

# Natural selection of body size differentiation in Spiny mice, *Acomys*

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## Abstract

Tested morphometrics of spiny mice, *Acomys*, of 181 specimens from 7 localities in Israel and Sinai, to evaluate the factors effecting body size differentiation. These specimens represent 3 karyotypes (2 formal species) comprising 5 populations of *Acomys cahirinus* ( $2n = 38$ ); 2 populations of *A. cahirinus* ( $2n = 36$ ); and 3 populations of *Acomys russatus* ( $2n = 66$ ). Each population of the latter is sympatric with *A. cahirinus*. The 7 localities represent a general southward transect of increasing aridity. The results indicate that: 1. body characters varied significantly between localities. Body weight and length decreased, whereas tail, ear and relative forefoot and hindfoot lengths generally increased with aridity in accordance with the Bergmann rule. 2. Morphology was found to be partly correlated with allozymic variation.

The geographic patterns and climatic correlates and predictors of morphological variation in *Acomys* in Israel and Sinai indicate that natural selection, mediated by climatic and biotic factors, is a major cause of body size differentiation. The latter in turn contributes to improving thermoregulatory efficiency and optimizes the energetics balance.

## Introduction

Body size is subject to differentiation by both direct and indirect multiple evolutionary factors. These involve, among others, ecological (e.g., climatic, habitat, resource availability and biotic interactions), physiological (e.g., metabolism, food resources and energetics), demographic (e.g., population size, intra- and interspecific competition) and pathogenicity (e.g., parasites and diseases) factors. Their relative importance and complex interaction vary spatiotemporally, hence must be evaluated specifically in each case. For a general discussion of the functional significance of variation in body size among mammals, see CLUTTON-BROCK and HARVEY (1983). For a discussion of the general variation and correlates of body size in mammals, see EISENBERG (1981). Since heritability of body size in mammals is usually high (SHIELDS 1962), geographic variation in size differentiation must involve a relatively high genetic component subject to natural selection. The objective of this study was to investigate the body size differentiation in spiny mice, genus *Acomys*, in Israel, and hypothesize about its possible determinants.

Spiny mice, genus *Acomys*, are tropical murid rodents (Rodentia, Myomorpha, Murinae) involving about 18 species ranging in Africa and southwest Asia in rocky habitats. Two species of spiny mice, the common spiny mouse, *Acomys cahirinus*, and the golden spiny mouse, *Acomys russatus*, occur in Israel and Sinai (SHKOLNIK and BORUT 1969; HAIM and BORUT 1974, 1975). *A. cahirinus* is widely distributed in Israel and Sinai (Fig. 1), ranging in both mesic and xeric environments comprising the Mediterranean, steppe and desert climatic regimes and is thus a climatically euryoek species in range (Table 1). 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, and Fig. 1). 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. The two chromosome forms are morphologically indistinguishable, but 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. cabirinus* is an upper Palaeolithic colonizer in humid Mediterranean Israel, i.e., it presumably appeared some 20,000–30,000 years ago (TCHERNOV 1968). Therefore, its morphological differentiation in Israel is relatively recent and traceable over time.

*A. russatus* is similar in morphology and life history to the *A. cabirinus* complex, but it differs from the latter in karyotype ( $2n = 66$ , WAHRMAN and ZAHAVI 1953); in its restricted distribution in extreme desert habitats (either hot or cold), in its narrower niche, and in its unique physiological adaptations (SHKOLNIK and BORUT 1969; HAIM and BORUT 1974, 1975, 1981). It occurs sympatrically with *A. cabirinus* (either  $2n = 38$  or  $2n = 36$ ) and shares the same rocky habitat. However, while *A. cabirinus* is nocturnal, *A. russatus* is frequently diurnal (SHKOLNIK 1971). The genetic differentiation and speciation of spiny mice in Israel have been recently studied (NEVO 1985) and will be related to the morphometric differentiation in the discussion. Here I present evidence suggesting that body size differentiation in *Acomys* relates primarily to climatic and biotic determinants.

## Material and methods

### Sampling

A total of 181 (113 males and 68 females) specimens from 7 localities representing 10 populations and 3 karyotypes were sampled in Israel and in Sinai. These involved 5 (1–5) populations of *A. cabirinus* ( $2n = 38$ ); 2 populations (6, 7) of *A. cabirinus* ( $2n = 36$ ), and 3 populations (8–10) of *A. russatus*, each population being sympatric with a counterpart of *A. cabirinus* (8 with 4, 9 with 6 and 10 with 7). Data on localities and ecogeographical parameters are given in Table 1; distribution and sampling localities are shown in Fig. 1. Sampling was conducted in the autumns of 1975 (in Israel) and 1976 (in Sinai) and each sample was collected in an area of about one km<sup>2</sup>. The seven localities of the samples are distributed largely along a transect of increasing aridity (see Table 1 and Fig. 1).

### Morphological measurements

To demonstrate the range of phenotypic variation in the 3 karyotypes of *Acomys*, 6 measures were taken of each adult mouse (and averaged separately for each sex): body weight, and lengths of body, tail, forefoot, hindfoot and ear. The ratios of the last four measures to body length were calculated.

### Statistical analysis

Stepwise multiple regression (SPSS-x 1986) was used to determine whether phenotypic variation of morphological traits is influenced by and associated with environmental factors. In addition, Pearsonian correlations were computed between all variables including allozymic (see NEVO 1985) and morphological variation. The variance in morphology within and between populations was tested by analysis of variance, ANOVA.

## Results

### Patterns of morphometric variation

The means of morphometrics of body characters for the 10 populations examined are given for males and females separately (Tables 2a and 2b), and the regressions of body weight and relative tail and ear sizes on latitude, temperature and the aridity index as expressed by

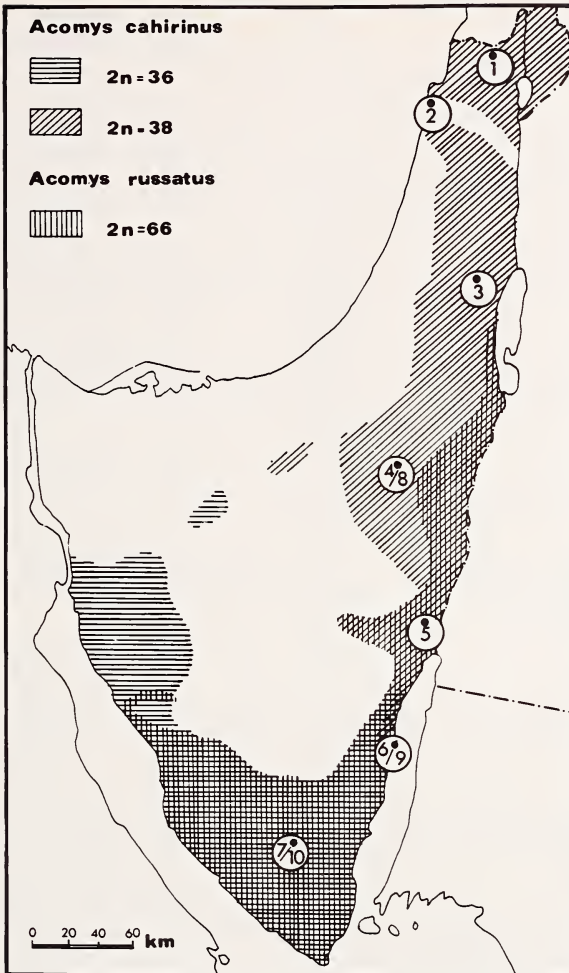


Fig. 1. The distribution of the three karyotypes of *Acomys*, and the sampled populations: *A. cahirinus* ( $2n = 38$ ): 1 = Hurfeish; 2 = Beit Oren; 3 = Jerusalem; 4 = Mitzpe Ramon; 5 = Timna. *A. cahirinus* ( $2n = 36$ ): 6 = Neviot; 7 = Santa Katharina. *A. russatus*: 8 = Mitzpe Ramon; 9 = Neviot; 10 = Santa Katharina

rainfall are given in Figure 2 in several scatter diagrams. A statistically significant amount of variation between localities (in most cases of *A. cahirinus*,  $p < 0.001$ ) was found for all body characters and ratios (Tables 2a and 2b). The following trends were found in *A. cahirinus* (note that males are better sampled than females). In general, body weight and length decreased southward (Fig. 2), whereas the lengths of tail, feet, ear and the ratios of all extremities of body length largely increased southward, along with an increase in aridity and temperature (Fig. 2). Body weight in *A. cahirinus* decreases from Hurfeish to Santa Katharina by 17.5 % and 19.7 % for males and females, respectively.

In *A. russatus*, which is represented by only 3 localities, the following trends were found. Body weight and length decreased in both sexes southward from the cool Negev highlands of Mitzpe Ramon to the hot Sinai lowlands of Neviot. Body weight decreased 32.7 % and 27.6 % for males and females, respectively. By contrast, a reverse trend is

Table 1. Geographical and climatological data for 7 localities in Israel and Sinai in which 3 karyotypes, *Acomys cabirinus*<sup>2</sup> and *Acomys russatus* and 10 populations of *Acomys* were sampled<sup>1</sup>

Species	Pop. No.	Locality	Sample size (N)	Longitude (Ln) (decimal)	Latitude (Lt) (decimal)	Altitude (Al) (m)	Mean Temperature (°C)			Annual rainfall (Rn) (mm)	Humidity at 14:00 (Hu) (%)	Annual evaporation (Ev) (cm)
							Annual (Tm)	Jan. (Tj)	Aug. (Ta)			
<i>A. cabirinus</i>	1	Hurfeish	19	35.40	33.03	800	18.0	8.0	26.0	750	40.0	192
<i>A. cabirinus</i>	2	Bet Oren	22	35.00	32.73	425	20.5	11.0	26.0	688	58.8	190
<i>A. cabirinus</i>	3	Jerusalem	17	35.23	31.78	700	18.5	10.0	25.0	486	54.0	220
<i>A. cabirinus</i>	4	Mitzpe Ramon	26	34.80	30.60	860	19.4	12.0	25.0	78	38.7	240
<i>A. russatus</i>	8		11									
<i>A. cabirinus</i>	5	Timna	14	35.03	29.88	80	25.0	14.0	36.0	32	27.0	360
<i>A. cabirinus</i>	6	Neviot	22	34.60	29.05	30	26.0	16.0	37.0	20	25.0	380
<i>A. russatus</i>	9		23									
<i>A. cabirinus</i>	7	Santa	13	33.92	28.58	2200	10.8	1.0	18.0	64	26.0	320
<i>A. russatus</i>	10	Katharina	14									

<sup>1</sup> Climatic data are multiple year averages reported by the Israel Meteorological Service. - <sup>2</sup> The *A. cabirinus* complex involves 2 chromosomal karyotypes.

apparent in body weight which increases again toward the cold mountain tops of southern Sinai in Santa Katherina. Body weight increased 33.1 % and 27.8 % in males and females, respectively.

An opposite trend was displayed by the relative tail and foot sizes of this species. In the better sampled males, they increased from Mitzpe Ramon to hot Neviot, but decreased again in cold Santa Katharina (see trends in Table 2). These reverse trends from Neviot to Santa Katharina are inconsistent in *A. cabirinus*.

### Environmental correlates and predictors of morphological variation

#### Pearsonian correlations

In the search for environmental correlates of morphological variation we used several geographic and climatic variables (Table 1): Longitude = Ln; Latitude = Lt; and Altitude = Al, were used as geographic variables. Temperature (mean annual = Tm; mean January = Tj; and mean August = Ta) and moisture (mean annual rainfall = Rn; mean mid-day relative humidity = Hu; and mean annual evaporation = Ev) were used as climatic variables. To assess the ecological background structure the correlation matrix of the ecological variables was analysed. Following are some correlations, where

Species	2n	Pop No.	Locality	Sample size N	Weight (g)		Body		Tail <sup>a</sup>		Forefoot		Hindfoot		Ear	
					Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
<i>A. cabirinus</i>	38	1	Hurfeish	12	45.12	9.1	106.3	7.4	98.8	6.1	9.08	0.7	18.58	0.7	12.50	0.9
		2	Bet Oren	11	44.66	6.8	117.1	5.6	98.2	9.0	9.56	0.9	19.00	0.5	11.78	0.8
		3	Jerusalem	11	39.65	4.8	108.5	7.0	97.3	8.2	8.64	0.9	18.27	0.5	13.00	0.9
		4	Mitzpe Ramon	11	50.03	11.9	112.0	7.2	106.3	6.6	9.09	0.7	17.64	2.4	16.00	2.6
		5	Timna	12	38.27	8.1	100.8	9.9	109.9	6.4	9.58	1.0	18.92	1.4	14.08	0.9
	36	6	Neviot	15	36.35	4.6	102.2	8.0	111.8	5.0	9.60	1.2	18.73	1.0	15.07	1.1
	7	7	Santa Katharina	8	37.24	8.2	105.5	6.7	105.8	7.3	9.13	1.4	19.50	0.8	15.75	1.0
		Total		80	41.58	8.9	106.9	9.0	104.2	8.6	9.26	0.90	18.63	1.3	14.07	1.9
		F <sup>b</sup>			4.67***		5.87***		5.55***		1.81 n.s.		2.28*		15.96***	
<i>A. russatus</i>	66	8	Mitzpe Ramon	7	63.31	7.1	112.4	3.6	72.3	5.3	9.14	0.9	18.00	1.0	11.43	2.0
		9	Neviot	15	42.61	9.4	105.3	7.0	69.6	6.7	9.47	1.1	18.53	1.1	10.53	1.1
		10	Santa Katharina	11	56.72	17.9	114.7	6.9	61.8	16.9	9.09	1.3	19.27	1.7	12.55	2.6
			Total	33	51.71	15.1	110.0	7.6	68.3	10.0	9.27	1.1	18.67	1.4	11.39	2.1
		F <sup>b</sup>			7.75**		7.47**		1.29 n.s.		0.42 n.s.		2.06 n.s.		3.50*	

<sup>a</sup> Only 47 tails were measured in *A. cabirinus* others being broken (N = 10, 5, 6, 4, 7, 9, 6 in each population, respectively) and 16 tails in *A. russatus* (N = 4, 8, 4 respectively). - <sup>b</sup> F represents the statistic of ANOVA; degrees of freedom for *A. cabirinus* 6,7 except in tail and tail/body ratio where they were 6,40; and for *A. russatus* 2,30, and for tail and tail/body 2,13. \* =  $p < 0.05$ ; \*\* =  $p < 0.01$ ; \*\*\* =  $p < 0.001$ ; n.s. = non significant.

Table 2a. continued

Species	2n	Pop. No.	Locality	Sample size N	Tail/Body <sup>a</sup>		Forefoot/Body		Hindfoot/Body		Ear/Body	
					Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
<i>A. cabirinus</i>	38	1	Hurfeish	12	0.936	0.068	0.086	0.007	0.176	0.011	0.118	0.011
		2	Bet Oren	11	0.861	0.063	0.082	0.009	0.163	0.007	0.101	0.008
		3	Jerusalem	11	0.913	0.062	0.080	0.008	0.169	0.013	0.121	0.008
		4	Mitzpe Ramon	11	0.937	0.081	0.081	0.006	0.157	0.019	0.144	0.027
		5	Timna	12	1.122	0.099	0.096	0.015	0.188	0.010	0.141	0.012
	36	6	Neviot	15	1.100	0.079	0.095	0.015	0.184	0.014	0.148	0.013
	7	7	Santa Katharina	8	1.020	0.049	0.087	0.006	0.186	0.014	0.150	0.008
		Total		80	0.995	0.115	0.087	0.012	0.175	0.017	0.133	0.022
		F <sup>b</sup>			12.08***		4.48***		9.33***		17.16***	
<i>A. russatus</i>	66	8	Mitzpe Ramon	7	0.639	0.058	0.081	0.006	0.160	0.010	0.102	0.017
		9	Neviot	15	0.666	0.036	0.090	0.013	0.177	0.016	0.100	0.008
		10	Santa Katharina	11	0.551	0.136	0.079	0.008	0.168	0.008	0.109	0.018
			Total	33	0.631	0.086	0.085	0.011	0.170	0.014	0.103	0.014
		F <sup>b</sup>			3.11 n.s.		4.57*		4.38*		1.32 n.s.	

Table 2b. Morphometrics of *Acomys cabirinus* and *Acomys russanus* accompanied by analysis of variance (ANOVA); Females

Species	2n	Pop No.	Locality	Sample size N	Weight (g)		Body		Tail <sup>a</sup>		Length (mm)		Hindfoot		Ear		
					Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	
<i>A. cabirinus</i>	38	1	Hurfeish	7	42.94	5.1	108.3	5.9	100.2	3.0	9.14	0.7	18.14	2.8	13.57	2.1	
		2	Bet Oren	11	43.45	7.5	108.8	6.6	98.0	5.2	9.27	0.8	18.55	0.7	11.55	0.7	
		3	Jerusalem	6	32.20	5.9	100.0	7.8	96.8	6.1	8.33	0.8	17.83	1.0	12.67	0.5	
		4	Mitzpe Ramon	15	47.67	8.2	111.3	7.5	105.8	6.7	9.07	0.5	17.67	2.1	16.80	2.6	
		5	Timna	2	42.20	9.8	106.5	12.0	118.5	2.1	9.50	0.7	16.50	2.1	17.50	3.5	
		36	6	Neviot	7	35.81	5.3	100.9	7.4	114.2	4.9	8.43	0.8	18.43	0.8	14.86	1.7
		7	7	Santa Katharina	5	34.48	6.8	103.4	7.2	107.5	10.6	9.00	0.7	19.00	0.7	15.40	0.9
		Total F <sub>b</sub>		53	41.40	8.7	106.8	8.0	103.8	8.4	8.96	0.7	18.11	1.7	14.23	2.5	
					5.44***		2.98*	8.35***		2.28 n.s.		0.91 n.s.		8.47***			
<i>A. russatus</i>	66	8	Mitzpe Ramon	4	59.73	11.0	104.3	9.4	74.5	2.1	8.50	1.2	18.75	1.0	10.25	1.0	
		9	Neviot	8	43.24	8.5	103.8	9.5	73.4	3.5	9.13	0.6	18.63	0.9	10.88	0.6	
		10	Santa Katharina	3	55.27	16.7	116.7	11.2	58.0	-	10.00	1.7	20.00	2.0	13.00	1.8	
		Total F <sub>b</sub>		15	50.04	12.7	106.5	10.5	72.2	5.6	9.13	1.1	18.93	1.2	11.13	1.8	
					3.46 n.s.		2.05 n.s.	9.67**		1.67 n.s.		1.56 n.s.		2.68 n.s.			

<sup>a</sup> Only 42 tails were measured in *A. cabirinus* others being broken (N = 5, 9, 6, 13, 2, 5, 2 in each population, respectively), and 11 tails in *A. russatus* (2, 8, 1 respectively). - <sup>b</sup> F represents the statistic of ANOVA; degrees of freedom for *A. cabirinus* 6,46 except in tail and tail/body ratio where they were 6,35, and for *A. russatus* 2,12, and for tail and tail/body 2,8. \* = p < 0.01; \*\* = p < 0.05; \*\*\* = p < 0.001; n.s. = not significant.

Table 2b. continued

Species	2n	Pop No.	Locality	Sample size N	Tail/Body <sup>a</sup>		Forefoot/Body		Hindfoot/Body		Ear Body	
					Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
<i>A. cabirinus</i>	38	1	Hurfeish	7	0.949	0.052	0.085	0.008	0.168	0.026	0.126	0.025
		2	Bet Oren	11	0.921	0.049	0.085	0.008	0.171	0.011	0.106	0.008
		3	Jerusalem	6	0.970	0.038	0.084	0.010	0.179	0.020	0.127	0.030
		4	Mitzpe Ramon	15	0.964	0.064	0.082	0.007	0.159	0.017	0.145	0.028
		5	Timna	2	1.119	0.106	0.089	0.004	0.157	0.038	0.164	0.015
<i>A. russatus</i>	36	6	Neviot	7	1.148	0.101	0.084	0.012	0.184	0.015	0.147	0.008
		7	Santa Katharina	5	1.085	0.045	0.087	0.006	0.184	0.014	0.149	0.013
		Total F <sub>b</sub>		53	0.989	0.096	0.084	0.008	0.170	0.020	0.134	0.025
					9.89***	0.47 n.s.		2.56*		6.85***		
<i>A. russatus</i>	66	8	Mitzpe Ramon	4	0.738	0.031	0.082	0.015	0.181	0.015	0.099	0.010
		9	Neviot	8	0.713	0.075	0.089	0.011	0.181	0.015	0.106	0.014
		10	Santa Katharina	3	0.479	-	0.086	0.011	0.172	0.006	0.110	0.022
	Total F <sub>b</sub>		15	0.696	0.097	0.086	0.012	0.179	0.013	0.105	0.014	
					5.19*	0.41 n.s.		0.55 n.s.		0.59 n.s.		

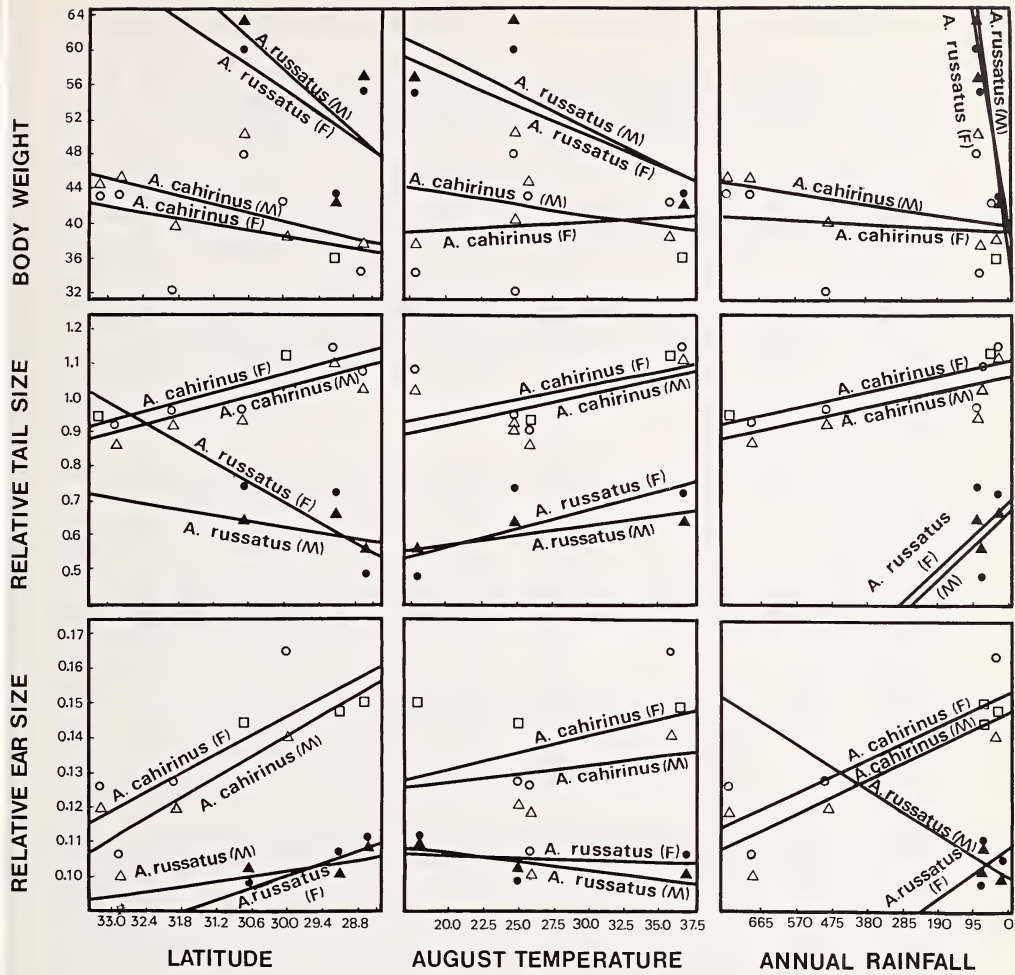


Fig. 2. Regressions of body weight and of relative ear and tail size of *Acomys cahirinus* and *A. russatus* on latitude, August temperature and annual rainfall.  $\Delta$  Population mean of males of *Acomys cahirinus*,  $\circ$  population mean of females of *Acomys cahirinus*,  $\blacktriangle$  population mean of males of *Acomys russatus*,  $\bullet$  population mean of females of *Acomys russatus*,  $\square$  both sexes of *Acomys cahirinus*, (M) males, (F) females

figures in parentheses are Pearsonian  $r$ 's for all 7 localities of *Acomys*. All 3 temperature variables,  $T_m$ ,  $T_j$  and  $T_a$ , are highly correlated (0.88–0.97);  $A_l$  and  $T_m$  (–0.97);  $R_n$  and  $T_a$  (–0.29);  $R_n$  and  $H_u$  (0.92);  $E_v$  and  $T_a$ ,  $R_n$  and  $H_u$  (0.55, –0.86, –0.94, respectively). The low correlation between  $R_n$  and temperature is due to the reversed temperature trend in Santa Katharina. When the latter locality is excluded, the correlation between  $R_n$  and temperature is negatively high as usual across the studied area ( $r$  between  $R_n$  and the temperature variables are from –0.67 to –0.86).

In general, rainfall increases and temperature decreases northward with latitude;  $r$  ( $R_n$ – $L_t$ ) = 0.94;  $N = 7$ ; and  $r$  ( $T_j$ – $L_t$ ) = –0.93 for 6 localities excluding Santa Katharina. In other words, aridity increases southward toward the Negev and Sinai deserts.  $T_m$  and  $H_u$  were eliminated from the multiple regression analysis in order to reduce the level of intercorrelations between the environmental variables.

Table 3. Pearson correlation between morphology and climatic variables in *Acomys cahirinus* 7 populations<sup>1</sup>

Variable	Sex	Geographical			Ecogeographical variables					Water availability	
		Longitude (Ln)	Latitude (Lat)	Altitude (Al)	Annual (Tm)	Jan. (Tj)	Aug. (Ta)	Annual rainfall (Rn)	Midday humidity (Hu)	Evaporation (Ev)	
Body weight	♂ ♂	.404	.600	-.005	-.696	-.547	-.762 <sup>o</sup>	.395	.632	-.726 <sup>o</sup>	
	♀ ♀	.323	.361	-.251	-.170	-.139	-.232	.125	.343	-.323	
Body length	♂ ♂	.174	.599	.109	-.616	-.469	-.784 <sup>o</sup>	.550	.803*	-.788*	
	♀ ♀	.235	.399	-.021	-.325	-.301	-.385	.211	.418	-.442	
Tail length	♂ ♂	-.520	-.850*	-.181	.861*	.903*	.845*	-.908**	-.886**	.921**	
	♀ ♀	-.375	-.765*	-.260	.884*	.832*	.905*	-.827*	-.856**	.923**	
Forefoot length	♂ ♂	-.173	-.263	-.480	.781 <sup>o</sup>	.659	.703	-.274	-.235	.501	
	♀ ♀	.077	.159	.016	.025	-.125	.009	.069	.142	-.092	
Hindfoot length	♂ ♂	-.485	-.308	.304	.490	.195	.511	-.030	-.237	.359	
	♀ ♀	-.506	-.037	.554	-.267	-.209	-.330	.231	.164	-.192	
Ear length	♂ ♂	-.726 <sup>o</sup>	-.852*	.364	.397	.627	.361	-.894**	-.803*	.625	
	♀ ♀	-.352	-.707 <sup>o</sup>	.023	.542	.561	.589	-.835*	-.815*	.721 <sup>o</sup>	
Tail/body ratio	♂ ♂	-.372	-.783*	-.202	.874*	.781 <sup>o</sup>	.947**	-.774*	-.906**	.959***	
	♀ ♀	-.537	-.873**	-.097	.925**	.863*	.968***	-.803*	-.934**	.991***	
Forefoot/body ratio	♂ ♂	-.213	-.584	-.371	.892**	.717	.966**	-.562	-.719 <sup>o</sup>	.862	
	♀ ♀	-.202	-.305	.031	.526	.247	.581	-.202	-.360	.474	
Hindfoot/body ratio	♂ ♂	-.357	-.604	.041	.721	.481	.863*	-.440	-.726 <sup>o</sup>	.779*	
	♀ ♀	-.492	-.303	.367	.094	.114	.095	-.010	-.184	.184	
Ear/body ratio	♂ ♂	-.660	-.916**	.237	.589	.712	.619	-.932**	-.945**	.807*	
	♀ ♀	-.431	-.819*	.047	.634	.648	.699	-.889**	-.929**	.838*	

<sup>o</sup> = p < 0.10, \* = p < 0.05, \*\* = p < 0.01, \*\*\* = p < 0.001. <sup>1</sup> The correlations with the 3 temperature variables were performed on 6 populations only, excluding Santa Katharina.



### Morphological correlates with climate

As can clearly be seen in Table 3, high and significant correlations, above those expected by chance, relate morphometrics and climatic factors. Body size significantly decreases ( $r$ , for males, =  $-0.79$ ;  $p < 0.05$ ) southward with evaporation whereas the relative tail size in males increases southward with evaporation ( $r = 0.96$ ;  $p < 0.001$ ). Even single climatic factors explain significantly the morphological variance in body ratios, but much more of the variance is explained by two or three variable combinations (see later, multiple regression analysis, Table 5).

### Morphological correlates with allozymes

The frequencies of some allozymes show significant correlations with morphometric means (Table 4). The analysis is based on the assumption that there is no real difference in allozyme frequencies between the sexes. The reliance on male morphometrics stems from their better sampling. Because of the high correlation between the morphometrics of both sexes, the analysis of females gave similar results. The following alleles showed significant correlations with morphometrics, the numbers in parentheses indicate the number of body variables correlated with the alleles: Aat-1<sup>a</sup> (3); Est-2<sup>a</sup> (2); Est-2<sup>c</sup> (1); Est-3<sup>a</sup> (1); Est-5<sup>b</sup> (3); Est-6<sup>b</sup> (1) and Est-7<sup>b</sup> (2). In addition, in females only: Pept-2<sup>c</sup> ( $r = -0.81^*$  =  $p < 0.05$  with forefoot); Est-6<sup>c</sup> ( $r = 0.78^*$  with ear, and  $r = -0.82^*$  with hindfoot-body ratio). It thus appears that allozymic and morphological diversities are at least partly significantly correlated, primarily with the allele frequency in several esterase loci. Both allozymic and morphological variations are correlated with environment.

### Multiple regression analysis

A test of the best predictors of the morphological variables of the populations of the *A. cahirinus* complex was conducted by stepwise multiple regression analysis, MR (SPSS-x 1986), employing the aforementioned variables as dependent variables and ecogeographic factors as independent variables. The results are given in Table 5. A substantial

Table 4. Pearsonian correlations between male morphometric means and allozymic frequencies in 7 populations of the *Acomys cahirinus* complex

Variable	Aat-1 <sup>a</sup>	Est-2 <sup>a</sup>	Est-2 <sup>c</sup>	Est-3 <sup>a</sup>	Est-5 <sup>b</sup>	Est-6 <sup>b</sup>	Est-7 <sup>b</sup>	Ao <sup>a</sup>
Weight	-	-	-	-	-	-	-	0.925 <sup>e</sup>
Body length	0.715 <sup>e</sup>	-	-	-	-	-	-	-
Tail length	-0.795 <sup>*</sup>	-	-	-	-	-0.732 <sup>e</sup>	0.973 <sup>**</sup>	-
Forefoot length	-	-0.864 <sup>*</sup>	-	0.800 <sup>*</sup>	-	-	0.817 <sup>e</sup>	-
Hindfoot length	-	-0.681 <sup>e</sup>	-	-	-	-	-	-
Ear length	-	0.672 <sup>e</sup>	-	-	-	-0.746 <sup>e</sup>	0.827 <sup>e</sup>	-
Tail/Body ratio	-0.870 <sup>*</sup>	-	-	-	0.744 <sup>e</sup>	-	-	-
Forefoot/Body ratio	-0.913 <sup>**</sup>	-	-	-	-	-0.685 <sup>e</sup>	-	-
Hindfoot/Body ratio	-	0.801 <sup>*</sup>	-	-	-	-	-	-
Ear/Body ratio	-	-	-	-	-0.812 <sup>*</sup>	-0.795 <sup>*</sup>	0.977 <sup>**</sup>	-

Aat-1 = aspartate aminotransferase, Est-2-7 = Esterases 2-7, Ao = aldehyde oxidase. All upperscripts a-c are allele designations. <sup>e</sup> =  $p < 0.10$ , \* =  $p < 0.05$ , \*\* =  $p < 0.01$ , - = non significant correlations.

Table 5. Coefficients of multiple determination ( $R^2$ ) employing as dependent variables 6 morphological variables and 4 morphological ratios of *Acomys cahirinus* and as dependent variables geographic + climatic, and climatic factors

Variable	Stepwise model					
	Geographic + Climatic variables			Climatic variables		
Weight ♂♂	Same as for climatic variables			Ev 0.53 <sup>e</sup>	EvRn 0.73 <sup>e</sup>	EvRnTa 0.84
Body length ♂♂	Ev 0.62*	EvLn 0.72 <sup>e</sup>	EvLnAl 0.95*	Ev 0.62*	EvRn 0.68 <sup>e</sup>	EvRnTj 0.70
Tail length ♂♂	Same as for climatic variables			Ev 0.85**	EvRn 0.90*	EvRnTa 0.93*
Forefoot length ♂♂	Ta 0.39	TaLn 0.54	TaLnLt 0.85 <sup>e</sup>	Ta 0.39	TaEv 0.43	TaEvRn 0.45
Hindfoot length ♂♂	Ln 0.24	LnRn 0.38	LnRnEv 0.83	Tj 0.20	TjTa 0.64	TjTaRn 0.65
Ear length ♂♂	Same as for climatic variables			Rn 0.80**	RnTa 0.90*	RnTaEv 0.91*
Tail/Body ratio ♂♂	Ev 0.92***	EvLn 0.96**	EvLnAl 0.98**	Ev 0.92***	EvTa 0.93**	EvTaTj 0.97*
Forefoot/Body ratio ♂♂	Ev 0.75*	EvLt 0.93**	EvLtAl 0.96*	EV 0.75*	EvRn 0.87*	EvRnTa 0.91*
Hindfoot/Body ratio ♂♂	Same as for climatic variables			Ev 0.58*	EvRn 0.80*	EvRnTj 0.94*
Ear/Body ratio ♂♂	Rn 0.87**	RnAl 0.90**	RnAlTa 0.94*	Rn 0.87**	RnTj 0.90**	RnTjTa 0.91*

Abbrev. of environmental variables: Ln = Longitude, Lt = Latitude, Al = Altitude, Ta = mean August temperature; Tj = mean January temperature, Rn = annual rainfall, Ev = annual evaporation. <sup>e</sup> =  $p < 0.10$ , \* =  $p < 0.05$ , \*\* =  $p < 0.01$ , \*\*\* =  $p < 0.001$ .

amount of the geographic variation in body characters was explained by the climatic factors of water availability (evaporation and rainfall) and temperature. Note that the variance in body ratios, which represents the relative estimates of body extremities (tail, ear, fore- and hindfoot lengths) is significantly explained by a single factor (either evaporation or rainfall), but a two or three variable combination explains above 90 % of the variance.

## Discussion

I will subdivide the discussion into two parts, 1. general, including other examples of geographic variation of body size in both space and time across Israel and in other regions, and 2. specific, analysing the results of the *Acomys* complex.

### General comments on body size and energetics

The usual explanation of the positive correlation of body weight with latitude in homoiotherms (Bergmann's rule) relates to the physics of heat exchange, providing a thermoregulatory device for conserving energy in colder climates by a larger body size, and dissipating energy in warmer climates by a smaller size. This interpretation of Bergmann's rule was criticized by SCHOLANDER (1955) on several grounds. First, many species did not follow the rule and those that did show clinal increases in weight were

physiologically unimportant. Second, many of the characters supposedly associated with the rule have no significance in heat exchange. The rule was also questioned when some poikilotherms reflected it (RAY 1960). RENSCH (1932) concluded that when factors other than temperature affect body size the maximum is reached in the optimal portion of the species range. MAYR (1970) emphasized that diametrically opposed size trends occur in species differing in life cycle patterns, sexual maturity, and optimal habitats.

In a series of studies on the patterns and evolution of endothermy in the phylogeny of mammals and other vertebrates McNAB (1970, 1971, 1974, 1979, 1980, 1983) has critically analysed the influence of body size on the energetics, food habits and population biology of mammals. In his analysis of the ecological significance of Bergmann's rule, McNAB (1971) emphasized that those species which do conform to the Bergmann rule "are usually carnivores or granivores; a change in their body size reflects a change in the size of their prey. A latitudinal change in the size of available prey is due either to the distribution of the prey species or to the distribution of other predators utilizing the same prey species. Only the smallest species of a set of similar predators normally will conform to Bergmann's rule, and then only beyond the limits of distribution of the largest species. These changes in size seem to be another example of character displacement."

McNAB concluded that Bergmann's rule usually is a special case of a more general phenomenon related to food frequency and its size and the presence of other species that utilize the same food resources. In a recent analysis McNAB (1983) analysed the complex relationship between energetics and body size and the limits to endothermy. Most vertebrates follow a Kleiber relation down to a "critical" mass, below which the scaling of metabolism must be changed to ensure the maintenance of endothermy. Critical mass varies inversely with the level of energy expenditure. The perfection of endothermy may always require an evolutionary decrease in mass. These considerations may not only be true at higher taxonomic levels, but also intraspecifically.

#### Body size as a "niche difference"

Body size variation may permit the coexistence of close species, thus providing an important niche parameter. The reason is that different sized animals eat different sized foods, hence utilize differential resources, at least partly nonoverlapping in size, to allow coexistence (MACARTHUR 1972). WILSON (1975) describes patterns of convergence and divergence of body size unifying in his model seemingly contradictory concepts: 1. the concept that differences in body size promote a niche difference (HUTCHINSON 1959; BROWN and WILSON 1956; SCHOENER 1965, 1967, 1970, 1974a, b; GRANT 1968, 1972), and 2. the concept that differences in body size set up a competitive gradient whereby the larger can exclude the smaller (BROOKS and DODSON 1965; GALBRAITH 1967).

#### Spatiotemporal variation in size of other rodents in Israel

Several studies analyse the spatial and temporal morphological variation in Israeli rodents. Size variation of *Meriones tristrami* was analysed by CHETBOUN and TCHERNOV (1983). Its size variation over the geographic range of Israel and northern Sinai and during the late Middle and Upper Quaternary of Israel is correlated with environmental factors. The allopatric fossil populations were found to fluctuate in accordance with Bergmann's rule (i.e., the maximum body size was obtained during colder phases). Recent populations did not show north-south body size gradient of high correlation with climatic factors. A sudden shift in body size of *M. tristrami* is observed when sympatry with its congener *M. sacramenti* occurs in the Coastal Plain, and another (and smaller) shift is noticeable when sympatry with a third congener (*M. crassus*) takes place in the Negev region. The allopatric convergence and sympatric divergence suggest an ecological interaction (character dis-

placement) among the congener species. A significant north-south increase in the relative volume of the bulla tympanica of *M. tristrami* is shown, with the mastoid portion playing the main role in geographic variation. The bulla volume is highly correlated with climatic factors and shows no divergent shifts within the sympatric region. It is suggested that in fossil populations the bulla tympanica can be used for evaluating palaeoclimatic fluctuations.

Size trends and Pleistocene paleoclimatic response of the murid genus *Apodemus* (subgenus *Sylvaemus*) were studied by TCHERNOV (1979). Eleven Pleistocene sites in Israel yielded samples of successive populations of *Apodemus*. Three species occur: two (*A. mystacinus* and *A. sylvaticus*) are continuously represented in the area, while the third, *A. flavicollis*, occurs only during colder periods. The separation of fossil populations is possible only on biometrical grounds. The observed distribution of coexisting populations revealed significantly different modes of each parameter, caused by strict ecological exclusion. Molars showed three well-defined morphological size-groups within each of the three species when they coexisted in closely related adaptive zones. Neither significant complication, simplification nor clinal variation occurred in tooth structure since early Middle Pleistocene.

In the Middle East three different lineages of *Apodemus*, which never overlapped in size, were present during the Middle and Upper Pleistocene. When all three species coexisted, parallel changes in size with time occurred in all of them simultaneously, apparently in accordance with Bergmann's rule. Yet when *Apodemus flavicollis* was temporarily eliminated from the scenario in warm periods, the other two species filled the vacated space independently of climate, and in contrast to Bergmann's rule. Two factors greatly affected the character displacement of the three chrono-species: interspecific competition and climate. As competitive exclusion of these three closely related species is and was heavy, it is suggested that no factor other than size was involved in their evolution during the last 700,000 years. The significant size changes of each of these lineages, with no overlap among them, were interpreted by correlations with climatic factors and by ecological exclusions.

In an extensive survey of faunal turnover and extinction rate in the Levant, TCHERNOV (1984) analysed size changes in the late Pleistocene and postglacial period. Size change is exemplified most drastically by postglacial radical dwarfing seen in several species of mammals in Israel: *Canis lupus*, *Ursus arctos*, *Sus scrofa*, and *Felis sylvestris* (KURTEN 1965); *Spalax ehrenbergi* and *Microtus guentheri* (TCHERNOV 1968); *Gazella gazella*, *Vulpes vulpes*, and *Canis lupus* (DAVIS 1977). DAVIS showed that the Aurignacian wolf of Israel attained the same dimensions as the present population of southern Sweden. Differences in mean temperature (for the hottest or coldest months) between the two regions is around 15 °C. According to DAVIS (1977), dwarfing commenced within the Natufian period (10,000 to 12,000 B.P.) and was completed approximately during the Neolithic. It is obvious that a conspicuous climatic change took place in the eastern Mediterranean region, an effect not clearly shown by the mammalian fauna turnover.

A detailed analysis on differentiation of body size in general (NEVO et al. 1986) and on 42 skull and body characters (NEVO et al. 1988) have been conducted on the four chromosomal species (2n = 52, 54, 58 and 60) of subterranean mole rats of the *Spalax ehrenbergi* complex in Israel. For differentiation of body size, the weight of 1,653 subterranean mole rats comprising 12 populations of the four chromosomal species were analysed. The results indicated that there is a southward latitudinal gradient in body size. Northern animals living in cooler and more productive mesic environments are larger than southern animals living in warmer and less productive xeric environments. Body size is negatively correlated with temperature variables, and positively correlated with plant cover (reflecting productivity or food resources) and rainy days. The best predictors of body size, explaining up to 87 % of the variation in size included various combinations of

temperature variables and plant cover. The conclusions were that in both adaptation and speciation natural selection is a major agent of differentiation of body size in accordance with multiple factors, primarily temperature and food resources operating on the energetics balance.

In a complementary study (NEVO et al. 1988) the morphometrics of 327 adult subterranean mole rats comprising 44 populations distributed across the ranges of the four chromosomal species of the *Spalax ehrenbergi* superspecies in Israel has been studied on a total of 42 skull and body variables. The results indicated that climatic variable combinations of temperature and water availability explain a significant part of the variance of most skull and body variables. Morphological diversity displays a southward gradient of decreasing size in skull and body variables which are significantly explained by climatic selection (and indirectly by decreasing resource availability southward). Hence it is adaptive and explicable on even very low selective pressures over evolutionary time.

Geographic variation of decreasing body size southward occurs in Israel in other homoiotherm mammals (e.g., wolves, leopards and hedgehogs; in MENDELSSOHN 1982) and in birds (partridges; in NISANI 1974). In contrast, increase in body size southward occurs in some poikilotherms (e.g., toads; in NEVO 1972). The decrease in body size southward in mammals and birds may be due to the sole or combined effects of higher temperatures and lower productivity in the xeric southern Negev and Sinai deserts. The increase in size of toads southward may be due to the fact that larger toads, having a relatively smaller evaporative body surface area, are capable of withstanding longer periods of desiccation and are therefore selectively superior in arid habitats.

### Ecophysiological, genetical and morphological differentiation of spiny mice, *Acomys*

What are the evolutionary forces molding body size differentiation in spiny mice in Israel? I will first summarize the ecophysiological background structure, then discuss body size differentiation, relate it to allozymic diversity and assess the evidence indicating that natural selection is a major architect in population differentiation at both the molecular (i.e., genetic) and organismal (i.e., morphological) levels. See ENDLER (1986) for a critical review of natural selection in the wild.

#### *Ecophysiological background*

1. *A. cabirinus* is a climatically generalist species ranging over widespread mesic and xeric habitats across Israel and part of the Sinai, whereas *A. russatus* is a habitat specialist species restricted to extreme xeric desert conditions in these regions. Recently, *A. russatus* was described from the colder mountain tops of the southern Sinai desert at altitudes of up to 2650 m (HAIM and TCHERNOV 1974). Physiological analysis of the Sinai mountain top populations of *A. russatus* indicates that it is adapted to cold-stress physiology by means of a higher nonshivering thermogenesis (HAIM and BORUT 1974, 1975, 1981), whereas animals from the En-Gedi Judean Desert population were unable to produce enough heat to keep warm below 18 °C (SHKOLNIK and BORUT 1969). However, both species (*A. cabirinus* and *A. russatus*) are narrow-niched species restricted to life in rocky crevices where microclimatic conditions in their microhabitats are relatively constant and far more moderate than the surrounding climates (SCHMIDT-NIELSEN 1964; SHKOLNIK 1966); yet they differ in their thermal niche-breadth (see below).

2. *A. cabirinus* is able to regulate its body temperature over a much greater range of ambient temperatures than *A. russatus* in accordance with its larger habitat range (WEISSENBERG 1977; WEISSENBERG and SHKOLNIK 1977). However, *A. russatus* is physiologically better adapted for a diurnal life than nocturnal *A. cabirinus* by its ability to withstand

high ambient temperatures and generate less heat by metabolism, as well as its capacity to derive water from salty, succulent plants (SHKOLNIK and BORUT 1969; SHKOLNIK 1971).

3. Both species are adapted to desert conditions through an adaptive syndrome which is more pronounced in *A. russatus* than in *A. cabirinus*. Their metabolic rates deviate from the expected based on weight, 34.5 % in the former and 13.5 % in the latter, thereby reducing the water required for evaporation. Likewise, maximum chloride concentration is higher in the urine of *A. russatus* (1500 mN), and it is almost twice that of *A. cabirinus*. Finally, both species have among the very highest mammalian urine concentration (4700–4800 mN; SHKOLNIK and BORUT 1969).

4. High ratios of evaporative water loss characterize both species, but more so in *A. russatus* than in *A. cabirinus*, involving a high cutaneous water loss, about 60–70 % of the total. The high cutaneous water evaporation, particularly in diurnal *A. russatus*, allows it to dissipate at an ambient temperature of 30 °C, over the third of the heat it generates. This efficient cooling device through a high evaporation rate, which appears very high even when compared to other diurnal rodents, is compensated by a very efficient kidney, by food choice comprising snails and succulent plants and by behavioral adaptations of shade-path selection (SHKOLNIK 1971). All four ecophysiological factors suggest a tropical (hot and humid) evolutionary origin of *Acomys* (SHKOLNIK 1966), as is also substantiated by taxonomic (ELLERMAN and MORRISON-SCOTT (1951), paleontological (TCHERNOV 1968, 1975, 1984) and cytogenetic (WARHMAN and GOITEIN 1972) studies.

#### *Genetic and morphological patterns*

The genetic differentiation and speciation in *Acomys* has been described elsewhere (NEVO 1985). Here I summarize the major genetic and morphological patterns. 1. Low levels of genic diversity (A, P, H) characterized *Acomys* but they were higher in the *A. cabirinus* complex than in *A. russatus*. 2. A substantial proportion of the variant loci, 40–50 % were either localized or sporadic, suggesting sharp local and regional differentiation of alleles across the mesic-xeric ranges of *Acomys* in Israel and Sinai. 3. In both *A. cabirinus* and *A. russatus* the level of polymorphism and number of alleles increased southward with aridity. 4. Levels of A, P and H varied at enzyme and protein loci in different functional classes. Loci whose enzymes utilize substrates originating from the external environment are far more genetically diverse than loci whose enzymes utilize internal metabolites (GILLESPIE and KOJIMA 1968; JOHNSON 1974). Likewise, regulatory enzymes were more variable than nonregulatory enzymes (JOHNSON 1974). 5. Significant linkage disequilibria were found in *A. cabirinus* in three populations involving six alleles. 6. Deviations from Hardy-Weinberg equilibria owing to heterozygote paucity were found in eight populations involving five loci. 7. Significant heterogeneity between 14 polymorphic loci in their effective inbreeding coefficients suggest the operation of natural selection. This test was criticised on statistical grounds (EWENS and FELDMAN 1976) and I use it here only as a supportive, and not a conclusive result. 8. Polymorphism and allozymic variant at six polymorphic loci were correlated with and predicted by climatic factors of water availability and temperature. 9. Body characters vary significantly between geographical localities: Body weight and length decreased, whereas tail, ear and relative fore- and hindfoot lengths increased and were correlated significantly with aridity and temperature. 10. Morphology was found to be partly correlated with allozymic variation. 11. Genetic patterns of *A. cabirinus* and *A. russatus* varied in three sympatric localities. 12. Mean genetic distance, D, was very small within *A. cabirinus* (2n = 38 and 2n = 36), and within *A. russatus*. It was also very small between the karyotypes of *A. cabirinus* (2n = 38 and 2n = 36), but high between the *A. cabirinus* complex and *A. russatus*.

### Adaptive differentiation of body size in spiny mice

The interspecific size differences between nocturnal *A. cabirinus* and diurnal *A. russatus* may relate to their striking pattern of competitive exclusion (SHKOLNIK 1966, 1971) which results in opposed patterns of circadian activity. This variation of body size between the species may represent niche differences (see WILSON 1975). The heavier body weight of *A. russatus*, as compared with *A. cabirinus* (Table 2) may be associated with its diurnal life, where a relatively small surface to volume ratio may be adaptively superior in dry and high-radiation environments.

In general, in both *A. cabirinus* and *A. russatus*, sizes decrease and extremities increase with aridity and temperature (Fig. 2). 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). Both patterns appear to better adapt *Acomys* to a progressively increasing heat load southward by improving its thermoregulation capacity through larger dissipating heat surfaces. Most fossorial mammals conform to these trends, although the interpretation of the trend in other mammals is often complex, and may involve inter-species interaction or character displacement (e.g. McNAB 1979; CHETBOURN and TCHERNOV 1983; TCHERNOV 1979; WILSON 1975).

Although one could suggest character displacement as a factor involved in body size differentiation of spiny mice, it appears very unlikely. In all three populations where both *A. cabirinus* and *A. russatus* coexist (localities 4–8, Mitzpe Ramon; 5–9, Neviot; and 7–10, Santa Katharina) the size difference appears to reflect an extension of general regional gradient of each of the species, rather than local character displacement, as is evident by the general ranking pattern in each of the species and in both sexes, i.e., decrease in size southward from the Central Negev desert (Mitzpe Ramon) to the Sinai desert (Neviot). The increase in size of *A. russatus* in both sexes at the mountaintop of Sinai (Santa Katharina) appears to support the thermoregulatory hypothesis. The contribution of a bigger body size to thermoregulatory efficiency in mountaintop colder environments complements the physiological adaptation by nonshivering thermogenesis of this population (HAIM and BORUT 1974, 1975, 1981).

The involvement of natural selection in genetic and morphological population differentiation is suggested by points number 1–11 mentioned above for both allozymes and body characters, which are intercorrelated and are explicable at least partly by the environment. Neither gene flow nor genetic drift can explain satisfactorily the genetic and morphological patterns found. If gene flow was a major factor, sporadic and localized alleles would not comprise about half of the variant alleles, and clines should have been more abundant. If genetic drift was a major factor, fixation of alternative alleles should have been more pronounced within the *A. cabirinus* complex and allele distribution would not be explained, at least partly, by climatic factors. Likewise, it is unlikely that small size population effects are responsible for the regional patterns. Both species are very abundant in the continuous rocky habitats across Israel and parts of Sinai. The intercorrelation between allozymic and morphological diversities reinforce their adaptive component.

In sum the morphological differentiation of body size, like the genetic one (NEVO 1985) appears to relate to environmental factors. Climatic factors appear substantial in molding body size as a contributor to thermoregulatory efficiency interacting with genetic, physiological and behavioral factors to optimize the energetics balance. Additional factors such as decline in resource availability southward may also contribute to the decrease in body size toward the hot Negev and Sinai deserts. It is noteworthy that desert rodents in Israel show a peaked curve of diversity over productivity, drastically declining in the deep desert (ABRAMSKY and ROSENZWEIG 1984).

While in general temperature and aridity (i.e., lower productivity) increase southward across the *Acomys* range, they are correlated and impossible to disentangle. Partial

separation of both factors may be achieved between hot and arid Neviot populations and cold and arid Santa Katharina populations, both in the Sinai desert. Here, while aridity (hence productivity) is similar, temperature differences are extreme. Therefore, size differentiation between both sites appear largely to be determined by temperature, in accordance with the Bergmann rule. This is observed primarily in *A. russatus*. However, the relative importance of declining food resources in the southward decrease in size remains to be further evaluated by critical, specifically designed experiments.

Natural selection appears to be a major architect of size as well as allozyme (NEVO 1985) differentiation in spiny mice and of their interaction. A critical discussion of the operation of natural selection in natural populations has been presented by MANLY (1985) and ENDLER (1986).

### Evolutionary history and the rate of morphological differentiation

The evolutionary center of origin of spiny mice based on taxonomic grounds (ELLERMAN and MORRISON-SCOTT 1951; WAHRMAN and GOITEIN 1972 and references therein) is the Ethiopian Region, and Israel represents a northern extension from this center. The African genus *Acomys* existed apparently in the Near East since the Pliocene, as it is found in Cyprus which separated from the mainland not later than the early pleistocene. This Pliocene ancestor presumably radiated into several closely related species (e.g. ATALLAH 1967). No *Acomys* remains were found however, in the Pleistocene of Israel until as late as the Aurignacian in the upper Palaeolithic, i.e., some 20,000 years ago (TCHERNOV 1968, 1975). *A. cabirinus* is a recent colonizer to the mesic but deforested Mediterranean region, particularly in the Epipaleolithic period, i.e., 15,000 B.P. Noteworthy, in the Mediterranean region *A. cabirinus* occurs primarily on warm and dry south-facing wadi slopes, presumably reflecting its derivation from steppic or desert origins, whereas the cooler and more humid north-facing slopes in Mount Carmel, for example, are primarily inhabited by the European *Apodemus* (NEVO, unpubl.). *A. russatus* may have originated in the extreme southwest Asiatic arid zones.

The three chromosomal forms of *Acomys* in Israel, *A. cabirinus* ( $2n = 38, 36$ ) and *A. russatus* ( $2n = 66$ ) appear to represent two speciation events: an old and a recent one. This deduction is based on both karyotypic differentiation (WAHRMAN and ZAHAVI 1953) and genetic distances (NEVO 1985). The genetic distance separating *A. russatus* and *A. cabirinus* is  $D = 0.30$ . A rough evolutionary divergence time for a pair of species estimated from electrophoretic data based on their genetic distance can be obtained by  $t = 5 \times 10^6 D$  (NEI 1975). On this basis, *A. russatus* and *A. cabirinus* separated  $1,500,000 \pm 50,000$  years ago. On the same basis, and in sharp contrast to this older speciation event, the karyotypic differentiation within *A. cabirinus* occurred  $115,000 \pm 40,000$  years ago. This figure is in accordance with the fossil record which reveals *A. cabirinus* in Israel only as late as 20,000 years ago (TCHERNOV 1975). It supports the hypothesis that the Israeli form of *A. cabirinus* ( $2n = 38$ ) has probably been derived from the Sinaitic form ( $2n = 36$ ) through fission of one metacentric chromosome, rather than the reversed, cytologically simpler process (WAHRMAN and GOITEIN 1972).

The evolutionary recency of the *Acomys cabirinus* complex in Israel, i.e., 20,000 years, suggests that natural selection must have been instrumental in driving a relatively high evolutionary rate of size differentiation.

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## Zusammenfassung

### Natürliche Selektion in der Differenzierung von Körpermaßen bei der Stachelmaus, *Acomys*

Untersucht und miteinander verglichen wurden 181 Stachelmäuse des Genus *Acomys* von 7 Lokalitäten aus Israel und dem Sinai. Diese Tiere entsprechen 3 Karyotypen (2 Arten), welche 5 Populationen von *Acomys cabirinus* (2n = 38), 2 Populationen von *A. cabirinus* (2n = 36) und 3 Populationen von *A. russatus* (2n = 66) umfassen. Jede Population von *A. russatus* ist mit einer von *A. cabirinus* sympatrisch. Die 7 Lokalitäten erstrecken sich von Norden nach Süden und entsprechen Regionen mit schnittweise zunehmender Aridität. Die Ergebnisse der Untersuchungen zeigen: 1. Die Tiere der verschiedenen Lokalitäten unterscheiden sich in den erfaßten körperlichen Merkmalen signifikant voneinander. In Übereinstimmung mit der Bergmann'schen Regel zeigen Körpergewichte und -längen Abnahmen mit zunehmender Aridität, die absoluten Längen von Schwanz und Ohr sowie die relativen von Vorder- und Hinterfuß nehmen hingegen allgemein zu. 2. Die morphologischen Besonderheiten sind teilweise korreliert mit enzymatischen Variationen. Die Beziehungen zwischen geographischen Faktoren sowie klimatischen Besonderheiten und morphologischen Unterschieden bei *Acomys* in Israel und dem Sinai zeigen an, daß die natürliche Selektion als wichtigster Faktor für die Differenzierungen der Körpermaße angesehen werden muß. Diese Differenzierungen tragen bei zur Verbesserung der Thermoregulation. Durch sie wird die Energiebalance optimiert.

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