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Genotypic and phenotypic divergence of rodents (*Acomys cahirinus* and *Apodemus mystacinus*) at "Evolution Canyon": Micro- and macroscale parallelism

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Genetic allozyme and RAPD diversities were examined for ecological-genetic patterns in two rodents, the spiny-mouse *Acomys cahirinus* (Desmarest, 1819) and woodmouse *Apodemus mystacinus* (Danford and Alston, 1877), from the ecologically contrasting opposite slopes of the Lower Nahal Oren microsite, Mt. Carmel, Israel, designated by us "Evolution Canyon". Likewise, morphological measurements were compared. Samples of both rodent species were collected from six stations: 3 (upper, middle and lower) on the "tropical" xeric South-facing slope (SFS) and 3 on the opposite "temperate" mesic North-facing slope (NFS) which vary dramatically physically and biotically. Higher solar radiation on the SFS than on the NFS makes it warmer, drier, spatiotemporally more heterogeneous and climatically more fluctuating and stressful than the cooler and more humid NFS. Consequently, the SFS exhibits an open park forest representing an "African" savanna landscape, in sharp contrast with the "European" lush liveoak maquis forest. Inter- and intraslope allozyme, RAPD, and morphological divergence was found in both rodents. Local variation in solar radiation, temperature and aridity stress caused interslope and intraslope adaptive genotypic (proteins and DNA) and phenotypic (morphological, physiological and behavioural) differences paralleling regional patterns across Israel in *Acomys* and in northern and central Israel in *Apodemus*. This suggests that, at both the micro- and macroscales, diversifying natural (microclimate) selection appears to be the major evolutionary driving force causing inter- and primarily SFS intraslope adaptive genotypic and phenotypic divergence. "Evolution Canyon" proved in small rodents, as previously in other organisms, an optimal model for unravelling evolution in action across life and organization.

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Contents

Introduction 10
"Evolution Canyon" 11
The predominant rodents at "Evolution Canyon" 11
The ecological-genetics of rodents at "Evolution Canyon": The problem of local versus regional divergence 13
Problems investigated at "Evolution Canyon" 14
Material and methods 14
Ecological background 14
Sampling and analysis 14
Results 18
Morphological variation 18
Genetic diversity 18
Acomys cahirinus 18
Allozymic variation 18
RAPD diversity 21
Apodemus mystacinus 24
Allozymic variation 24
RAPD diversity 26
Discussion 26
"Evolution Canyon": the model background 26
The local genetical, morphological, physiological and behavioural patterns 26
The regional morphological, physiological, behavioural, and genetic patterns 27
Acomys cahirinus 27
Apodemus mystacinus 29
The evolutionary driving forces causing genotypic and phenotypic divergence of rodents at "Evolution Canyon" 31
References 32

Introduction

Microgeographical studies provide powerful tools to evaluate the relative importance of the forces driving evolution, particularly if they parallel macrogeographic patterns (eg Nevo 1995, 1997). In particular, microscale studies could assess the relative roles of migration and natural selection in moulding the genetic structure of populations at both the genotypic and phenotypic levels. While phenotypic divergence is usually attributed to Darwinian selection, genotypic divergence is still considered by some as neutral (Kimura 1983) or nearly neutral (Ohta and Tachida 1990) rather then largely selective (Nevo 1988, 1998). Our long term research program of genetic diversity in natural populations involved both macro- and microscale studies (Nevo 1978, 1988, 1990, 1995, 1997, 1998, Nevo *et al.* 1984, 1996, 1998). These studies suggested that natural selection in its various forms appear to be a major differentiating and orienting force of evolutionary change in both genotypes (proteins and DNA) and phenotypes (morphology, physiology and behaviour).

Recently, we embarked upon a microsite research program designated by us "Evolution Canyon" at Lower Nahal Oren, Mt. Carmel, Israel (Nevo 1994, 1995, 1997) attempting to explore some major unresolved problems of evolutionary biology.

"Evolution Canyon"

"Evolution Canyon" (32°43'N; 34°58'E) is a Plio-Pleistocene canyon presumably 3–5 million years ago (Ma). It is eroded in tectonically uplifted Upper Cenomanian limestones (Karcz 1959) geologically identical on the opposite slopes in a regional Mediterranean climate (Atlas of Israel 1970). However, the opposite slopes, separated by only 100 m (at bottom) and 400 m (at top), represent dramatic physical and biotic contrasts and divergence due to the higher (up to 300%) solar radiation on the South-facing slope (SFS) (H. Kutiel and G. Sher, unpubl.). The SFS is therefore warmer, drier, microclimatically more fluctuating and less predictable than the North-facing slope (NFS), as is true for valleys north of the equator (Cottle 1932). Spatiotemporally, the SFS represents a "broader-niche" (Van Valen 1965), tropical, dry savanna-like biota. The SFS consists spatially of more microhabitat patches and subdivisions than the NFS, involving a mosaic of habitats, comprising of open park forest, savanna plant formations and bushy islands. Notably, small variations in aridity in the savanna-like habitats amplify the biotic divergence on the SFS, both in space and over time. In particular, the lower third of the SFS obtains the runoff, hence is covered by more vegetation and is less expossed to solar radiation, heat and drought. By contrast, the milder and more homogeneous NFS consists of lush and dense liveoak maquis forest with a few island openings (Fig. 1). The sharply contrasting physical and biotic inter- and intraslope differences provide an ideal model for studying the interaction of population ecology, genetics and evolution in action [Nevo 1995, 1997; Israel Journal of Zoology 42 (4), 1996].

The predominant rodents at "Evolution Canyon"

Out of the 8 rodent species at "Evolution Canyon" (Blaustein *et al.* 1996) the two predominant species are African *Acomys cahirinus* (Desmarest, 1819) and southeast European and Levantine *Apodemus mystacinus* (Danford and Alston, 1877). Our rodent survey at "Evolution Canyon" (Broza and Nevo 1994, Blaustein *et al.* 1996) revealed the predominance of African derivative *A. cahirinus* on the SFS with scarce *A. mystacinus*, and an opposite pattern, ie predominance of European derivative *A. mystacinus* on the NFS, with scarce *A. cahirinus*. Because this pattern, ie African versus European derivation of taxa, is true at "Evolution Canyon" across phylogeny (ie in diverse organisms from cyanobacteria to mammals, Nevo 1995, 1997) we designated the SFS as the "African" slope and the NFS as the "European" slope. Clearly, colonizations of AfroAsian versus EuroAsian taxa occur into a generally Mediterranean climate and biota (Nevo 1995, 1997).

Spiny mice of the genus *Acomys*, are tropical murid rodents (Rodentia, Myomorpha, Muridae) involving about 25 species ranging in Africa and southwest

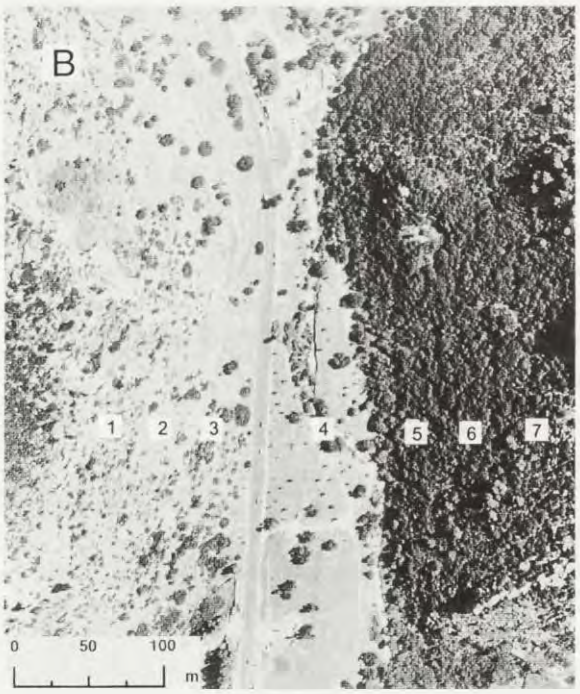

Fig. 1. (A) "Evolution Canyon", Lower Nahal Oren, Mt. Carmel, Israel. Note the plant formations on opposite slopes: the green lush "European" north-facing slope (NFS), sharply contrasting with the open park forest or xeric "African-Asian" savanna on the south-facing slope (SFS).
(B) Air view of "Evolution Canyon". Below the "African" savanna plant formation with an open park forest of *Ceratonia siliqua* and *Pistacia lentiscus* on the SFS; Above the south "European" evergreen dense maquis forest of *Quercus calliprinos – Pistacia palaestina* on the NFS. The 7 stations are indicated: three on the SFS (1–3), on Valley bottom (4) and three on the NFS (5–7).

Asia in rocky habitats. Two species of spiny mice, the common spiny mouse, *A. cahirinus*, and the golden spiny mouse *Acomys russatus*, occur in Israel and Sinai (Shkolnik and Borut 1969, Nevo 1989). *A. cahirinus* is widely distributed across Israel and Sinai ranging in both mesic and xeric environments comprising the Mediterranean, steppe and desert climatic regimes and is thus a climatically euryoek species in range (Fig. 1 in Nevo 1989). However, it lives only in rocky areas, and is therefore relatively stenotopic, or narrow in niche structure. Two chromosome forms of *A. cahirinus*, which differ by a single Robertsonian change, occur in Israel and Sinai (Wahrman and Goitein 1972; Fig. 1 in Nevo 1989).

The Israeli populations possess 2n = 38 chromosomes, and those from Sinai have 2n = 36 chromosomes. The two chromosome forms are completely homozygous except for a hybrid zone, about 16 km long and 15 km wide, where 2n = 37 hybrids were also found. Morphologically, the two karyotypes are indistinguishable, but they have not as yet reached complete reproductive isolation. Although designated as the northern or "Israeli Form" and southern or "Sinaitic Form" (Wahrman and Goitein 1972) they may be viewed, owing to their chromosomal homozygosity across vast ranges, as derivatives of a relatively recent event of speciation, displaying currently its final stages (Nevo 1985). The fossil record indicates that *A. cahirinus* is an Upper Paleolithic colonizer from the southern deserts into humid Mediterranean Israel, ie, it presumably appeared some 20 000 years ago (Tchernov 1968). Therefore, its phenotypic differentiation in Israel is relatively recent, rapid and traceable over time.

The Palearctic genus *Apodemus* is represented in Europe by five species: *A. agrarius*, belonging to the subgenus *Apodemus*; *A. flavicollis*, *A. sylvaticus*, *A. microps*, and *A. mystacinus*, belonging to the subgenus *Sylvaemus*. *A. mystacinus* ranges in the Balkan Peninsula, Anatolia and the Near East and can be clearly distinguished from the other three species of the subgenus *Sylvaemus*. For this reason *A. mystacinus* was recently considered as belonging to a separate subgenus: *Karstomys* (Filippucci *et al.* 1989). *Apodemus* colonized Israel from the north in the early Pleistocene and the succession record of *Apodemus* fossils in Israel appears in Tchernov (1968:65). *A. mystacinus* becomes dominant in the Levallois--Mousterian Upper Pleistocene, emerging in the Oumm Qatafa cave 160 000 years ago. At "Evolution Canyon" *A. mystacinus* was described from the Um Usba Mousterian cave 40–50 000 years ago (Tchernov 1968).

The ecological-genetics of rodents at "Evolution Canyon": The problem of local versus regional divergence

Here we asked the question whether at "Evolution Canyon" the intraspecific population genetic pattern of *Acomys cahirinus* and *Apodemus mystacinus* show inter- and intraslope phenotypic and genotypic divergence in accordance with the dramatic physical and biotic divergence between and within the slopes. Likewise, whether the local microclimatic divergence (Nevo 1995, 1997) parallels the regional macroclimatic one (for the regional perspective of *Acomys* and *Apodemus* see Nevo

1985 and Filippucci *et al.* 1989, respectively). Our results indeed reflect local genetic divergence largely paralleling the regional macroclimatic mesic-xeric genetic and phenotypic (morphological and physiological) divergence across Israel. This local-regional parallelism in *Acomys* and *Apodemus* suggests that climatic natural selection, primarily the aridity stress, is a major evolutionary driving force shaping population genotypic and phenotypic structures.

Problems investigated at "Evolution Canyon"

At the "Evolution Canyon" model we explore among others, the following problems: What is the relative importance of the forces driving evolution? What is the relative role of neutrality and deterministic factors in genetic population structure and differentiation? Can one demonstrate convergent evolutionary patterns at the molecular and organismic levels across different taxa, ie, across phylogeny, caused by shared environmental stresses? Does the local microscale divergence parallel macroscale patterns, thereby highlighting the causal factors of divergence? Our attempt to answer these and other problems is interdisciplinary and covers microorganisms, fungi, plants (lower and higher) and animals (invertebrates and vertebrates), at both the genotypic (molecular) and phenotypic (organismal) levels (Nevo 1995, 1997). Here we present the first interslope genotypic and phenotypic divergence in two murid rodents, the spiny mouse *Acomys cahirinus*, and the woodmouse *Apodemus mystacinus*, henceforward referred to as *Acomys* and *Apodemus*.

Material and methods

Ecological background

The sharp physical and biotic contrast (Nevo 1995) of the opposite SFS and NFS is seen in Fig. 1a, b. The highly solar radiated SFS is warmer and drier than the NFS. Consequently, the steep SFS (dip ~ 35°) displays an open park forest of *Ceratonia siliqua* – *Pistacia lentiscus* with savanna grassland on a very rocky and stony background, a perfect tropical habitat for *Acomys*. By contrast, the less steep NFS (dip ~ 25°) displays a dense maquis forest of *Quercus calliprinos* and *Pistacia palaestina*, with much less rocky background excepting the NFS cliff, a perfect habitat for *Apodemus*. Hence, the opposite slopes harbour African versus European rodent representatives. The small subpopulations of *Acomys* on the NFS and *Apodemus* on the SFS both face harsh stressful habitat on a very short geographic distance. This microscale pattern resembles the distribution near each species boundaries.

Sampling and analysis

Sampling allozymic diversity. We trapped altogether 172 mice of both species at "Evolution Canyon" including 1995/96 captures (Table 1). We analyzed for allozyme diversity 83 mice from "Evolution Canyon", Lower Nahal Oren, Mt. Carmel, Israel, one km upstream from the 6 permanent sampling stations described in Nevo (1995). The allozymic analysis included 33 spiny mice, *Acomys*, and 50 woodmice, *Apodemus*, sampled on the opposite slopes, South-facing slope (SFS) and North-facing slope (NFS) at 5 and 6 stations, respectively, as shown in Table 1. The 6 stations involved 3 on the SFS (Upper, middle and lower, 1–3) and 3 on the NFS (Lower, middle and upper, 5–7). The lower, middle and upper stations on each slope were at 60, 90 and 120 m above sea level. The interslope distance at the valley bottom is 100 m, and at top valley 400 m.

Table 1. I. Sampling data and molecular (allozyme and RAPD) analysis and II. Morphological body measurements of A. *Acomys cahirinus* and B. *Apodemus mystacinus* from 6 stations on two opposite slopes of "Evolution Canyon" in Lower Nahal Oren, Mt. Carmel, Israel. SFS – South-facing slope, NFS – North-facing slope. Weight in grams and length in milimeters. The values: average ± SE and in parenthesis relative length to weight. W – weight, HBL – body + head length, TL – tail length, HFL – hind foot length, EL – ear length.

I. Sampling data

	1	2	3	5	6	7	SFS	NFS	Total
				A. *Acomys cahirinus*					
Collected	16	22	10	1	10	8	54	19	73
Allozyme analysis	7	10	7	0	5	4	24	9	33
DNA RAPD analysis	3	5	5	0	4	4	13	8	21
Animals whose station is unknown							6		6
				B. *Apodemus mystacinus*					
Collected	15	14	9	19	17	21	39	60	99
Allozyme analysis	8	7	4	13	10	8	19	31	50
DNA RAPD analysis	4	4	4	6	7	3	12	16	28
Animals whose station is unknown							1	3	4
Grand total (collected)	31	36	19	20	27	29	93	79	172

II. Morphology
(1) Slopes

Sex	Slope facing	*n*	W	HBL	TL	HFL	EL
				A. *Acomys cahirinus*			
Males	SFS	28	46.98 ± 1.33	113.36 ± 1.36 (2.413)	100.32 ± 1.66 (2.135)	19.75 ± 0.16 (0.420)	19.50 ± 0.15 (0.415)
	NFS	10	49.86 ± 1.94	113.60 ± 2.16 (2.278)	104.50 ± 3.02 (2.096)	19.60 ± 0.28 (0.393)	19.80 ± 0.20 (0.397)
Females	SFS	18	40.94 ± 2.32	107.24 ± 1.74 (2.619)	97.00 ± 2.41 (2.369)	19.08 ± 0.28 (0.466)	19.03 ± 0.35 (0.465)
	NFS	9	42.78 ± 2.88	106.67 ± 3.61 (2.493)	100.13 ± 4.10 (2.341)	18.78 ± 0.40 (0.439)	19.00 ± 0.47 (0.444)
				B. *Apodemus mystacinus*			
Males	SFS	20	39.68 ± 1.79	111.00 ± 1.85 (2.797)	120.47 ± 2.33 (3.036)	25.28 ± 0.22 (0.637)	19.40 ± 0.24 (0.489)
	NFS	33	33.14 ± 1.42	109.95 ± 1.69 (3.318)	115.12 ± 1.73 (3.474)	25.70 ± 0.17 (0.775)	19.33 ± 0.29 (0.583)
Females	SFS	18	30.78 ± 1.45	103.72 ± 1.76 (3.370)	116.93 ± 2.13 (3.799)	25.25 ± 0.18 (0.820)	19.33 ± 0.24 (0.628)
	NFS	24	37.71 ± 1.42	107.83 ± 1.69 (2.859)	116.00 ± 1.73 (3.076)	25.42 ± 0.17 (0.674)	19.42 ± 0.29 (0.515)

(2) Stations

Sex	Slope facing	*n*	W	HBL	TL	HFL	EL
				A. *Acomys cahirinus*			
Males	S1	10	46.71 ± 1.69	113.10 ± 2.64 (2.421)	99.17 ± 4.75 (2.123)	19.75 ± 0.29 (0.423)	19.30 ± 0.26 (0.413)
	S2	14	46.25 ± 1.61	113.64 ± 2.01 (2.457)	100.62 ± 1.85 (2.175)	19.75 ± 0.22 (0.427)	19.57 ± 0.20 (0.423)
	S3	3	49.10 ± 3.78	111.67 ± 1.67 (2.274)	100.50 ± 4.50 (2.047)	20.00 ± 0.58 (0.407)	20.00 ± 0.58 (0.407)
	N5	0					
	N6	6	48.50 ± 1.19	114.33 ± 2.17 (2.357)	102.50 ± 4.33 (2.113)	19.67 ± 0.44 (0.406)	20.00 ± 0.26 (0.412)
	N7	4	51.90 ± 4.72	112.50 ± 4.73 (2.168)	108.50 ± 0.50 (2.091)	19.50 ± 0.29 (0.376)	19.50 ± 0.29 (0.376)
Females	S1	5	49.45 ± 2.86	110.00 ± 1.58 (2.224)	104.00 ± 0.71 (2.103)	19.30 ± 0.44 (0.390)	19.50 ± 0.39 (0.394)
	S2	6	38.45 ± 3.37	104.20 ± 3.02 (2.710)	95.00 ± 3.45 (2.471)	18.67 ± 0.61 (0.485)	18.00 ± 0.58 (0.468)
	S3	6	35.67 ± 3.50	106.50 ± 3.96 (2.986)	93.00 ± 5.99 (2.607)	19.50 ± 0.43 (0.547)	19.67 ± 0.71 (0.551)
	N5	1	28.38	97 (3.428)	78 (2.756)	19 (0.671)	17 (0.601)
	N6	4	42.20 ± 4.56	105.00 ± 5.34 (2.488)	99.67 ± 2.91 (2.362)	18.50 ± 0.65 (0.438)	19.00 ± 0.41 (0.450)
	N7	4	46.98 ± 2.34	110.75 ± 5.96 (2.358)	106.00 ± 4.69 (2.257)	19.00 ± 0.71 (0.404)	19.50 ± 0.87 (0.415)
				B. *Apodemus mystacinus*			
Males	S1	8	39.99 ± 2.67	111.25 ± 2.86 (2.782)	122.43 ± 3.05 (3.062)	25.13 ± 0.39 (0.628)	19.87 ± 0.35 (0.497)
	S2	7	43.89 ± 2.33	114.14 ± 2.93 (2.601)	122.71 ± 3.45 (2.796)	25.79 ± 0.31 (0.588)	19.29 ± 0.42 (0.440)
	S3	4	30.00 ± 1.94	102.75 ± 2.29 (3.425)	110.00 ± 5.02 (3.667)	24.50 ± 0.29 (0.817)	18.75 ± 0.63 (0.625)
	N5	13	37.68 ± 1.88	107.50 ± 1.33 (2.853)	113.12 ± 1.73 (3.002)	25.38 ± 0.30 (0.674)	18.85 ± 0.30 (0.500)
	N6	8	39.45 ± 3.17	109.88 ± 2.63 (2.785)	116.20 ± 1.77 (2.946)	25.69 ± 0.39 (0.651)	20.38 ± 1.00 (0.516)
	N7	12	37.77 ± 2.30	112.67 ± 2.51 (2.983)	117.00 ± 2.29 (3.098)	26.04 ± 0.22 (0.690)	19.17 ± 0.21 (0.508)
Females	S1	7	28.81 ± 2.45	102.57 ± 3.14 (3.560)	114.40 ± 2.38 (3.971)	25.79 ± 0.21 (0.895)	19.57 ± 0.48 (0.679)
	S2	7	34.86 ± 1.84	107.00 ± 2.37 (3.069)	121.50+4.11 (3.485)	24.86 ± 0.14 (0.713)	19.00 ± 0.22 (0.545)
	S3	4	27.10 ± 2.10	100.00 ± 3.54 (3.690)	113.25 ± 3.25 (4.179)	25.00 ± 0.58 (0.923)	19.50 ± 0.65 (0.720)
	N5	5	40.88 ± 3.92	109.20 ± 4.03 (2.671)	114.25 ± 3.90 (2.795)	25.40 ± 0.40 (0.621)	18.80 ± 0.80 (0.460)
	N6	10	36.01 ± 2.10	105.80 ± 2.57 (2.938)	117.33 ± 3.04 (3.258)	25.45 ± 0.32 (0.707)	19.40 ± 0.52 (0.539)
	N7	9	37.84 ± 2.14	109.33 ± 2.87 (2.889)	115.17 ± 2.18 (3.043)	25.39 ± 0.20 (0.671)	19.78 ± 0.32 (0.523)

Trapping with Sherman live traps (details in Blaustein *et al.* 1996) was conducted at the 6 locations during summer (28 June to 14 July), winter (7–22 December) 1994; and January–February 1995, one kilometer upstream from our permanent transect (Nevo 1995). Trapping results appear in Table 1. Morphological measurements were taken of all trapped animals. Tissues of 83 animals collected in 1994 and 1995 were preserved in the laboratory at −80°C untill processed for protein (allozymes) and DNA (RAPDs) diversities.

Electrophoretic procedure and loci studied. Homogenates for electrophoresis were obtained from portions of muscle and kidney tissues crushed in distilled water. Genetic diversity of structural genes encoding for enzymatic and non-enzymatic proteins was assessed using standard horizontal starch-gel electrophoresis (the procedures were those described by Filippucci *et al.* 1987, Nevo *et al.* 1994). All gels were prepared using an 11% suspension of Connaught hydrolyzed starch.

Homogenates obtained from muscle were processed for the following enzymatic proteins involving 35 and 33 putative gene loci in *Acomys* and *Apodemus*, respectively: α-glycerophosphate dehydrogenase (E.C. 1.1.1.8; *α-Gpdh*), alcohol dehydrogenase (E.C. 1.1.1.1.; *Adh*), sorbitol dehydrogenase (E.C. 1.1.1.14; *Sdh*), lactate dehydrogenase (E.C. 1.1.1.27; *Ldh*-1 and *Ldh*-2), malate dehydrogenase (E.C. 1.1.1.37; *Mdh-1* and *Mdh-2*), malic enzyme (E.C. 1.1.1.40; *Me-1* and *Me-2*), isocitrate dehydrogenase (E.C. 1.1.1.42; *Idh-1* and *Idh-2*), 6-phosphogluconate dehydrogenase (E.C. 1.1.1.44; *6Pgdh*), glucose-6-phosphate dehydrogenase (E.C. 1.1.1.49; *G6pdh*), glyceraldehyde- 3-phosphate dehydrogenase (E.C. 1.2.1.12; *G3pdh*), indophenol oxidase (E.C. 1.15.1.1; *Ipo-1* and *Ipo-2*), nucleoside phosphorilase (E.C. 2.4.2.1; *Np*), glutamate- oxaloacetate transaminase (E.C. 2.6.2.1.; *Got-1* and *Got-2*), hexokinase (E.C. 2.7.1.1; *Hk-1* and *Hk-2*), creatine kinase (E.C. 2.7.3.2; *Ck*), adenylate kinase (E.C. 2.7.4.3; *Adk*), phosphoglucomutase (E.C. 2.5.7.1; *Pgm-1* and *Pgm-2*), esterases (E.C. 3.1.1.1; *Est-2*, *Est-3* and *Est-4*), aminopeptidase (E.C. 3.4.11; *Ap-1*, *Ap-2* and *Ap-4*), leucyl aminopeptidase (E.C. 3.4.11; *Lap*), adenosine deaminase (E.C. 3.5.4.4; *Ada*), aldolase (E.C. 4.1.2.13; *Ald*), fumarase (E.C. 4.2.1.2; *Fum*), mannose phosphate isomerase (E.C. 5.3.1.8; *Mpi*), glucose phosphate isomerase = phosphoglucose isomerase (E.C. 5.3.1.9; *Pgi*).

Isozymes were numbered in order of decreasing mobility from the most anodal one. Allozymes were designated numerically according to their mobility, relative to the most common allele (= 100), (< 100 = slower mobility; > 100 = faster mobility) in the reference population for *Apodemus mystacinus* (Filippucci *et al.* 1989) and at "Evolution Canyon" for *Acomys cahirinus*.

Intrapopulational genetic diversity was estimated by the following genetic indices: the mean heterozygosity per locus per individual (observed heterozygosity – H), gene diversity (equals to expected heterozygosity under panmixia – H_e), the proportion of polymorphic loci in the population (P–5%: a locus is considered polymorphic if the frequency of the most common allele is not greater than 0.99 and 0.95, respectively), and the average number of alleles per locus (A). The amount of genetic divergence between populations was estimated with the index of standard genetic distance (D) (Nei 1978) and the chord distance (Cavalli-Sforza and Edwards 1967). The statistics was computed by the Biosys-1 (Swofford and Selander 1989).

The high number of loci analyzed, 35 and 33 alozymic loci, and 106 and 81 RAPD loci in *Acomys* and *Apodemus*, respectively, compensates for the small sample size of some subpopulations, for *Apodemus* on the SFS and *Acomys* on the NFS. Values of heterozygosity and genetic distance are therefore reliable with a reasonable margin of precision (Sarich 1977, Nei 1978, Gorman and Renzi 1979). Nevertheless, we plan additional future sampling and analysis.

RAPD PCR diversity. We also analyzed 21 and 28 individuals of *Acomys* and of *Apodemus* for RAPD PCR analysis (Table 1). The RAPD method allows the detection of DNA sequence polymorphisms using single primers of arbitrary sequences across the genome in the polymerase chain reaction (Williams *et al.* 1990). The method is useful in genetic analysis when the variation in banding pattern represents allelic segregation at independent loci (Clark and Lanigan 1993). Polymorphism is detected as band presence versus absence, and band absence may be caused either by failure to prime a site in some individuals because of nucleotide sequence differences or by insertions or deletions in fragment between two conserved primer sites. We analyzed 106 and 81 bands considered as loci in *Acomys* and *Apodemus*, respectively. Following are the technical details:

DNA isolation and arbitrary primers. High molecular weight genomic DNA was extracted from kidney, following Holland (1983). We selected 10 primers that showed reliably reproduced polymorphisms for *Acomys* out of 140 10-mer primers of RAPD primer Kit 11×, University of British Columbia: Nos. 306, 323, 333, 337, 350, 363, 371, 405, 408, and 411; and for *Apodemus* 12 primers were selected from RAPD primer kits (Operon Technologies, Almeda, CA, USA; 11 X University of British Columbia, Canada: A-1 Operon, Nos. 312, 313, 318, 319, 322, 326, 328, 329, 349, 419, and 431. Each primer was dissolved in water to yield the final concentration of DNA 10 mg/ml and stored at −20°C.

PCR and agarose gel electrophoresis. Each amplification reaction (20 µl) contained 2 µl DNA sample for *Acomys* and 1 µl for *Apodemus* (10 ng/µl), 1.2 µl primer (10 ng/µl), 2.1 µl storage buffer, 1.6 µl $MgCl_2$ (25 mM), 2 µl dNTPs (1mM), 2 ml reaction buffer (10×), 0.1 µl enzyme and 9 and 10 µl H_20, for *Acomys* and *Apodemus*, respectively. 25 µl of light paraffin oil was overlaid on each reaction mixture before starting the reaction. DNA amplification was performed using the Perkin-Elmer DNA thermal cycler programmed for 45 cycles of 1 min at 94°C (denaturation), 1 min at 37°C (primer annealing) and 2 min at 72°C (primer extension) followed by storage at 4°C until use. 2 µl of gel loading dye solution were added directly to the reaction tubes. Depending on species, a total of 20 µl DNA samples were loaded for electrophoresis on 1.2% agarose gel. DNA fragments were then visualized and photographed under UV light.

Data scoring and statistical analysis. Photographs from ethidium bromide stained agarose gels were used to score the data for RAPD analysis. To estimate gene diversity for RAPDs we used formulas published by Lynch and Milligan (1994). In total, 106 and 81 bands ("loci") were obtained for *Acomys* and *Apodemus*, respectively. As recommended by Lynch and Milligan (1994), the genetic analysis was restricted to bands whose observed frequency is less than 1-(3/N), where N is the sample size. In this analysis we regarded the animals from each slope as a subpopulation (pooled data). After the restriction, 77 relevant bands were selected for *Acomys* and 33 bands for *Apodemus*. The results are presented in Table 2.

Beside this estimation, we used another approach to compare the two populations. PCR-phenotype of each animal is described by 106 and 81 bands each of which can be equal to 0 or to 1 for *Acomys* and *Apodemus*, respectively (presence or absence of each of the bands). We used the proximities program of the SPSS package (SPSS, 1990) for calculations of the Eucledian distances between localities using the band frequency data. The results of these calculations are presented in Table 3.

Results

Morphological variation

Morphological measurements of *Acomys* and *Apodemus* appear in Table 1, II. In general, body weight in both species is smaller on the SFS, except in *Apodemus* males, where the opposite is true. Extremities (tail, TL, hindfoot, HFL, and ear lengths, EL, relative to body weight) were longer on the SFS than on the NFS except in HFL and EL of *Apodemus* males. These patterns of body weight and extremities length coroborate the Bergmann and Allen rules, ie displaying positive and negative correlation with latitude, respectively, on a local scale.

Genetic diversity

Acomys cahirinus

(1) Allozymic variation

Interslope genetic divergence. We tested 24 animals from 3 stations (Nos 1–3) on the SFS and 9 animals from 2 stations (Nos 6 and 7) on NFS (Table 1). Only

Table 2. Allozyme allele frequencies of polymorphic loci of A. *Acomys cahirinus* and B. *Apodemus mystacinus* at "Evolution Canyon", Lower Nahal Oren, Mt. Carmel, Israel. *S and *N means an allele retricted to SFS or NFS, respectively. *n* – sample size, *He* – gene diversity. A. 28 monomorphic loci: *a-G6pdh, Sdh, Ldh-1,2, Mdh-1,2, Me-2, Idh-1,2, 6Pgdh, G6pdh, G3pdh, Ipo, Np, Got-1,2, Hk-1,2, Adk, Pgm-1,3, Ap-1,2, Lap, Est-4, Ald, Pgi, Adh*. B. 25 monomorphic loci: *a-G6pdh, Sdh, Ldh-1,2, Mdh-1,2, Idh-1,2, Mpi, G3pdh, Ipo-1,2, Fum, Np, Adh, Got-2, Hk-2, Adk, Pgm-2, Ap-2,4, Ck, Lap, Ald, Pgi*.

	Slope facing:	SFS			NFS			Slopes (pooled data)	
	Station:	high	middle	low	low	middle	high	SFS	NFS
Locus	Allele	1	2	3	5	6	7		
				A. *Acomys cahirinus*					
Ada	*a*	1.000	0.850	1.000	–	1.000	1.000	0.938	1.000
	*b**S	0.0	0.150	0.0		0.0	0.0	0.063	0.0
He		0.0	0.255	0.0		0.0	0.0	0.116	0.0
n		7	10	7	–	5	4	24	9
Mpi	*a*	0.643	0.600	0.643	–	0.600	0.625	0.625	0.611
	b	0.071	0.050	0.071		0.100	0.0	0.063	0.056
	c	0.286	0.350	0.286		0.300	0.375	0.313	0.333
He		0.500	0.515	0.500		0.540	0.469	0.507	0.513
n		7	10	7	–	5	4	24	9
Me-1	*a*	0.786	0.944	1.000	–	0.800	0.500	0.913	0.667
	b	0.214	0.056	0.0		0.200	0.250	0.087	0.222
	*c**N	0.0	0.0	0.0		0.0	0.250	0.0	0.111
He		0.336	0.106	0.0		0.320	0.625	0.159	0.506
n		7	9	7	–	5	4	23	9
Ck	*a*	0.929	0.850	1.000	–	1.000	1.000	0.917	1.000
	*b**S	0.0	0.050	0.0		0.0	0.0	0.021	0.0
	*c**S	0.071	0.100	0.0		0.0	0.0	0.063	0.0
He		0.132	0.265	0.0		0.0	0.0	0.155	0.0
n		7	10	7	–	5	4	24	9
Est-2	*a*	1.000	0.750	1.000	–	0.900	0.875	0.896	0.889
	b	0.0	0.250	0.0		0.100	0.125	0.104	0.111
He		0.0	0.375	0.0		0.180	0.219	0.186	0.197
n		7	10	7	–	5	4	24	9
Est-3	*a*	0.917	0.950	1.000	–	0.900	1.000	0.957	0.944
	b	0.083	0.050	0.0		0.100	0.0	0.043	0.056
He		0.152	0.095	0.0		0.180	0.0	0.082	0.106
n		6	10	7	–	5	4	23	9
Fum	*a*	0.750	0.938	1.000	–	0.900	1.000	0.921	0.944
	b	0.250	0.063	0.0		0.100	0.0	0.079	0.056
He		0.375	0.116	0.0		0.180	0.0	0.146	0.106
n		4	8	7	–	5	4	19	9
Average *n*		6.4	9.6	7	0	5	4	23	9

Table 2 – concluded.

Locus	Slope facing: / Station: / Allele	SFS high 1	SFS middle 2	SFS low 3	NFS low 5	NFS middle 6	NFS high 7	Slopes (pooled data) SFS	Slopes (pooled data) NFS
				B. *Apodemus mystacinus*					
Ada	*a**N	0.0	0.0	0.0	0.0	0.0	0.063	0.0	0.016
	b	1.000	1.000	1.000	0.923	1.000	0.938	1.000	0.952
	*c**N	0.0	0.0	0.0	0.077	0.0	0.0	0.0	0.032
He		0.0	0.0	0.0	0.142	0.0	0.116	0.0	0.092
Me-1	*a**N	0.0	0.0	0.0	0.0	0.0	0.063	0.0	0.016
	b	0.688	0.857	0.750	0.654	0.800	0.750	0.763	0.726
	c	0.313	0.143	0.250	0.346	0.200	0.188	0.237	0.258
He		0.429	0.245	0.375	0.453	0.320	0.398	0.362	0.406
Me-2	*a**N	0.0	0.0	0.0	0.038	0.050	0.0	0.0	0.032
	b	0.500	0.857	0.625	0.885	0.950	0.750	0.658	0.871
	c	0.500	0.143	0.375	0.077	0.0	0.250	0.342	0.097
He		0.500	0.245	0.469	0.211	0.095	0.375	0.450	0.231
6Pgdh	*a**S	0.0	0.0	0.125	0.0	0.0	0.0	0.026	0.0
	b	1.000	1.000	0.875	0.923	0.850	1.000	0.974	0.919
	*c**N	0.0	0.0	0.0	0.077	0.150	0.0	0.0	0.081
He		0.0	0.0	0.219	0.142	0.255	0.0	0.051	0.149
G6pdh	*a*	1.000	0.929	1.000	0.962	1.000	1.000	0.974	0.984
	b	0.0	0.071	0.0	0.038	0.0	0.0	0.026	0.016
He		0.0	0.132	0.0	0.073	0.0	0.0	0.051	0.031
Got-1	*a*	0.875	0.929	1.000	0.846	0.900	0.938	0.921	0.887
	b	0.125	0.071	0.0	0.154	0.100	0.063	0.079	0.113
He		0.219	0.132	0.0	0.261	0.180	0.116	0.146	0.200
Est-3	*a*	0.688	0.071	0.250	0.269	0.150	0.063	0.368	0.177
	b	0.313	0.929	0.750	0.692	0.850	0.938	0.632	0.806
	*c**N	0.0	0.0	0.0	0.038	0.0	0.0	0.0	0.016
He		0.152	0.132	0.375	0.447	0.255	0.116	0.465	0.319
Pgm-1	*a*	1.000	1.000	1.000	0.962	0.950	1.000	1.000	0.968
	*b**N	0.0	0.0	0.0	0.038	0.050	0.0	0.0	0.032
He		0.0	0.0	0.0	0.073	0.095	0.0	0.0	0.062
n		8	7	4	13	10	8	19	31

one *Acomys* was caught at station 5 (NFS-low), despite successive trap setting, suggesting that this lower station is an unfit habitat for *Acomys*, possibly because it is largely rockless. Seven loci out of 35 (20%) (*Me-1*, *Ck*, *Ada*, *Mpi*, *Fum*, *Est-2*, *Est-3*) were polymorphic (Table 2). All the 7 loci were polymorphic on SFS and

only 5 on NFS. Four alleles were slope-specific, one to NFS and 3 to SFS (Table 2). All other loci were monomorphic on both slopes (*Adh*, *αGpdh*, *Sdh*, *Ldh-1,2*, *Mdh-1,2*, *Me-2*, *Idh-1,2*, *6Pgdh*, *G-6pdh*, *G3pdh*, *Ipo*, *Got-1,2*, *Hk-1,2*, *Adk*, *Pgm-1,2*, *Np*, *Lap*, *Ap-1,2*, *Est-4*, *Ald*, *Pgi*).

Genetic indices. Results appear in Table 3. The general level of diversity is low. It is obvious that in all indices (*A*, *P*, *H*, and *He*) the relatively more mesic and vegetated low station of SFS (S3) had the lowest diversity in Nahal Oren, whereas the more xeric middle station (S2) only 30 m above had the highest level of diversity, except for *H*, for which the exposed rocky upper station 7 on NFS was more diverse. Thus, genetic intraslope divergence was larger on the ecologically heterogeneous SFS than the interslope divergence.

Comparing the slopes reveals that in A and P SFS shows higher diversity, whereas *H* and *He* are higher on NFS. This contradiction between the *P* and *H* estimates may be caused by the extreme drop in *H* and *He* in S3, and the high *H* and *He* of *Me-1* in N7 (100% heterozygotes). Overall, however, if the 2 xeric stations of SFS (Nos 1 and 2) are compared with the 2 mesic stations of NSF (Nos 6 and 7) then the SFS animals are more genetically diverse than the NFS animals (excepting *H*), as is also true regionally across Israel (Nevo 1985, and see Discussion).

Genetic distances. Nei's genetic distances were too small to be used here (*D* = 0.00 – 0.003). Therefore, we used the Cavalli-Sforza and Edwards (1967) chord distance which appear in Table 4. The closest stations were S1 and N6 (= 0.051), whereas the most distant stations were S1 or S2 and N7 (= 0.103). The average interslope distance is less than the distances between the SFS stations and is equal to the within NFS distance (Table 4).

A dendrogram based on the genetic distance matrix shows that N6 and S1 are the closest subpopulations and then S2, S3 and N7 are sequentially joining the first pair (Fig. 2).

Gametic phase disequilibria. We found 8 gametic phase disequilibria (D) on the SFS and 6 on NFS with $|D| > 0.010$ (Table 5). No D was significant, presumably because of the small sample sizes. Two pairs showed the same signed D on both slopes, so they can be regarded as general Ds (*Mpi* × *Me-1* and *Mpi* × *Est-2*) while the other 10 Ds are presumably slope-specific, 6 on the SFS and 4 on the NFS.

(2) RAPD diversity

Altogether we obtained 106 bands, considered putatively as loci, by using 10 primers as described in Material and methods. The results based on phenotypic band counting appear in Table 3.

Band counting. Polymorphic band number was higher on the SFS than on NFS (75 versus 72). The opposite was true if station S3 was omitted in order to compare interslope parallel stations, ie, S1 and S2 versus N6 and N7. A gradual decrease of polymorphic band percentage was displayed upward on the SFS from station S3 through S2 to the most xeric S1 (52, 47 and 43, respectively) (Table 3).

Table 3. Genetic summary of proteins and RAPD polymorphism in A. *Acomys cahirinus*, and B. *Apodemus mystacinus*, as a function of interslope differential solar radiation in a microsite at "Evolution Canyon", Lower Nahal Oren, Mt. Carmel, Israel. Genetic diversity of I. Allozymic loci and II. DNA RAPD bands or loci, at six stations, 3 on the South-facing slope (SFS) (1–3) and 3 on the North-facing slope (NFS) (5–7). Genetic indices of RAPDs according to Lynch and Milligan (1994). *n* – sample size, *P* – proportion of polymorphic loci, *A* – mean number of alleles per locus, *H* – observed heterozygosity, *He* – gene diversity.

Slope:	SFS			NFS			Pooled		Contrast of S1+S2 vs N6+N7 (pooled data)	
Station:	upper	middle	lower	lower	middle	upper	SFS	NFS		
	1	2	3	5	6	7			SFS	NFS
					A. *Acomys cahirinus*					
I. Protein diversity: Allozymes (35 loci):										
Average *n*	6.9	9.9	7.0	0	5.0	4.0	23.8	9.0	16.8	9.0
P – 5%	0.143	0.200	0.029	–	0.143	0.086	0.171	0.143	0.200	0.143
A ± SE	1.17±0.08	1.26±0.09	1.06±0.06	–	1.17±0.08	1.11±0.07	1.26±0.09	1.20±0.09	1.26±0.09	1.20±0.09
H ± SE	0.033±0.018	0.047±0.021	0.020±0.020	–	0.040±0.024	0.057±0.036	0.035±0.017	0.048±0.026	0.042±0.018	0.048±0.026
He ± SE	0.047±0.022	0.052±0.021	0.015±0.015	–	0.044±0.021	0.043±0.026	0.040±0.017	0.043±0.022	0.050±0.019	0.043±0.022
II. DNA diversity: RAPDs (77 loci):										
n	3	5	5	0	4	4	13	8		
P – 5% criterion							0.86	0.70		
A							1.86	1.70		
He							0.23	0.19		
Polymorphic bands (out of 106)	43	47	52		50	53	75	72		
					B. *Apodemus mystacinus*					
I. Protein diversity: Allozymes (33 loci):										
Average *n*	8.0	7.0	4.0	13.0	10.0	8.0	19.0	31.0		
P – 5%	0.121	0.152	0.121	0.182	0.121	0.152	0.121	0.152		
A ± SE	1.12±0.06	1.15±0.06	1.12±0.06	1.30±0.10	1.18±0.07	1.18±0.08	1.18±0.07	1.36±0.12		
H ± SE	0.045±0.024	0.030±0.014	0.045±0.023	0.051±0.019	0.030±0.014	0.034±0.017	0.040±0.019	0.040±0.016		
He± SE	0.051±0.025	0.029±0.013	0.050±0.025	0.057±0.022	0.038±0.016	0.036±0.018	0.047±0.022	0.046±0.018		
II. DNA diversity: RAPDs (33 loci):										
n	4	4	4	6	7	3	12	16		
P – 5% criterion							0.79	0.85		
A							1.79	1.85		
He							0.22	0.22		
Polymorphic bands (out of 81)	22	28	17	27	29	23	40	46		

Table 4. Genetic distances I. (*C*, Cavalli-Sforza and Edwards, 1967) based on allozymic data or II. Euclidean distances based on RAPD band frequencies, among the subpopulations of A. *Acomys cahirinus*. B. *Apodemus mystacinus* at "Evolution Canyon", Lower Nahal Oren, Mt. Carmel, Israel. SFS – South-facing slope, NFS – North-facing slope.

	A. *Acomys cahirinus*				B. *Apodemus mystacinus*				
Slope:	SFS		NFS		SFS		NFS		
Station:	middle 2	low 3	middle 6	high 7	middle 2	low 3	low 5	middle 6	high 7
				I. *C* distance based on allozymic data					
S1	0.085	0.087	0.051	0.103	0.097	0.077	0.094	0.120	0.094
S2	–	0.094	0.070	0.102	–	0.073	0.074	0.078	0.053
S3	–	–	0.078	0.096	–	–	0.096	0.106	0.071
N5					–	–	–	0.062	0.088
N6	–	–	–	0.083	–	–	–	–	0.091
	Distance between SFS and NFS: 0.060 (pooled data) 0.083 (average)				Distance between SFS and NFS: 0.070 (pooled data) 0.087 (average)				
				II. Euclidean distance based on RAPD data					
S1	2.322	2.906	3.368	3.343	1.577	1.820	1.945	1.699	1.822
S2	–	2.272	2.871	2.940	–	1.635	1.436	1.267	2.183
S3	–	–	2.994	2.909	–	–	1.687	1.562	2.191
N5					–	–	–	1.320	2.248
N6	–	–	–	2.208	–	–	–	–	2.181
	Distance between SFS and NFS: 2.447 (pooled data) 3.071 (average)				Distance between SFS and NFS: 0.964 (pooled data) 1.755 (average)				

Band slope specificity. RAPD band-slope specificity was higher on the SFS than on NFS (23 versus 11). Nine slope-specific high frequent bands (> 0.10) occurred on SFS and 3 on NFS. These bands reinforce the apparently lack of migration between the slopes, deduced from mark-recapture studies (Blaustein *et al.* 1996).

RAPD genetic summary. The genetic summary statistics of RAPDs appear in Table 3, together with sample size and band numbers. All genetic estimates of genic diversity, *He*, polymorphism *P*-5%, and allele diversity, *A*, estimates were higher for SFS than NFS animals, as was the case for allozymes. This suggests that RAPD and allozyme loci are subjected to the same selective regime, and similarly represent genetic diversity across the genome.

Genetic distances. We calculated the interslope phenotypic distance based on presence/absence of each of the 106 bands. We used the SPSS proximities program to calculate Eucledian distances (SPSS, 1990). The RAPD average interslope distance was 3.071 larger than the intraslope distances on the SFS (2.500) and NFS (2.208). The interslope distance between the pooled slope data sets was 2.447.

Apodemus mystacinus

(1) Allozymic variation

We sampled 19 animals from the SFS and 31 animals from the NFS. Among 33 loci, 8 loci (24%) were polymorphic. Seven slope-specific alleles were found on the NFS whereas only a single allele was found on the SFS (Table 2B). Presumably, the SFS stress on mesic *Apodemus* selects for a restricted subset of alleles, adapted to xeric conditions typifying the SFS, as was also shown for *Apodemus* allozymes regionally (Filippucci *et al.* 1989) and for other organisms tested experimentally under heavy pollution controlled laboratory experiments (eg Nevo *et al.* 1981).

Genetic indices. Results appear in Table 3B. The interslope and intraslope differences are milder in *Apodemus* than in *Acomys*. The most polymorphic (*P*, also in *H*, *He*, and *A*) station was N5 (NFS-low), whereas the least polymorphic stations were S1, S3 and N6. Heterozygosity (*H*) and genic diversity (*He*) were equal on both slopes. In *A* and *P* NFS is more diverse than SFS, in contrast to *Acomys*.

Genetic distance. Nei's genetic distance was again inappropriate. Only S1 was separated from S2, N6 and N7 by D's larger than 0.010. In Cavalli-Sforza and Edwards Chord distance (Table 4B), and in other distance measures, the largest

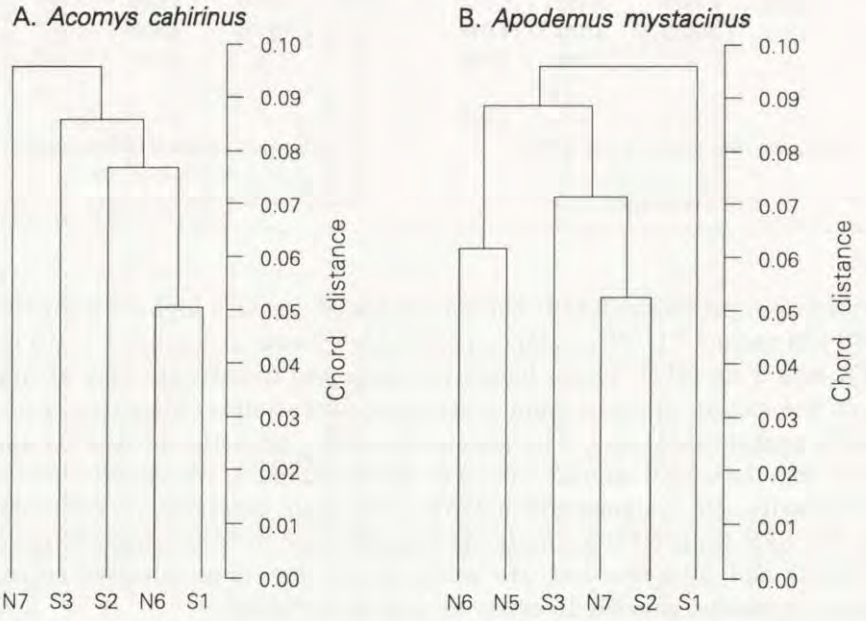

Fig. 2. (A) Dendrogram based on genetic distances between stations calculated from allozymic variation (Table 4) of *Acomys cahirinus* from 5 stations on the SFS (South upper, S1, South middle, S2, and South low, S3) and NFS (North middle, N6, and North upper, N7). (B) Dendrogram based on genetic distances between station calculated from allozymic variation (Table 4), of *Apodemus mystacinus* from 3 stations on the SFS (upper, middle, low, S1, S2, S3, respectively) and 3 stations on the NFS (lower, middle and upper, N5, N6, N7).

distance was between S1 and N6 (0.120) whereas S2 and N7 were the genetically closest stations (0.053). This is exactly the opposite than in *Acomys*. Also, in contrast to *Acomys*, in *Apodemus* the interslope average distance was larger than the within slope distances (0.087 > 0.082 and 0.080). We used the Cavalli-Sforza and Edwards Chord estimates to construct the dendrogram (Fig. 2B). Three clusters are obvious: S2 with N7 and S3, N5 with N6, and S1 is the farthest subpopultion.

Gametic phase disequilibrium. We found 3 allozyme Ds on the SFS and 4 Ds on NFS with $|D| > 0.010$. Of those, *Me-1* × *Est-3* seems to be general while the other disequilibria are slope-specific, 2 on the SFS and 3 on the NFS (Table 5B).

Table 5. Gametic phase disequilibria, absolute (D) and relative (D'), between paired loci of A. *Acomys cahirinus* and B. *Apodemus mystacinus* at "Evolution Canyon", Lower Nahal Oren, Mt. Carmel: (1) general (2) specific to NFS and (3) specific to SFS. c – complete association: one gametic type is missing (Clegg *et al.* 1976).

Locus and allele	NFS		SFS	
	D	(D')	D	(D')
	A. *Acomys cahirinus*			
(1) General disequilibria				
Me-1 a – Mpi c	0.040	(0.518)	0.019	(0.950)
Est-2 a – Mpi c	0.017	(0.798)	0.018	(0.851)
(2) Specific to NFS				
Me-1 a – Est-2 a	0.038	(0.818)	−0.006	(0.931)
Fum a – Mpi c	0.019	(1.0, c)	0.003	(0.095)
Est-3 a – Me-1 a	−0.019	(1.0, c)	−0.001	(0.811)
Fum a – Me-1 a	−0.019	(1.0, c)	−0.004	(1.0, c)
(3) Specific to SFS				
Est-2 a – Ada b	–		−0.038	(0.950)
Fum a – Ada b	–		−0.020	(0.275)
Est-2 a – Fum a	−0.006	(1.0, c)	0.016	(0.233)
Est-3 a – Mpi c	–			
Ada b – Mpi c	–		−0.013	(0.938)
Ck a – Mpi c	–		0.012	(0.856)
	B. *Apodemus mystacinus*			
(1) General disequilibria				
Me-1 b – Est-3 b	0.028	(0.229)	0.035	(0.289)
(2) Specific to NFS				
Est-3 b – 6Pgdh a	0.017	(0.262)	–	
Pgm-1 a – 6Pgdh a	0.014	(0.472)	–	
Me-1 b – 6Pgdh a	−0.012	(0.896)	–	
(3) Specific to SFS				
Me-2 b – Est-3 b	−0.005	(0.213)	0.032	(0.148)
Got-1 a – Est-3 b	0.006	(0.473)	−0.019	(0.921)

(2) RAPD diversity

Altogether we obtained 81 bands (= loci) by using 10 primers as described in Material and Methods. The results based on phenotypic band counting appear in Table 3B.

Band counting. Polymorphic band number was higher on the NFS than on the SFS (46 versus 40). A decrease of polymorphic band percentage was displayed upward on the NFS (from stations N5 and N6 to the most xeric station on this slope, N7 (27, 29 and 23, respectively), (Table 3B).

Band slope specificity. RAPD band-slope specificity was lower on the SFS than on the NFS (5 versus 7, for N = 12 and 16, respectively).

Band genetic summary. The RAPD genetic indices, calculated according to Lynch and Milligan (1994) equations were based on only 33 bands. The value of *P*-5%, and *A*, are higher on the NFS, and *He* is equal on both slopes.

Conclusion. The comparison of genetic patterns of both allozymes and RAPDs in *Apodemus* and *Acomys* indicated opposite trends in the two rodents. The "xeric", climatically more generalist, *Acomys* showed more diversity on the warmer and drier SFS, while the mesic, climatically more specialist, Ap*odemus* showed more diversity on the cooler and wetter NSF. Only a subset of the genetic variation of *Apodemus* persists in the subpopulation hostile SFS. Likewise, except in *H*, the *Acomys* subpopulations on the NSF display lower genetic diversity (see a parallel case in controlled pollution biology experiments in Nevo *et al.* 1981). Remarkably, beside a general gametic phase disequilibria, each slope has its unique ensemble of D's.

Discussion

"Evolution Canyon": the model background

"Evolution Canyon". The sharp physical and biotic inter- and intraslope contrasts are remarkable: the SFS represents a very heterogeneous dry tropical "African" savanna on a very rocky formation. By contrast, the NFS represents a mesic and cooler temperate "European" lush and dense liveoak maquis forest, with restricted rocky habitats (Fig. 1; Nevo 1995, 1997), except in its cliff. This dramatic biotic contrast derives from the physical climatic interslope divergence. The SFS obtains up to 300% more solar radiation deduced from computer simulations (H. Kutiel and G. Sher, unpubl.), and partly documented by direct automatic micro-climatic measurements around the clock measurements (in preparation). The sharp physical and biotic interslope habitat divergence results in the high predominance of tropical *Acomys* and temperate *Apodemus* on the SFS and NFS, respectively (Table 1). This local divergence reflects their original regional-global biogeographical origins, African for *Acomys* and European for *Apodemus*.

The local genetical, morphological, physiological and behavioural patterns

The inter- and intraslope genetic differences, over a very short geographical transect of 300 m, displayed by both *Acomys* and *Apodemus* in multilocus allozyme

and RAPD polymorphisms, heterozygosity, genic diversity, unique alleles, and gametic phase disequilibria indicate microsite genetic divergent patterns presumably caused by micro-climatic natural selection. The relatively small sample sizes are compensated by the large number of allozyme and RAPD loci, 141 and 114 in *Acomys* and *Apodemus*, respectively. Interslope migration is excluded as a major evolutionary factor, since it was not observed in mark-recapture experiments (Blaustein *et al.* 1996), and factually because of its largely homogenizing effect which can not explain the interslope divergent genetic patterns observed. Morphologically, in general, both rodents (excepting *Apodemus* males) showed smaller size and longer extermities on the warmer SFS, displaying locally the Bergmann and Allen rules, respectively. Physiological comparison indicated higher activity pattern and metabolism (20% higher oxygen consumption) in *Acomys* from the NSF than *Acomys* from the SFS (A. Haim *et al.*, in prep.).

The local genetic patterns, in both *Acomys* and *Apodemus* parallel regional genetic patterns across Israel, ie, higher genetic diversity in local and regional xeric environments in *Acomys* (Nevo 1985) and lower genetic diversity in local and regional xeric environments for *Apodemus* (Filippucci *et al.* 1989). Moreover, the local morphological (Table 1), physiological and behavioural (A. Haim *et al.*, in prep.) interslope divergent patterns of *Acomys* parallel the regional morphological (Nevo 1989) and physiological (Weissenberg and Shkolnik 1994) divergent patterns of *Acomys* mesic-xeric across Israel. The *Apodemus* morphological results are less clear regionally (Table 2 in Filippucci *et al.* 1989) probably because the geographical spread of the more specialist *Apodemus* is restricted in Israel than that of *Acomys*. Southern *Apodemus* boundary extends only to the Judean Mountains near Jerusalem, whereas climatically more generalist *Acomys* ranges across mesic and xeric Israel into the Negev and Sinai. This parallelism between local and regional patterns suggest that the genetic, morphologic and physiologic diversities represent a complex adaptive syndrome contributing to fitness across a gradient of increasing aridity. Climatic natural selection, through aridity and temperature stresses, appears to be the major differentiating factor of this syndrome at both the micro- and macroscales. Following is an overview of the regional morphological physiological and genetic differentiation of *Acomys cahirinus* across mesic and xeric Israel, and the morphological and genetic differentiation of *Apodemus mystacinus*.

The regional morphological, physiological, behavioural, and genetic patterns

Acomys cahirinus

Regional morphological adaptations. The genus *Acomys* involves 25 species, largely African, and only few species colonized the Near East, Cyprus and Crete. *A. cahirinus* ranges in Israel in rocky habitats across mesic (Mediterranean) and xeric (steppic, Irano-Turanian, and desert, Saharo-Sindian) environments. Regionally, across Israel, body weight and length decreased, whereas extremities, ie tail, ear and relative forefoot and hind foot lengths generally increased with increasing aridity and temperature southwards into the Negev and Sinai deserts

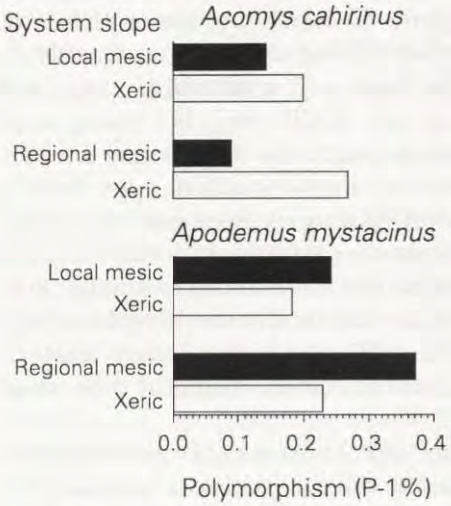

Fig. 3. Local and regional comparison of genetic polymorphism (P–1%) of *Acomys cahirinus* (mesic population, Hurfesh; xeric population, Timna; both in Nevo 1985) and *Apodemus mystacinus* (mesic-Galilee Mts.; "xeric" – Judean Mts, Jerusalem, both in Filippucci *et al.* 1989). The local estimates are from "Evolution Canyon" (this study).

(Nevo 1989). These two trends reflect a positive correlation of weight with latitude (Bergmann's rule) and a negative correlation of body extremities with latitude (Allen's rule). Colour becomes also lighter southward towards the desert. These regional morphological patterns appear to better adapt *Acomys* to a progressively increasing heat and drought load (Nevo, 1989). Complementarily, physiological, behavioural and genetic adaptations to increasing aridity were reported regionally across Israel (see later) (Fig. 3).

The fossil record indicates that *A. cahirinus* is a recent colonizer of the Mediterranean region, dating from the Upper Paleolithic period, some 20 000 years ago (Tchernov 1968). Hence, the geographic variation in morphology, physiology, behaviour and genetics must have taken place during a relatively short period of time, when presumably the northern 2n = 38 speciated from the southern 2n = 36 (Nevo 1985), by colonizing the Mediterranean region from the desert. This northward colonization, shared by many African taxa (Atlas of Israel 1970) is opposite to other rodents, eg, *Spalax*, which colonized the steppes and northern Negev desert originating in the more mesic north (Nevo 1991), as did *Apodemus* which colonized only northern and central Israel (Filippucci *et al.* 1989).

Regional physiological and behavioural adaptations. Physiological adaptation to the environment has been studied in two populations of the common spiny mouse, *A. cahirinus*, one from the extreme desert (Elat), the other from the Galilee, an area characterized by temperate Mediterranean conditions (Weissenberg and Shkolnik 1994). The resting metabolic rate at thermoneutrality in the Elat animals was 0.71 ± 0.13 ml $0_2 g^{-1} h^{-1}$. A 20% higher oxygen consumption was recorded in the animals from the Galilee. The lower critical points for the desert and the Galilee animals were 30°C and 28°C, respectively. When measured in the laboratory (ambient temperature = 28°C), the water turnover rate in the Elat animals was 7.14 ± 1.7ml $(100)^{-1}$ day^{-1}, and in the animals from the Galilee, 11.22 $\pm$ 0.45 ml $(100g)^{-1}$ day^{-1}. The maximal urine concentration obtained in animals maintained on a high protein, high salt diet was 5663 $\pm$ 737 mosml/kg in the animals from Elat and 3895 $\pm$ 224 mosmol/kg in the animals from the Galilee. These results unravel intraspecific geographic variation in metabolism and water

economy, in accordance with increasing aridity and temperature, and decreasing food productivity (Shkolnik 1988). A resting metabolic rate lower than expected from their body mass is known for many desert rodents (eg Dawson 1955). A low metabolic rate and low water turnover and a lower activity pattern are adaptive in the desert because they imply low rate of heat generation, hence prevent overheating, water expenditure and excessive food requirement (Shkolnik 1988).

Regional genetic adaptations. Genetic adaptations to the regional environmental gradient were also found for *Acomys*. Allozymic variation encoded by 35 loci was analyzed in specimens from 7 localities involving 2 populations of *A. cahirinus* 2n = 36, and 5 populations of *A. cahirinus* 2n = 38 (Nevo 1985). The 7 localities represent a general southward transect of increasing aridity from northern Israel to southern Sinai. Polymorphism, *P*, and gene diversity, *He*, significantly increased southwards with aridity, as was the case in additional 21 unrelated taxa in Israel (Nevo and Beiles 1988), including even subterranean mammals (Nevo *et al.* 1994). Higher levels of genetic diversity in micro- and macrogeographic spatiotemporally varying environments are effective adaptations to heterogeneous and stressful environment (Nevo 1978, 1988, 1990, 1995, 1998).

Apodemus mystacinus

Evolutionary biology. The woodmouse *A. mystacinus* is known from the Balkans, Turkey, Iraq, Syria, Lebanon and Israel (Filippucci *et al.* 1989). It is frequent in terrace walls, in olive and fig groves, vineyards, orchards and wheat fields, as well as rocky scrubland and Mediterranean maquis. In Israel it is a common species, primarily in Mount Hermon, the Golan Heights, Galilee and the Carmel Mountains and its southern range is around Jerusalem. It is much more restricted in distribution than that of *Acomys cahirinus*. According to paleontological analysis by Tchernov (1979), three species of *Apodemus* (*A. mystacinus, A. flavicollis* and *A. sylvaticus*) occurred in Israel during the Pleistocene. Moreover, whereas *A. mystacinus* and *A. sylvaticus* have been continuously present in this area, *A. flavicollis* occurred only during colder periods (Tchernov 1979).

The evolutionary biology of the genus *Apodemus* Kaup 1829 in Israel was studied allozymically and biometrically (Filippucci *et al.* 1989). The analysis of 36 gene loci, combined with biometric analysis indicated the existence of a new species *Apodemus hermonensis* on Mt. Hermon at about 2000 m. The most common species in Israel after *A. mystacinus* is *A. flavicollis* and not *A. sylvaticus* as commonly believed. *A. flavicollis* coexisted in low numbers with *A. mystacinus* on the NFS of "Evolution Canyon" but it disappeared during recent years from that site, since it was first recorded and apparently fluctuates around the threshold of a very low population density (Blaustein *et al.* 1996). It is found still elsewhere in Mount Carmel even nearby to "Evolution Canyon" (Hofman and Dolev, unpubl. report,

1996). The genus *Apodemus* invaded the Near East, probably from southeastern Europe, relatively late (Tchernov 1979). According to current estimates of evolutionary divergence time from genetic distance data the separation between Israeli and Balkan populations occurred 100 000 years ago (Filippucci *et al.* 1989). *A. mystacinus* was found in Israel from the Middle Pleistocene; *A. sylvaticus* appeared in the Upper Levalloise- Mousterian, about 40 000 years ago and reached its peak in the Natufian-Neolithic period, about 10 000 B.C. (Tchernov 1968, 1979).

On Mount Hermon *A. mystacinus* ranges with *A. flavicollis* in the lowest belt (300–1300 m) characterized by evergreen Mediterranean maquis. In the steppic zone belt above the former (1300–1900 m) only *A. mystacinus* is present. In the alpine tragacanthic belt above 1900 m *Apodemus* is represented only by the new species, *A. hermonensis*. Elsewhere in Israel the two existing species are primarily *A. mystacinus* and secondarily (and fluctuating) *A. flavicollis* (Filippucci *et al.* 1989).

Regional morphological adaptations. The mean values of body characters for *A. mystacinus* from six geographic groups of populations (Mount Hermon, Golan Heights, Hula Valley, Tel Dan, Galilee Mountains, Mount Carmel and Judean Mountains) are given in Filippucci *et al.* (1989; Table II, p. 365). The Golan Heights and Mount Carmel populations showed higher mean values for head and body length (HBL). The population of Mount Hermon showed slightly lower mean values for most body characters. On average, the populations from Mount Hermon, Golan and Jerusalem showed lower mean values of the hind-foot length (HFL). In fact, in these populations average HFL was $24.2 < HFL < 24.8$, whereas in those from Galilee and Mount Carmel it was $25.3 < HFL < 25.7$. Body weight within Israel increased from the Galilee through Mt. Carmel to Judea (Fig. 3 in Filippucci *et al.* 1989). This size increase within Israel may derive from the aridity stress on mesic *Apodemus* from the Galilee to the Judean Mountains rather than thermoregulatory response. On the other hand, the body characters in Israeli groups showed lower mean values than those in Turkey, Lebanon and Syria populations (Lewis *et al.* 1967), confirming the existence of a clinal variation in *A. m. mystacinus* (Felten *et al.* 1973), conforming regionally with the Bergmann rule.

Regional genetic adaptations. Regional levels of genetic variation within populations of *A. mystacinus* appear in Table VII, p. 372 of Filippucci *et al.* (1989). The overall mean of *A*, *P*1%, *H* and *He* were 1.366, 0.308, 0.04, and 0.055, respectively. In general these values decrease from the Galilee through Mount Carmel to the Judean Mountains. Likewise, altitudinally, they decrease upwards from low (300 m) to high (1200 m) altitude on Mt. Hermon. In other words, genetic diversity of European *A. mystacinus* decreases in stressful (drier, colder or warmer) environments, close to its species boundaries, both regionally and locally (eg, locally at the SFS in "Evolution Canyon"). This suggests that the genetic strategy of *A. mystacinus* is opposite to that of *A. cahirinus*. Under stress regimes its genetic diversity declines, reflecting its more specialist ecological nature.

The evolutionary driving forces causing genotypic and phenotypic divergence of rodents at "Evolution Canyon"

The genotypic, morphological, physiological and behavioural results obtained at "Evolution Canyon" for both *Acomys* and *Apodemus* can not be explained by mutation, migration, stochastic or neutral models. Mutation rate is excluded because of its low rates and the many generations needed for its accumulation by mutation pressure without any selective advantage of the mutants. Migration is ruled out as explanatory model on two grounds, experimental and theoretical. First, mark-recapture data indicated that individual rodents tended to remain largely within the same or the adjacent elevetional location within the same slope. We did not recover a single marked animal on the opposite slope (Blaustein *et al.* 1996). Presumably, as is true in other organisms studied at "Evolution Canyon", even in flying *Drosophila* (Nevo *et al.* 1998) interslope migration is very limited (Nevo 1995, 1997). Second, the interslope genetic divergence suggest that migration which is a homogenizing rather than heterogenizing force, does not play a major role in either genotypic or phenotypic inter- and intraslope differentiation, as is indicated by slope-specific alleles and gametic phase disequilibria (see results).

Stochasticity is ruled out as an explanatory model because the local interslope mesic-xeric divergence largely parallels genotypically and phenotypically the regional mesic-xeric pattern across Israel. This parallelism suggest that macro- and microclimatic diversifying selection is a major differentiating force of both genotypes and phenotypes which lead to complex inter- and intraslope adaptive complexes contributing to fitness.

The rodent results discussed here complement biodiversity and genetic diversity results on phenotypes and genotypes at "Evolution Canyon" in diverse groups of organisms across phylogeny, including cyanobacteria, plants, earthworms, landsnails, scorpions, beetles, ants, fruit flies, reptiles and birds [Nevo 1995, 1997 and a series papers in Israel Journal of Zoology 42 (4), 1996]. The results across life involves both species richness, phenotypic and genotypic adaptations. The latter include interslope adaptive complexes in germination pattern in wild barley (Gutterman and Nevo 1994), temperature preference, drought resistance and longevity in *Drosophila* (Nevo *et al.* 1998), mutation rate in the fungus *Sordaria fimicola* (Lamb *et al.* 1998), and desiccation tolerance in landsnails (Arad 1993, Rankevich *et al.* 1996). In the rodents themselves, while no interslope gene flow appears to operate, within slope interannual and spatiotemporal rodent adaptive dynamics (Blaustein *et al.* 1996) and predation (Broza and Nevo 1994) were distinct. Thus, adaptive patterns both in the plants and animals tested suggest that natural selection overrides migration which is presumably selected against even in locomotory (rodent) and flying (eg *Drosophila*) animals. Transplant experiments in wild barley support these results demonstraing slope-adaptations and fitness (Lavie *et al.* 1993).

"Evolution Canyon" is a rich evolutionary model appropriate for unfolding adaptive patterns and regularities across life and organizational levels (Nevo 1995,

1997). Similar, convergent adaptive patterns have been shown earlier locally (Nevo 1988, 1998), regionally (Nevo and Beiles 1988) and globally (Nevo *et al.* 1984). The advantage of studying contrasting patterns at "Evolution Canyon" lies in displaying global biodiversity patterns and ongoing adaptive evolution in action on a local scale across life's diversity and organization. The single key factor leading to a whole interslope microclimatic differential syndrome is the differential stress of solar radiation. Interslope migration appears to be low not only in sedentary organisms but also in moving organisms such as *Drosophila* and mice. Effective population sizes of most tested species (more than 1600 species studied todate) are either absolutely or relatively large, hence small size stochastic population effects may be negligent. Likewise, migration can be ruled out as a major evolutionary force because it can not generate the observed phenomena.

The available evidence suggests that microclimatic diversifying natural selection seems to be the major evolutionary force causing adaptive differentiation of genotypes and phenotypes in rodents and other organism between and within slopes. We now plan additional transplant, genetic experiments and genetic mapping to assess adaptive fitness components of some model organisms to the contrasting slopes. "Evolution Canyon" proves an optimal microscale ecological model for unfolding a long-term (several millions of years) evolution in action across life and organization.

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