

Longevity and Mortality in 15 Rodent Species and Subspecies Maintained in Laboratory Colonies¹

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Morrison P., Dieterich R. & Preston D., 1977: Longevity and mortality in 15 rodent species and subspecies maintained in laboratory colonies. *Acta theriol.*, 22, 23: 317—335 [With 5 Tables & 9 Figs.].

Longevity/mortality data are presented for 15 wild rodent taxa as maintained in laboratory colonies: *Microtus pennsylvanicus tananaensis*, *M. oeconomus macfarlani*, *M. o. operarius*, *M. miurus*, *M. abbreviatus*, *Lemmus lemmus*, *L. sibiricus trimucronatus*, *Dicrostonyx stevensoni*, *Clethrionomys rutilus*, *Peromyscus maniculatus borealis*, *P. m. bairdii*, *Baiomys taylori*, *Calomys ducilla*, *C. callosus* and *Acomys cahirinus*. Infant mortality (1st week) averaged 11 percent (0 to 23%) and infant + juvenile mortality (1st month) averaged 23 percent (10 to 38%). Median life spans for animals weaned at 1 month averaged 50 wk and ranged from 25 to *L. s.* to 108 wk in *A. c.* The range was 25 to 40 wk in microtines and 44 to 105 wk in the cricetines excluding *B. t.* Most microtine survival curves were linear or »oblique« ($dS/dt = -k$) rather than logarithmic ($dS/Sdt = -k$) or Gompertzian ($\log dS/Sdt = A = kt$) and could be characterized by 2 constants describing a linear increase in mortality with time: $dS/Sdt = -k$ ($t = t^0$) or $2 \ln S/S_0 = -k(t + t^0)^2$. Unmated *B. t.* showed logarithmic survival which, on regrouping into successful breeding pairs, changed to $1/3$ the rate and a linear configuration. Other species showed much smaller effects of grouping or of sex on survival. Early mortality in *M. o. m.*, *L. l.* and *L. s.* was correlated with an early incidence of fatty livers and in *D. s.*, of respiratory pathology.

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I. INTRODUCTION

The life spans of mammals vary enormously ranging from a few weeks to scores of years. A considerable portion of this variation can be related to size as an intrinsic property of any species and, among morphological and physiological characters, brain weight and metabolic rate have been suggested as functionally correlated with potential longevity or maximum life span (Sacher, 1959). Besides such intrinsic factors, various environmental influences can increase mortality in natural populations. Survival curves (survivors, *S.* vs time or life span,

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t) dominated by environmental influences are quite different from those of protected animals and ideal or limiting forms for the respective types have been suggested as exponential with constant mortality ($dS/dt = -k$) and »rectangular« with zero or minimum mortality through most of the life span ($t = k \pm \sigma$). De evey (1947) used various birds and the Dall sheep as examples of these respective limiting types. Conditions of captivity can decrease mortality in wild species to yield intermediate linear or »oblique« survival curves ($dS/dT = -k$) (C o m f o r t, 1957a, 1964) but limited data are available for such populations.

During the development and productive use of captive colonies of a series of wild rodent species (M o r r i s o n, 1971; D i e t e r i c h, 1974), data sets on their respective mortality/longevity have been accumulated. The present study presents and compares these data which provide useful base lines for ongoing production, and allow the identification of different mortality patterns and the comparison of different species for selection.

II. MATERIAL AND METHODS

The fifteen taxa used in this study were among the standardized animal colonies maintained at the Institute of Arctic Biology. The species used, their vernacular names, geographical origins and diets are listed in Table 1. Except for the old world *Acomys cahirinus*, a murid, all belong to the family *Cricetidae*, nine being from the characteristically northern subfamily *Microtinae* and the remaining five from the subfamily *Cricetinae* with its more characteristically temperate and subtropical distribution.

These rodents were born in captivity and maintained under continuous standard conditions of 20°C, 16 hr of artificial light and eight hr of darkness in 8" × 8" × 36" fiberglass boxes with expanded metal covers (M o r r i s o n, 1960). Bedding of wood shavings and nesting material of facial tissues was changed weekly. Water and food were available *ad libitum*. The animals were weaned at three to four weeks as sibling groups of the same sex. Rodents were paired for breeding at a minimum age of two months. Animals not paired were continued in their original groupings.

The colony was under the supervision of a veterinarian and conventional practice and precautions were maintained. Access to the animals was restricted but not prohibited. New animals were maintained under quarantine before joining the colony. Gross and microscopic examination of dead or dying individuals was carried out by an experienced veterinary pathologist (Table 2). Except for *Dicrostonyx* which showed unusual susceptibility among our species, the pathologic data do not show infectious disease as a preponderant cause of death. Pulmonary + bacterial mycosis + middle ear infection together amounted to 23 percent of the observed pathology and pulmonary lesions may represent secondary rather than primary involvement. No epidemic losses occurred during these studies. Serum was tested periodically for evidence of a number of common murine pathogens: reo virus, Sendai virus, ectromelia (mousepox), mouse hepatitis virus, lymphocytic choriomeningitis and Theiler's mouse encephalomyelitis. The only positive reactions

Table 1

Identification and diets of Rodent subjects.

Species ¹	Common name	Geographical origin	Diet supplement ²
<i>Microtus pennsylvanicus tananaensis</i>	Meadow vole	Cent. AK.	Barley sprouts
<i>Microtus oeconomus macfarlani</i>	Tundra vole	E. AK. + Yukon + NWT	" "
<i>Microtus oeconomus operarius</i>	Tundra vole	W. AK.	" "
<i>Microtus miurus muriei</i>	Singing vole	Brooks Range to W. Coast AK.	" "
<i>Microtus abbreviatus (a)</i>	Insular vole	St. Matthew I., AK.	Sunflower seeds, carrots & sprouts
<i>Lemmus lemmus (b)</i>	Norwegian lemming	Norway	Carrots & sprouts
<i>Lemmus sibiricus trimucronatus</i>	Brown lemming	Arctic Coast AK.	" "
<i>Dicrostonyx stevensoni (a)</i>	Collared lemming	Umnak I., AK.	" "
<i>Clethrionomys rutilus</i>	Red-backed vole	AK. & N. Canada	None
<i>Peromyscus maniculatus borealis (e)</i>	Deer mouse	N. W. Canada	Sunflower seeds
<i>Peromyscus maniculatus bairdii (d)</i>	Deer mouse	Mid. W. U. S.	" "
<i>Baiomys taylori (e)</i>	Pygmy mouse	Coastal Texas & Mexico	" "
<i>Calomys ducilla (f)</i>	Vesper mouse	Andes, Peru	" "
<i>Calomys callosus (g)</i>	Laucha de campo	Lowland Bolivia	" "
<i>Acomys cahirinus (h)</i>	Egyptian spiny mouse	Egypt & Near East	Carrots, orange & sunflower seeds

¹ Original stocks of these rodents were obtained through the kindness of (a) Dr. R. Rausch, Arctic Health Research Center, Fairbanks; (b) Dr. E. Ostbye, Univ. Oslo, Blindern; (c) Dr. W. Fuller, Univ. Alberta, Edmonton; (d) Dr. R. Reeder, Univ. Wisconsin, Madison; (e) Dr. J. Hudson, Rice University, Houston; (f) Dr. O. P. Pearson, Univ. California, Berkeley (= *C. lepidus ducillus*); (g) Dr. K. M. Johnson, USPHS, NIAID, Middle America Research Heights, CZ (Pearson and Patton, 1976, have recently referred these animals to *C. fecundus* on the basis of chromosome morphology.); (h) National Zoological Park, Washington.

² Basic diet for all animals was Mouse Breeder Chow (Ralson Purina Co.), wheat germ, and rolled oats; except lemmings who received rabbit pellets instead of chow.

were to reo III virus (11/86 in three species) but no symptoms of active infection could be found .

Population losses were of three kinds: (1) withdrawal for sacrifice or other experimental use (44%), (2) other artificial loss as by escape or failure of the water supply (5%) and (3) »natural« loss. The natural loss ($\Delta S/S$) was referred to the number of individuals beginning that month and these values were used to construct corrected survival tables for natural attrition alone (Table 3). A more precise form uses the average population at risk during the month or even computes on a day-to-day basis (Storer, 1962). However, such correction factors for table 2 would only average 1.10 for monthly mortality and 0.87 for survivors at 10 mo, and the forms of the mortality and survival curves would not be changed. Since early losses are of a different character than later losses, they have been excluded in most of the graphical comparisons which use the number of animals weaned at one month as the base.

Table 2

Pathological lesions grouped according to diagnostic category ¹.

Species	N	Skin-Pelage	Musculo-Skeletal	Respiratory	Cardio-Vascular	Hemic & Lymphatic	Digestive	Uro-Genital	Endocrine	Nervous	Organs of Sense ²	Misc. ²	Bacterial Mycotic	Parastic	Neoplasms	Nothing Found
<i>M. penn. ten.</i>	27		1	9			3	11				2		1		11
<i>M. oec. mac.</i>	50	1		13	3	1	24	14				10	1			8
<i>M. oec. oper.</i>	12			1		1	1				1	3		1	1	5
<i>Lemmus lemmus</i>	15			4			6	3			1	2	1		2	3
<i>Lemmus sib. tri.</i>	44	1	2	10	1		26	16	1		2	8	2	1		4
<i>D. stevensoni</i>	95	1	1	41	3	4	17	27		3	22	7	4		9	19
<i>C. rutilus</i>	26	1		7			7	8				2			2	8
<i>Calomys ducilla</i>	10	1		4		1	5	3				3			2	1
<i>Calomys callosus</i>	25	1	1	7	1	1		7	1	2	1	6	2	1	1	9
<i>Acomys cahirinus</i>	17			3			1	5				2				8
Total	321	6	5	99	8	8	90	96	2	5	27	45	10	4	17	76

¹ Observations by R. Dieterich and R. Van Pelt

² Includes cannibalism, malnutrition, stress, dehydration, toxemia

Other descriptive studies on these maintained populations include aspects of productivity (Morrison *et al.*, 1976a), growth (Morrison *et al.*, 1976b), organ weights (Dieterich *et al.*, 1973), biochemistry (Galster & Morrison, 1974) and physiology (Rosenmann & Morrison, 1974).

III. RESULTS

Basic survival data for the 15 taxa are given in Table 4 in relation to the total number of young identified after birth which averaged more than 300 and ranged from 200 to 670 in different groups. Values at one week defined infant or neonatal mortality which averaged 11 percent and ranged from 0 in the two species of *Calomys* to 23 percent in *Mi-*

Microtus pennsylvanicus and *M. oeconomus macfarlani*. Values at 1 month included an additional juvenile loss and averaged 23 percent in the different groups ranging from 10 percent in *Calomys callosus* to 38 percent in *Lemmus sibiricus*.

Figure 1 plots survivors against time for several representative groups. Without commitment to any particular function, these points can be

Table 3

Representative mortality table: *Microtus oeconomus macfarlani*.

Month or Final Age ¹	Monthly Natural Loss	Monthly Artificial Loss ²	Total Survivors	Monthly Mortality/1000	Monthly Survival/1000	Corrected Total Survivors		
						From Birth/1000	From 1 week/1000	From 1 Month/1000
0			671			1000		
1/4	151	0	520	151/671=210		775	1000	
1	62	15	443	62/520=119	(881)	683	881	1000
2	42	75	326	42/443=95	905	618	797	905
3	37	54	235	37/326=113	887	548	707	803
4	21	28	186	21/235=89	911	499	644	732
5	22	7	157	22/186=105	882	440	568	645
6	17	5	137	17/157=108	892	393	507	576
7	15	10	110	15/137=111	889	349	450	511
8	8	12	90	8/110=73	927	324	418	475
9	16	5	69	16/90=178	822	266	343	390
10	11	1	57	11/69=159	841	224	289	328
11	12	3	42	12/57=210	790	177	228	259
12	10	2	30	10/42=238	762	135	174	198
13	5	6	19	5/30=167	833	112	145	165
14	1	4	14	1/19=53	947	106	137	156
15	5	0	9	5/14=356	643	68	88	100
16	2	0	7	2/9=222	778	53	69	78
17	1	0	6	1/7=143	857	46	59	67
18	2	1	3	2/6=333	667	30	39	44
19	2	0	1	2/3=667	333	10	13	15
24	1	0	0		0	0	0	0

¹ Periods are lunar months of 28 days. ² Animals withdrawn for experimental use were selected for age only.

represented by one or more linear segments and figure 2 compares such linear representations for all the taxa. Survival curves for species and subspecies of *Microtus* (Fig. 2A) characteristically showed a single rate over the first 80% of loss followed by a much slower rate of loss over the remaining 20 percent. Curves for the lemmings (Fig. 2B) showed three segments, an initial phase through 60 percent of loss, a slower rate during the next 30 percent and a still slower rate for the final 10 percent. The curves for non-microtine species (Fig. 2C) are more diverse.

Table 4
Survivors per thousand from initial populations of 15 rodent species and subspecies.

Age in weeks	Species and initial numbers ^{1/}														
	M.p.t.	M.o.m.	M.o.o.	M.m.	M.s.a.	L.l.	L.s.	D.s.	C.r.	P.m.bo.	P.m.ba.	B.t.	C.d.	C.c.	A.c.
1 ^{2/}	769	775	820	840	877	917	847	840	885	909	980	952	999	999	885
4 ^{3/}	715	683	634	754	763	752	620	761	774	840	864	805	893	899	872
8	705	618	625	703	731	648	541	717	712	811	833	734	773	828	862
12	689	548	612	664	713	574	478	646	667	789	775	624	696	812	852
16	658	499	607	615	685	547	433	578	650	754	756	560	667	730	
20	632	440	548	570	647	480	384	539	600	729	740	516	636	703	829
24	582	393	507	525	617	436	347	498	581	649	703	465	613	686	823
28	531	349	473	489	582	373	252	450	514		674	393	596	649	816
32	512	324	450	416	554	318	224	402	458	639	656	357	569	608	752
36	469	266	402	343	510	292	194	378	424	623	628	317	538	543	
40	437	224	338	269	486	283	146	365	387	587	622	286	518	515	732
44	415	177	327	190	455	244	134	329	360	581	614	260	495	504	701
48	383	135	303	179	415	204	105	305	334	567	606	243	486	470	680
52	342	112		141	362	150	87	285	298	515	598	221	476		669
56	295	106	261	113	311	119	69	245	281	493		214	445		264
60	264	68	188	108	284	86		203	262	460		211	434	457	647
64	253	53	174	68	250	66	56	198	243	452	569	203	410	443	602
68	217	46		63	225	49		161		424		199	374	413	590
72	176	30	144	50	169		44	120	223			196	349	375	
76		10	108	36	142	32	31	107	182	401	556	175	335	307	579
80	160		90	22	99	24		99	160	378		158	306	239	
84			23			8	25	84		353	541	131	291	153	567
88					76	0	19	54	137	327		120	230	134	556
92	107				54		13	45	91	314	525	109	212	77	432
96		0			45		6		61	300	492	103		57	505
100			0					23	30	272	472	91	185		479
104	71				27				0		430				451
108					13					257	410	80	124		437
112			0				0	11		242	389	69			
116												63	82		387
120					0							50			370
124	0									194	359	44			353
128								0		161		36	41		335
132										144	320	30			301
136												22			282
140										125					
144										/83,		11	0		

¹ At 1 week; for species coding refer to table 1.

² 1-week values defines infant (neonatal) mortality.

³ 4-week value defines infant + juvenile mortality.

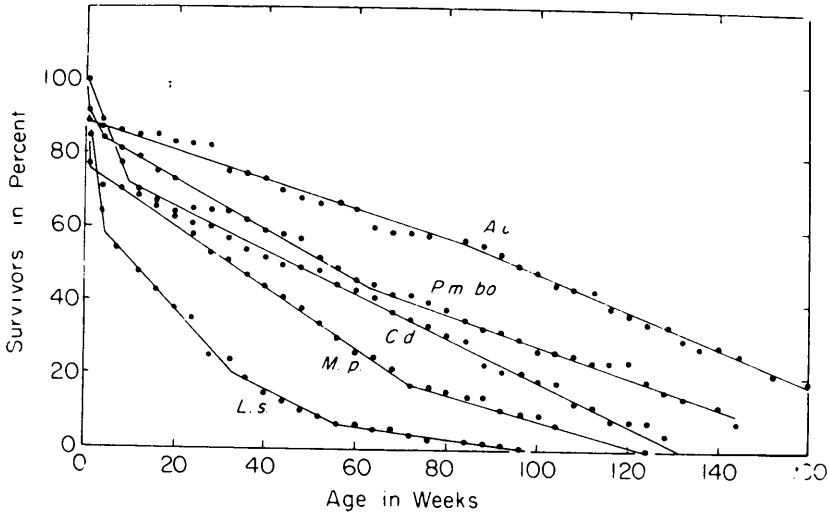


Fig. 1. Representative survival with data points fitted to linear segments by inspection. For species coding refer to Table 1.

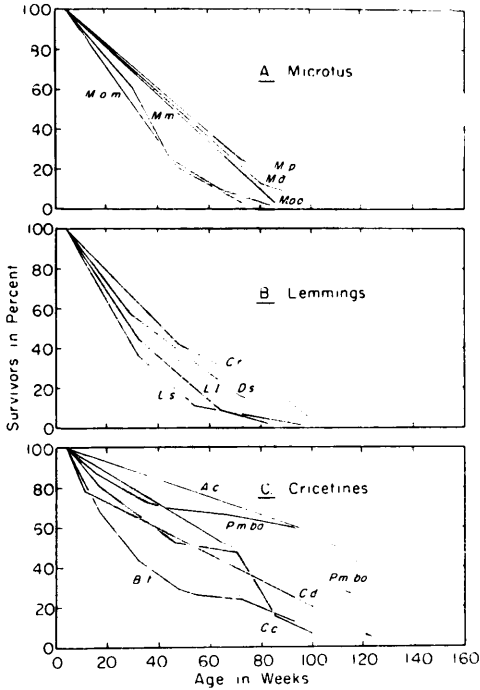


Fig. 2. Survival curves for all species by groups. (A) *Microtus*, (B) lemmings and *Clethrionomys*, (C) cricetines and *Acomys*. For species coding refer to Table 1.

Losses in *Calomys ducilla* are described (last 80 percent) by a single linear constant (0.65% S_0 /wk). In *Peromyscus* and *Acomys* which showed the greatest longevity with initial losses of < 1% S_0 /wk, the survival curves also showed little reduction in rate during later stages but *P. m. bairdii* showed a notable interim reduction between 40 and 90 weeks of age. *Baiomys* and *C. callosus* also showed bimodal curves with reduced mortality from 50 to 70 weeks.

Several time constants for the various curves are given in Table 5. The median life span (t_{50}) with values ranging from 23 to 120 weeks is a useful single index of survival under given experimental or natural

Table 5
Rate and time constants for rodent survival curves.

Species	t_{50}^1 wk	t_{max}^2 wk	t_{90}^3 wk	c.v. ⁴ %	k_1^5 %/wk	t^0 ⁶ wk	k^6 $\times 10^4$ /wk	k^5 %/wk ²
<i>Microtus pennsylvanicus</i>	50	124	104	66		4	4.8	2.6
<i>Microtus o. macfarlani</i>	31	96	60	60		12	8.9	
<i>Microtus o. operarius</i>	47	100	82	58		0 ⁷	6.2	
<i>Microtus abbreviatus</i>	48	120	88	60		4	5.2	
<i>Microtus miurus</i>	43	112	62	66		4	10.0	
<i>Lemmus lemmus</i>	30	88	64	67		16	7.7	
<i>Lemmus sibiricus</i>	26	96	64	72		16	10.0	4.0
<i>Dicrostonyx stevensoni</i>	37	128	86	73	2.0 ⁸	-4	5.2	
<i>Clethrionomys rutilus</i>	40	104	94	70	1.8 ⁹			
<i>Baiomys taylori</i>	23	170	108	92	3.2			
<i>Peromyscus m. borealis</i>	70	>160	160	69	1.0		1.1	
<i>Peromyscus m. bairdii</i>	105 ⁷		>160		1.0		0.3	
<i>Calomys ducilla</i>	60	160	114	77	1.0	-32	4.2	
<i>Calomys callosus</i>	(52)	>101	90	69	1.6		6.5	
<i>Acomys cahirinus</i>	110		>160			12	1.2	

¹ Median life span.

² Maximum observed life spans are lower than might be expected because of continuing experimental use of individuals.

³ Survival time to last decile (90th percentile).

⁴ Coefficient of variation, $100 \sigma_t/\bar{t}$

⁵ $dS/Sdt = -k$ or $\ln S/S_0 = -kt$

⁶ $dS/Sdt = -k(t+t^0)$ or $\ln S/S_0 = -k(t+t^0)^2$

⁷ Sacher & Staffeldt (1972) show a value of 170 wk for *P. leucopus*.

⁸ Data from Manning (1954) give a value > 1.7%/wk for *D. groenlandicus*.

⁹ Data from Buchalczyk (1970) also give a value of 1.8%/wk for *C. glareolus*.

conditions. The maximum life span (t_{max}) is another common index used as a measure of the potential or intrinsic longevity of the species (Sacher, 1959), but our values are lower than might be expected because of continuing experimental use of older individuals. As a limit, t_{max} is intrinsically more variable than a mean and Comfort (1959) has used the survival time for the last decile (t_{90}) as a measure of life span. Also given in Table 5 are values for the coefficient of variation, a common statistic which may be a useful index of the general form of

the survival curve including environmental influences together with genetic variability and any intrinsic variability of the mortality process (Sacher, 1956). Limiting values might range from near zero for a »rectangular« curve ($t = k \pm \sigma$), to near one half for a linear curve, to near one for an exponential curve ($dS/Sdt = -k$) or greater than one for forms in which mortality decreases with time ($dS/Sdt = f(1/t)$). Actual values range from 0.20 in strains of laboratory mice (Storer, 1966) and 0.24 in the grasshopper mouse (O'Farrell, 1975) in captivity to 1.1 — 1.4 in several heteromyid rodents in nature (French *et al.*, 1967). In our series the coefficient of variation was lowest in *M. o. operarius* (0.58) and highest in *Baiomys* (0.92).

The curve for the pigmy mouse *Baiomys* appeared bimodal so the data were examined more closely by separately plotting deaths for reproducing and non-reproducing, males and females. The sexes did not differ but segregation as successful breeding pairs reduced the loss rate by a

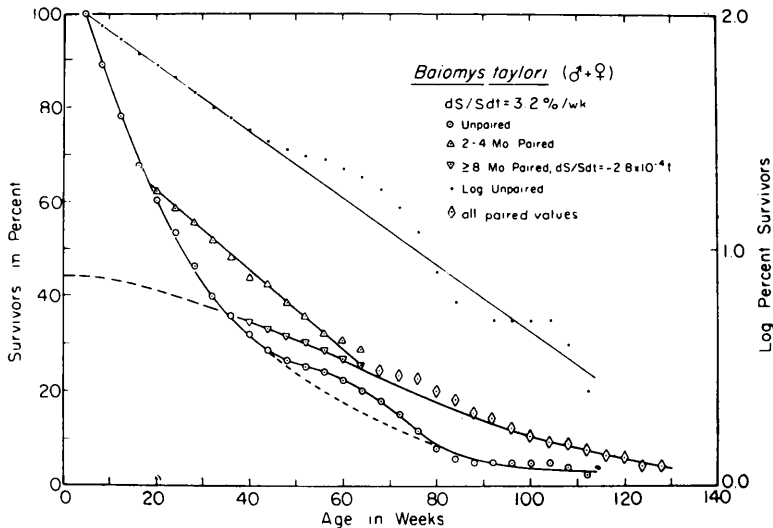


Fig. 3. Survival curves for *Baiomys taylori* (moving-3 averages).

factor of 3 (Figure 3) and changed the form from a logarithmic to a linear configuration. Thus *Baiomys* kept singly or in groups of the same sex after weaning through the 12th week showed much higher mortality before pairing, a higher mortality that was continued in the non-reproducing group through the following weeks. The survival curves for discrete groups paired at 8—16 and at 32—40 weeks showed a similar loss rate below $25^0/0S_0$ perhaps suggesting a resistant component in the population. The losses for unpaired *Baiomys* followed an exponential curve with $dS/Sdt = 3.2^0/0/wk$.

Separate analysis by sex and pairing showed a small advantage of pairing in *M. abbreviatus* with the curves displaced by +10 wk or +13% S_0 (40–80 wk) and a similar advantage for males over females (Figure 4). In *Clethrionomys* the curve for females was similarly displaced by +10 wk or +19% from that for males (Figure 4). The response in *Dicrostonyx* was less clear-cut since at 1 year there was no difference in survival between the four groups (paired and unpaired, males and females). During the first year paired animals and females had a temporary advantage (12–32 wk) but during the second year the males showed lower mortality. *Calomys callosus*, like *Baiomys* showed a

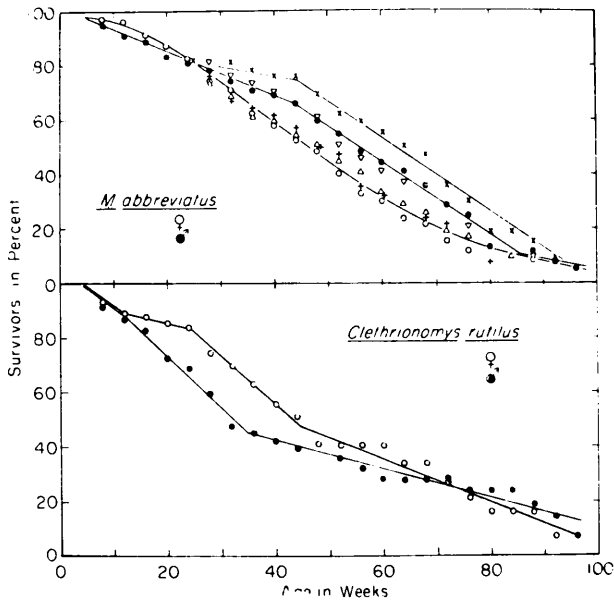


Fig. 4. Survival curves for male and female (●, ○), and paired and unpaired male (x, +) and male + female (△, ▽) *Microtus abbreviatus* (○ follows $dS/Sdt = -6.4 \times 10^{-4} t$); male and female (●, ○) *Clethrionomys rutilus*.

bimodal survival curve with little mortality from 50 to 65 weeks (Fig. 2c). In this case, however, separate grouping of the animals by sex or by pairing did not modify the survival curve.

IV. DISCUSSION

Patterns of longevity and mortality have been viewed as the resultant of two sets of influences, the one intrinsic relating to genetic characteristics of the population and the other extrinsic relating to various environmental factors (Deevey, 1947; Strehler, 1960; Comfort, 1964). Where losses from random predation or accident dominate, mortality would be constant during most of the life span resulting in ex-

ponential survival curves ($dS/Sdt = -k$) as described by Deevey (1947) for natural populations of several avian species. Other natural populations appear largely independent of environmental influences during much of their life span until the onset of degenerative changes of aging which follow some intrinsic schedule. The limiting pattern here would be the »skewed rectangular« curve ($t = k \pm \sigma$) in which mortality is very low through most of the life span but increases rapidly towards the end. This pattern as seen in Dall sheep (Murie, 1944) is much less common in nature but it may also be present in shrews in which older animals disappear from the population abruptly at about 15 months of age following severe tooth wear (Crowcroft, 1950; Hawes, 1975). This pattern is best known in relation to current human survival which has commonly been represented by the compound exponential (Gompertz) equation, $\log (dS/Sdt) = -(a + kt)$ (Comfort, 1959; Strehler, 1960; Cook, 1972), an empirical relation for which, however, theoretical rationales have been suggested (Sacher, 1956, 1960; Strehler, 1960).

Because laboratory populations are protected from major hazards encountered in nature they might be expected to follow the same pattern as man. Indeed, the laboratory mouse shows such delayed mortality (Murray & Hoffman, 1941; Finch, 1969; Russell, 1975; Storer, 1962). However, none of our species showed this behavior with nine survival curves being linear over most of the life span and six curves showing some positive curvature (segments with decreased slope). This observation follows Comfort (1957b) who reported that a variety of mammals in zoos including sheep, goats, wolves, voles and cavies were characterized by such linear survival curves and suggested that captivity may impose stresses or hazards that increase mortality.

Although the laboratory environments are free of some hazards, day-to-day contact with man or with other animals, even of their own species, is often stressful to captive wild species. Thus, Buchalczyk (1970) found a median life span of 20 months for successful breeding pairs of bank voles (*Clethrionomys glareolus*) but of only 7 months for animals housed communally. This effect is similar to our experience with *Baiomys* in which losses in the non-reproducing group were at 3 times the rate of the successful breeding pairs. Beyond such behavioral influences, conditions of caging, diet, temperature, radiation and risk of disease can modify survival in susceptible species. Accordingly, differences in rodent survival under equivalent conditions may be viewed as differing degrees of adjustment to or suitability for captivity. The carnivorous grasshopper mouse, *Onychomys*, in which an unselected

population taken from nature showed lower mortality than do inbred strains of white mice and rats (O'Farrell, 1975) may be thought of as »preadapted« for captivity. In addition, longer life spans might be expected in a maintained population since, to the degree that longevity is heritable, the composition of the population should shift progressively towards longer-lived individuals. Storer (1966) has estimated the »heritability« of longevity for laboratory mice as 0.36 in females and 0.21 in males. By contrast, in natural populations where most individuals die young, to the degree that longevity is inversely related to early maturation, the composition of the population might be expected to shift progressively towards shorter-lived individuals.

In comparing survival in various captive species a simple mathematical expression for these curves would be useful. Linear survival curves are easily characterized ($dS/S_0dt = -k$) but a relationship involving mortality increases with age, it may be noted that for the simplest function that might be proposed, ($dS/Sdt = -kt$), S is closely linear in t through the middle portion of the survival curve (80—30% S_0) (Leslie & Ransom, 1940). Furthermore, recognizing that the onset of mortality may be advanced or deferred by external circumstances with displacement of the survival curves on the time axis, we may propose an effective live span, $t + t^\circ$, for the actual life span, t . Figure 5A fits this relation to three examples from the genus *Microtus*, *M. o. macfarlani*, *M. o. operarius* and *M. agrestis* (Leslie & Ransom, 1940) with $t^\circ = 12$, 0 and -8 , respectively. Constants for these and other curves are given in Table 5. Comfort's (1957b) curve for *M. orcadensis* with $t^\circ = 4$ and $k = 5.8$ is close to ours for *M. pennsylvanicus*, *M. o. operarius* and *M. abbreviatus*, all of which show lower mortality than *M. o. macfarlani* and *M. agrestis* ($T_{50} = 50$ vs 35 wk). However in a later paper, Leslie *et al.* (1955) reports finding twice the mean life span for a subsequent population of *M. agrestis*. A similar but lesser difference was noted for earlier (1942) and later (1955) groups of *M. orcadensis*, the later value being almost twice that of Comfort (1957b). Leslie *et al.* (1955) suggest »differences in vitality between the two strains« »improved methods of feeding and housing« and »unconscious selection in favor of older-living animals« as possible explanations of these differences. We may note that we are currently observing comparable longevity ($t_{50} = 98$ wk) in another microtine, *M. xanthognathus*, the yellow-cheeked vole.

Even though a linear increase in mortality provides an effective description of survival this may be an approximation since careful examination of data as either survival or mortality curves often suggests a step function rather than a continuous change. These effects are shown in Figure 6 which gives mortality curves for all taxa. Although mortali-

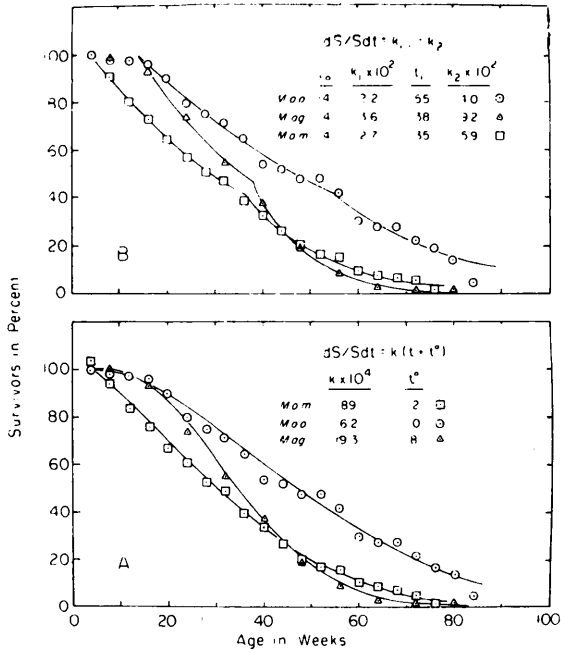


Fig. 5. Survival curves for *Microtus agrestis* (Leslie & Ransom, 1940), *M. oeconomus macfarlani*, and *M. o. operarius* fitted (A) as $dS/Sdt = -k(t+t^0)$ or $2 \ln S/S_0 = -kt(t+t^0)^2$; and (B) as $dS/Sdt = -k_1 - k_2$ or $\ln S/S_0 = -k_1t - k_2t^2$.

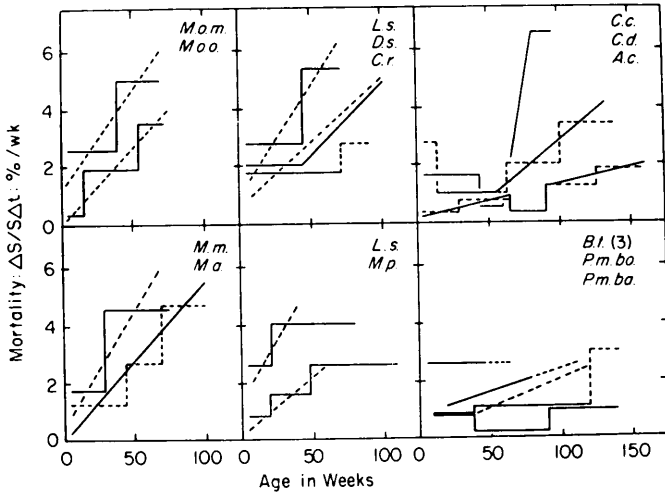


Fig. 6. Mortality ($\Delta S/S \Delta t$) in relation to age for all taxa. Oblique curves were fitted to least square deviations. Data favors »solid« configuration. For species coding refer to Table 1.

ty curves are more sensitive indices of change than are survival curves, the large dispersion of values often obscures the trends. However, in most cases the use of moving-three averages has smoothed the data sufficiently without blurring any steps. Such step changes could be in keeping with the phasic nature of mortality in which deaths during successive periods are characterized by specific pathologies as especially well documented in man (Strehler, 1975). Storer (1966) reported such bimodal distributions of survival associated with specific pathologies in four strains of white mice but in 40 other groups (sex and strain) survival times were »reasonably normally distributed«. Figure 5B compares the same three *Microtus* as fitted by two logarithmic mortality phases. Although the fit is good this is a much less economical description since two time plus two rate constants are required and so is correspondingly less useful for general comparisons of species.

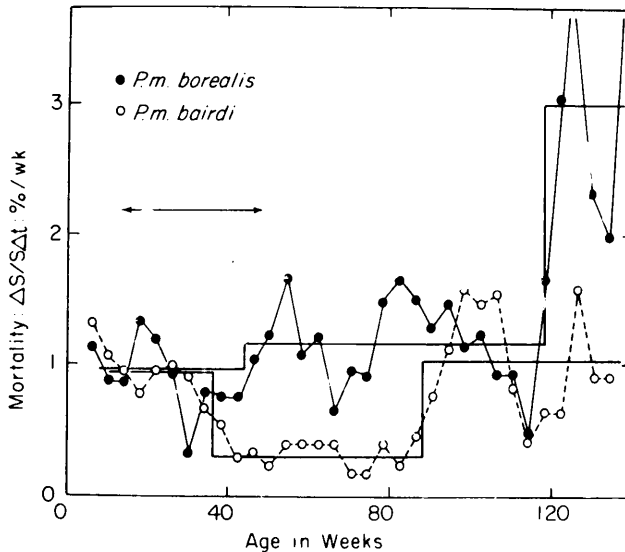


Fig. 7. Mortality as a function of age in 2 subspecies of *Peromyscus maniculatus*. Points are moving-3 averages. Arrows show period of arrested growth in *P. m. bairdii*.

During the first 120 weeks *P. m. borealis* maintained a steady mean mortality at $1.1^0\%/wk$ with values cycling between 0.5 and $1.6^0\%/wk$ (Fig. 7). Although *P. m. bairdii* began in this same manner, after 36 weeks mortality fell to a very low value ($0.35^0\%/wk$) which was maintained during the succeeding 50 weeks at which time it increased to the previous level ($1.0^0\%/wk$). This unusual behavior might be viewed as merely an accentuated bimodal distribution of deaths. However in eom-

paring other aspects of these two subspecies we find that *P. m. bairdii* also contrasts in exhibiting arrested growth during an extended period between 15 and 50 weeks of age (Morrison *et al.*, 1943). This dietary effect has been considered the only successful example of experimental deferral of aging (Comfort, 1964) so the association of delayed growth and delayed mortality in another species is of much interest. Between these two subspecies, *P. m. bairdii* has also shown an unusual metabolic lability associated with an alarm response (Rosenmann & Morrison, 1975).

In comparing survival curves it was a matter of some surprise that the inland *M. o. macfarlani* and *M. miurus* showed considerably higher

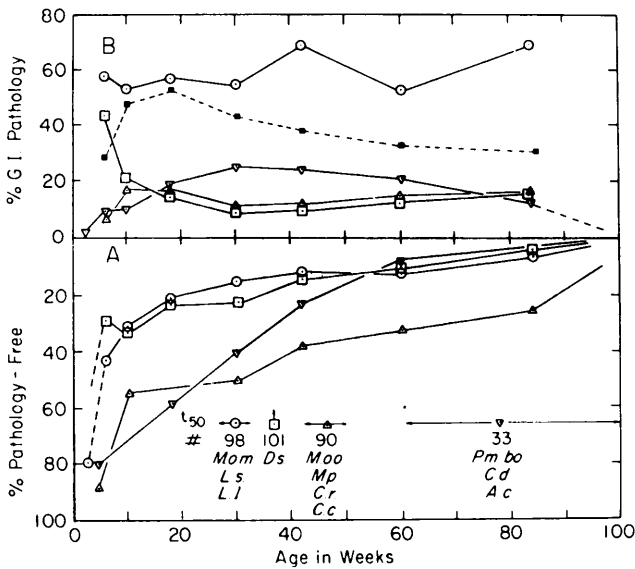


Fig. 8. Pathological findings in relation to age. Rodents are grouped by median life span as indicated with the number of necropsies shown below. »Pathology-free« means nothing found in necropsy. Closed squares compare incidence of respiratory pathology in *Dicrostonyx*. All points are moving-3 averages.

mortality than their coastal and insular close relatives, *M. operarius* and *M. abbreviatus*. A similar difference was seen between the two *Lemmus* and the *Dicrostonyx*. However, necropsy data (Table 2) revealed some interesting correlations between this higher mortality and the incidence of pathology. These are summarized in Figure 8 which divides the species into groups according to longevity and compares the fraction of individuals in which no pathology was found against age. The earlier incidence of overt pathology in the lemmings and *M. o. macfarlani* is clearly

seen. Figure 8 also compares GI pathology, largely fatty livers, and among the 4 groups the higher incidence in *Lemmus* and *M. o. macfarlani* is notable. *M. o. macfarlani* also showed some incidence of renal lipidosis not seen in the other species. This hepatic and renal lipidosis probably reflects the diet in captivity since more carbohydrate and fat was provided than is available to microtines in nature but the differential susceptibility of certain species or subspecies is still not explained. Finch (1969) maintained retired male C57B1/6J mouse breeders from the Jackson Laboratory and found an increased average life span as compared to the parent institution (122 vs. 104 wk). His only noted difference in handling was a reduction in the fat content of the diet from 12% to 4.3%.

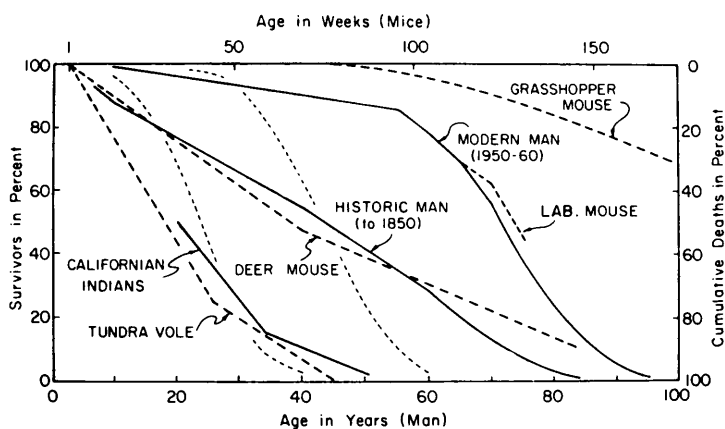


Fig. 9. Comparison of human and rodent survival curves. Solid curves: modern and historic man from Strehler (1975) and Californian Indians from Cook (1972); dashed curves; grasshopper mouse (*Onychomys leucogaster*) from O'Farrell (1975), deer mouse (*Peromyscus maniculatus borealis*) and tundra vole (*Microtus oeconomus macfarlani*) from this study, and laboratory mouse (C57 B1 6J♂) from Finch (1969). The latter is one of the longer-lived strains of laboratory mouse exceeding other strains by as much as 3-fold (Murray & Hoffman, 1941; Storer, 1966). Survival curves for shorter-lived strains of laboratory mouse correspond to the curves for neither man nor wild mice (dotted curves above).

The increased longevity seen in rats under restricted diet is also accompanied by a deferral of pathological changes (McCay *et al.*, 1943). O'Farrell (1975) has reported a similar picture in grasshopper mice, *Onychomys leucogaster*, with 95% survival through the first two years followed by increasing mortality during the next two years (median=3.9 yr) accompanied by a high incidence of pathological lesions not seen in younger individuals. In long-lived laboratory mouse strains mortality

stays at a lower level with 80% survival through the first two years, but increases rapidly in the third year (median = 2.5 yr) during which Finch (1969) observed a substantial incidence of postmortem pathology not seen during the earlier period. Barnett *et al.* (1974) also noted very limited pathology in two year old captive house mice.

Comfort (1964) commented on the resemblance of survival curves for captive mammals to some earlier human survival curves and it is possible to compare ranges of curves for mice and men. Thus, Figure 9 keys together survival curves for laboratory mice and modern man representing a scaling difference of 1 mo : 2.5 yr or 1 : 30 between mice and men. Curves for the deer mouse and »historic« man, and for the tundra vole and Californian indians then correspond respectively in both position (rate) and shape. However, in this representation there is no human analogue for the grasshopper mouse whose »longer« life span may present a goal for »future« man as projected by Strehler (1975). These parallels are interesting and possibly significant in reflecting similarities in mortality and aging but we cannot be sure that differences in various adapted species really correspond to different responses to environment in a single species.

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PRZEŻYWALNOŚĆ U 15 GATUNKÓW I PODGATUNKÓW GRYZONI TRZYMANÝCH W HODOWLI

Streszczenie

Przedstawiono dane o długości życia i śmiertelności 15 dzikożyjących gatunków i podgatunków gryzoni hodowanych w warunkach laboratoryjnych. Są to: *Microtus pennsylvanicus tananaensis*, *M. oeconomus macfarlandi*, *M. o. operarius*, *M. miurus*, *M. abbreviatus*, *Lemmus lemmus*, *L. sibiricus trimucronatus*, *Dicrostonyx stevensoni*, *Clethrionomys rutilus*, *Peromyscus maniculatus borealis*, *P. m. bairdii*, *Baiomys taylori*, *Calomys ducilla*, *C. callosus*, *Acomys cahirinus* (Tabela 1). Śmiertelność gryzoni w pierwszym tygodniu życia wynosi średnio 11% (0 do 23%), a ich śmiertelność w ciągu pierwszego miesiąca życia równa się 23% (10 do 38%). Przeciętna długość życia dla zwierząt odjętych od matki w wieku 1 miesiąca trwa średnio 50 tygodni i najniższa jest u *L.l.* — 25 tygodni a najwyższa u *A.c.* — 108 tygodni. Wskaźnik ten waha się u przedstawicieli *Microtinae* od 25 do 40 tygodni, a u *Cricetinae* od 44 do 105 tygodni, za wyjątkiem *B.t.* (Ryc. 6). Krzywa obrazująca przeżywanie jest dla większości *Microtinae* liniowa lub skośna ($ds/dt = -k$) a nie logarytmiczna ($dS/Sdt = -k$) czy też zgodna z równaniem Gompertza ($\log dS/Sdt = A = kt$) i może być charakteryzowana przez dwie stałe opisujące liniowy wzrost śmiertelności w czasie: $dS/Sdt = -k (t = t^0)$ lub $\ln S/S_0 = -k (t + t^0)^2$ (Tabele 2, 3, Ryc. 1—5). Niekojarzone *B. t.* cechują się logarytmiczną krzywą przeżywania, która po połączeniu tych zwierząt w rozradzające się pary zmienia swój kształt i poziom (Ryc. 3). Inne gatunki wykazują znacznie mniejszą zależność pomiędzy przeżywalnością a pięcią czy też trzymaniem w grupach. Duża śmiertelność młodych *M.o.m.*, *L.l.* i *L.s.* skorelowana była z objawami otłuszczenia wątroby i u *D.s.* chorobami układu oddechowego (Tabele 2, 3, Ryc. 7, 8).