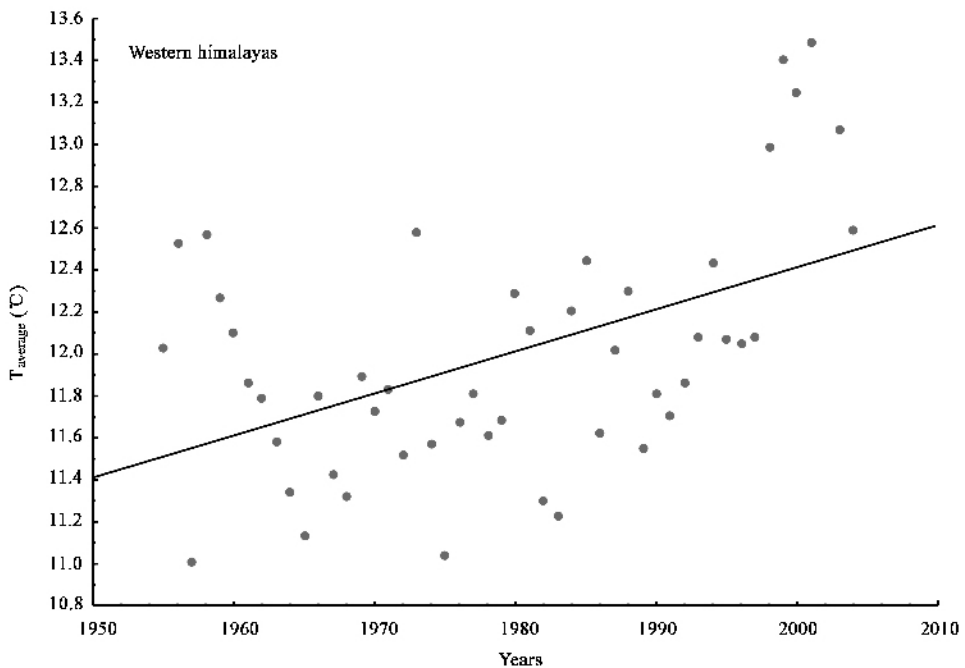


Fig. 2 Scatter plot of variations in average temperature (°C) for 48 years (1955 to 2003) in western Himalaya.

RESULTS AND DISCUSSIONS

A total of thirteen species comprising of six to seven thousand individuals were collected during the recent collections. Data for two consecutive collections (2003 – 2004 and 2005 – 2006) are given in Table 2. During the recent collections, cold adapted species – *D. nepalensis*, *D. takahashii* and *D. rufa* could be collected in significant numbers from the highlands only (> 1 500 m). Table 3 shows dominance index, relative abundance and species richness values, *e. g.* highest D (dominance) and R (relative abundance) values were obtained for *D. nepalensis* in 1961 – 1962 collection while lowest values were found for 2003 – 2004. Species richness index showed no significant changes except addition of new species, *i. e.* *D.*

repleta, *D. ananassae* and *D. bipectinata* in 2003 – 2004. When percent distributions of species (2003 – 2004 and 2005 – 2006) were compared with 1961 – 1962 collection, significant differences were found. In sixties, abundance for *D. nepalensis* was reported as 66.96% of total sample size. By contrast, the recent collections exhibit 1.70% *D. nepalensis* individuals particularly from the lowland regions. Four other cold adapted species (*D. punjabiensis*, *D. takahashii*, *D. bifasciata* and *D. rufa*) also evidenced significant decline in 2003 – 2004 collections as compared with 1961 – 1962. It may be noted that two other cold adapted species (*D. busckii* of subgenus *Dorsilopha* and *D. immigrans* – subgenus *Drosophila*) were not included in the surveys of 1961 – 1962 which focused mainly on Sophophoran species.

Table 2 Pooled data on *Drosophila* individuals sampled from seven geographical sites during 2003 – 2004 and 2005 – 2006 (percentages in parenthesis) from western Himalaya

Species	Year		Altitude of fly collection sites (m)	Developmental thermal range (°C)
	2003 – 2004	2005 – 2006		
<i>D. melanogaster</i>	565 (7.94)	801 (12.68)	400 – 2 200	12 – 31
<i>D. kikkawai</i>	1 070 (15.05)	500 (7.91)	400 – 2 200	12 – 31
<i>D. ananassae</i>	1 019 (14.33)	901 (14.26)	400 – 1 500	17 – 31
<i>D. jambulina</i>	260 (3.65)	215 (3.40)	< 600	14 – 31
<i>D. repleta</i>	2 730 (38.40)	2 200 (34.85)	600 – 1 500	14 – 30
<i>D. malerkotliana</i>	–	111 (1.75)	< 600	15 – 31
<i>D. busckii</i>	209 (2.94)	133 (2.10)	> 1 500	12 – 28
<i>D. punjabiensis</i>	70 (0.98)	141 (2.23)	~ 600	14 – 31
<i>D. biarmipes</i>	–	131 (2.07)	> 1 500	12 – 30
<i>D. nepalensis</i>	121 (1.70)	113 (1.78)	> 2 000	12 – 25
<i>D. immigrans</i>	810 (11.39)	910 (14.40)	600 – 2 200	12 – 28
<i>D. takahashii</i>	145 (2.03)	161 (2.50)	600 – 2 200	15 – 31
<i>D. bipectinata</i>	109 (1.53)	–	~ 600	15 – 31
Total	7 108 (100)	6 317 (100)	–	–

Data on altitudinal range as well as developmental thermal range are also given.

On the Indian sub-continent, *D. ananassae* and *D. bipectinata* are circumtropical stenothermal species whereas *D. kikkawai* (montium subgroup) and *D. melanogaster* occur all along the Indian sub-continent. The recent colonization of *D. kikkawai* in western Himalayas is reflected by four fold increase in its relative abundance as compared with 1961 – 1962 collections (Table 3). Another important finding is the collection of *D. ananassae* from low elevation sites. In 1961 – 1962 collections, there were no records of this warm adapted species whereas in the recent collections *D. ananassae* represented 14.33% of total sample size which indicated its invasive ability as well as colonizing strategy under changing climatic conditions in the western Himalayas.

For a detailed analysis of abundance as well as boundaries of *D. nepalensis* and *D. ananassae*,

samples were collected monthly (2003 – 2004) along an altitudinal cline during the complete winter season. The collection sites are situated across 450 km, but vary significantly in altitude, *i. e.* 400 to 2 200 m above sea level. *D. nepalensis* were collected from higher elevational sites in all the three periods (pre-winter, winter and post-winter). Recent collection surveys did not reveal *D. nepalensis* individuals from lowland sites except at 600 meters and that too in mid-winter ($r = -0.93 \pm 0.03$; Fig. 3). However, such data on *D. ananassae* suggested an opposite trend ($r = 0.90 \pm 0.05$; Fig. 4). *D. ananassae* showed a significant increase in lowland areas whereas number of individuals decreased while moving upwards (higher elevations). Collection of *D. ananassae* from these regions clearly indicated invasion of this species to low as well as midland areas. The invasive success of *D. ananassae*

Table 3 Estimates of dominance index (D) relative abundance (R) and species richness (S) for fourteen *Drosophila* species collected in two different time intervals (1961 – 1962 and 2003 – 2004)

Species	Dominance index (D)		Relative abundance (R)	
	1961 – 1962	2003 – 2004	1961 – 1962	2003 – 2004
<i>D. melanogaster</i> (P)	0.003395	0.005566	0.0632	0.0794
<i>D. kikkawai</i> (P)	0.000982	0.021298	0.0366	0.1500
<i>D. ananassae</i> (Wa)	–	0.019294	–	0.1433
<i>D. jambulina</i> (Wa)	0.000895	0.000977	0.0352	0.0365
<i>D. repleta</i> (Wa)	–	0.145066	–	0.3840
<i>D. malerkotliana</i> (P)	0.004589	–	0.0726	–
<i>D. busckii</i> (Ca)	–	0.000576	–	0.0294
<i>D. punjabiensis</i> (Ca)	0.000755	0.000000	0.0328	0.0098
<i>D. biarmipes</i> (P)	–	–	–	–
<i>D. nepalensis</i> (Ca)	0.446129	0.000120	0.6696	0.0170
<i>D. immigrans</i> (Ca)	–	0.011953	–	0.1139
<i>D. takahashii</i> (Ca)	0.002412	0.000211	0.0528	0.0203
<i>D. bipectinata</i> (P)	–	0.000081	–	0.0153
<i>D. bifasciata</i> (Ca)	0.000195	–	0.0198	–
<i>D. suzukii</i> (Wa)	–	–	–	–
<i>D. rufa</i> (Ca)	0.000120	–	0.0170	–

Species richness (S) = 9 (1961 – 1962); 11 (2003 – 2004)

P : Plastic species ; Wa : Warm adapted ; Ca : Cold adapted ; 1961 – 1962 data were used to calculate D , R and S values (Parshad and Paika, 1963)

may depend on their ability to respond to natural selection effects on physiological tolerance or plasticity. Changes in temperature may also affect viability, fertility and development time which influence survival of species. Life-history responses of British grasshoppers (Orthoptera : Acrididae) to temperature change have resulted in an increase, in growth and development rates (Willott and Hassall, 1998). With increasing temperature, insects are expected to pass through their larval stages faster and to become adults earlier (Hughes, 2000). A study on grasshoppers in UK suggests an advance in flight phenology of three to six days over past 25 years (Fleming and Tatchell, 1995). Mean temperature in England have risen by 0.4°C over the same period. Another similar kind of study on 104 species of most common Microlepidoptera in the Netherlands (1955 – 1994) shows a trend towards earlier (shifted earlier by 11.6 days) flight (Ellis *et al.*, 1997). Life-history traits such as oviposition preference may change as an evolutionary consequence of increased habitat fragmentation (Thomas *et al.*, 1998; Kuussaari *et al.*, 2000).

In last fifty years, a significant increase in the average temperature (Tave) has been observed in the western Himalaya. Regional Climatic Modeling system PRECIS (Providing Regional Climate for Impact Studies) developed by Hedley Center suggested that there can be an approximate 2°C to 6°C rise in temperature as 21st century progresses, with higher levels of warming in the northern parts of India (Kohli *et al.*, 2006). A temperature profile (Tave) from

1955 to 2003 is shown in Fig. 2. Beyond 1998 a significant increase in temperature (Tave) is evident in the western Himalayas and this is true on a global scale as well. This increase in temperature has affected the distribution and species richness and diversity in the recent decades. Habitat fragmentation may also change or disrupt predation and interspecific competition (Tschamtker and Kruess, 1999; Kareiva and Wennergren, 1995).

D. ananassae and *D. repleta* were not at all represented during the collections made in 1961 – 1962. However, both these species showed significantly higher incidence as compared with other *Drosophilids* collected during the recent years (2003 – 2004 and 2005 – 2006). Both the species are about fifty percent of total sample size. There are many variables that could affect dynamics of *Drosophila* communities. Number and type of resources available have changed due to massive urbanization. Recent collections from the different localities suggest that *D. repleta* is abundant when collections are made from public dustbins where all kind of food material gets decayed whereas *D. ananassae* is largely restricted to human households (unpublished data). Urbanization of western Himalayan region has played an important role in the increase of these two domestic *Drosophila* species. According to Lawton (1995) all the species are not equally affected by habitat fragmentation: species of higher tropic levels, rare species, species with specific habitat requirements, species with greatly fluctuating populations and species with poor dispersal

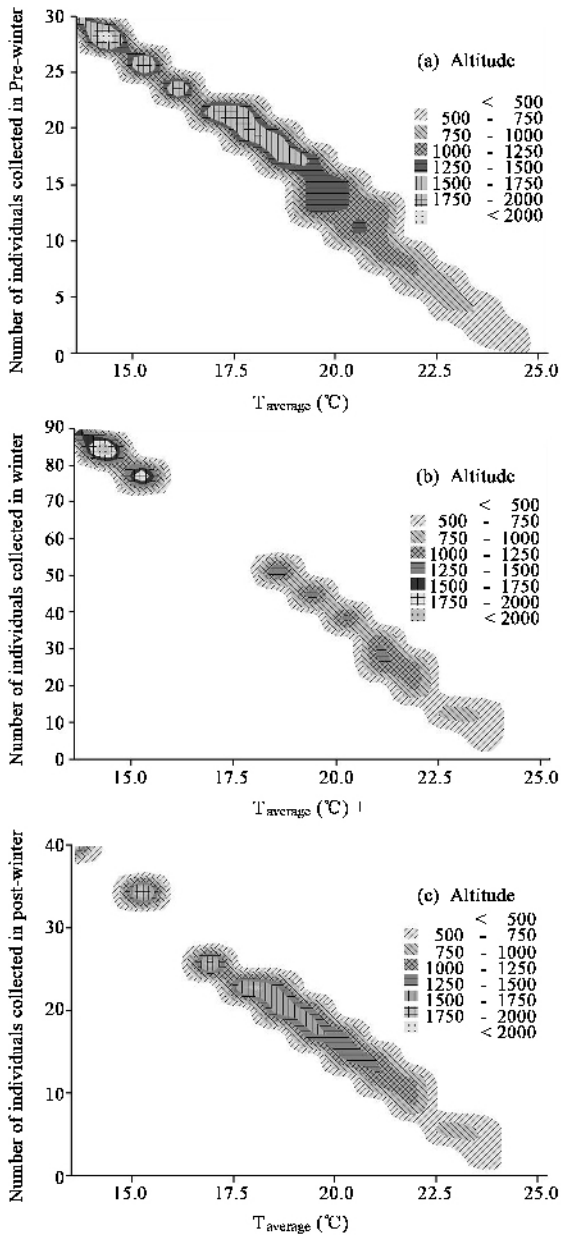


Fig. 3 Contour plots showing a negative correlation ($r = -0.93 \pm 0.03$) between *D. nepalensis* collected from altitudinal sites as a function of average temperature ($^{\circ}\text{C}$) of the site of origin of population.

Data obtained for the three seasons (pre-winter, winter and post-winter) are shown in a to c. Figure represents results of 2003–2004 data only.

abilities are expected to be more prone to extinction. Moreover, less competitive but highly mobile species, which are typically early successional strategists, may profit from habitat fragmentation at the cost of competitively superior but specialized and sedentary species (Tilman, 1994). Along with all these possible causes, biotic interactions (presence of predators, competitors, microbial pathogens, etc.) could also help in shaping the dynamics of these species. Indeed,

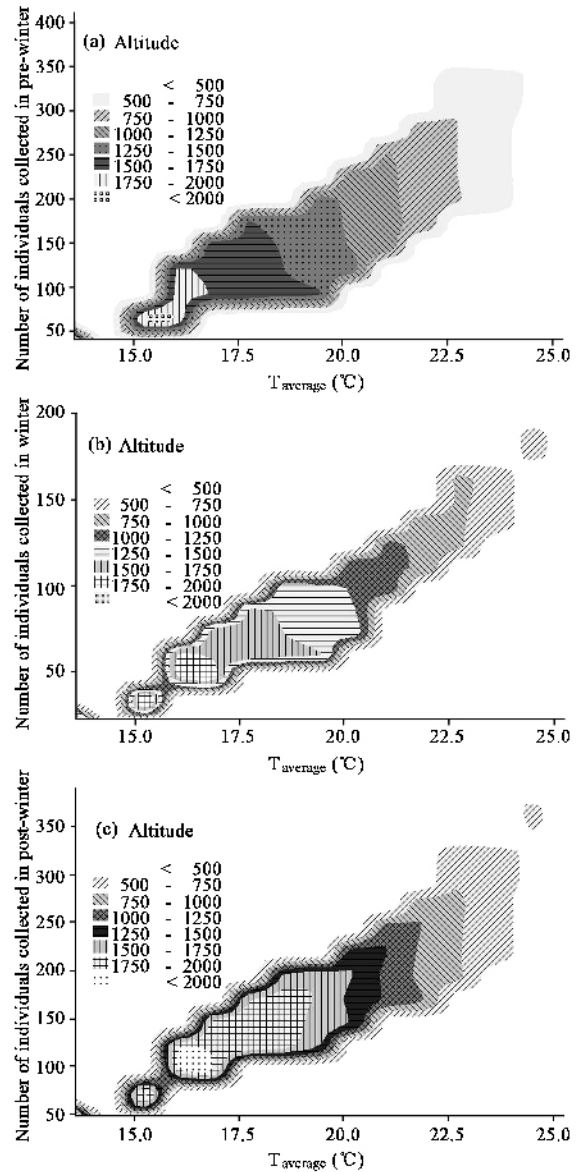


Fig. 4 A positive correlation ($r = 0.90 \pm 0.05$) between number of wild caught individuals of warm adapted *D. ananassae* and increasing average temperature ($^{\circ}\text{C}$) of the site of origin of populations.

Data on pre-winter (a), winter (b) and post-winter (c) collections show significant differences. Figure represents results of 2003–2004 data only.

there are a number of studies which investigate interactions between pathogens and/ or parasites in invertebrates (e.g. Ritters and Tanada 1978; Barbercheck and Kaya, 1990; Chandler *et al.*, 1993). As an extension of this suggestion, there is at present a considerable global interest in invasive species and emergent infectious diseases (Thomas *et al.*, 2003). We do have parallel explanations or reports which suggests that community structures is more likely to be influenced by predators in benign versus harsh abiotic regimes (Walde, 2004). Finally the assemblages of species in ecological communities reflect

interactions among organisms as well as between organisms and the abiotic environment. We might expect, therefore, that rapid climate change or extreme climatic events can alter community composition. Some of the range shifts involve community-level changes (Walther *et al.*, 2002).

Further studies are needed to analyze the interactions of species as well as ecosystem properties which determine species invasion in the western Himalayas. In conclusion, the comparison of *Drosophila* communities collected during 1961–1962 and 2003–2004 showed that cold adapted species are disappearing and warm adapted species are appearing and the data correlated with changes in the average temperature in the western Himalayas.

ACKNOWLEDGEMENTS We are grateful to the reviewers and to the editor Prof. Decheng YUAN for helpful comments on the manuscript.

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西喜马拉雅地区气候变化与果蝇分布界限的移动

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摘要 : 在长时间尺度上研究环境变化条件下的种群动态,有助于确定不同物种如何对新的生物和非生物条件做出反应。采纳类似的采集方法在相同的地点,分别于 1961 – 1962 年和 2003 – 2004 年在西喜马拉雅地区对果蝇种类进行了两次野外调查,对两次调查获得的种类的相对丰富度和优势度指数进行了比较。最近 50 年的气象数据显示西喜马拉雅平均气温 (T_{ave}) 发生了显著变化,对该地区的果蝇种类组成及分布界限产生了影响。本研究发现在低海拔的地带 *Drosophila nepalensis* 及其他一些冷适应种类的数量明显下降;而 *Drosophila ananassae* 及其他一些暖适应种类则进入了低海拔和中海拔地带。*D. nepalensis* 的丰富度与所调查地点的平均气温负相关 ($r = -0.93 \pm 0.03$),而对于 *D. ananassae* 则是相反趋势 ($r = 0.90 \pm 0.05$)。据此认为长期(42 年)的气候变化已对西喜马拉雅地区的果蝇种类的分布格局产生了影响。

关键词 : 果蝇;西喜马拉雅;温度分布;物种分布界限移动;气候适应

中图分类号 : Q968.1 文献标识码 : A 文章编号 : 0454-6296(2008)02-0328-08

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