Life Tables

Visualize Demography with Life Tables

- Summarizes mortality, survival, and growth potential over time
  - age-specific survival/mortality pattern within population
  - based on cohorts (often expressed per some round number, such as 1000 individuals)
  - requires age estimates
  - **cohort** (followed thru time) vs. **time-specific** or **static** (snapshot in time)

Cohort life table

also called ‘age-specific’ or ‘horizontal’

Age class	# Alive at start of year	Survival	Mortality	Mortality rate	Survival rate
x	f_x	l_x	d_x	q_x	p_x
0					
1					
2					
3					
4					
5					
6					
7					
8					
9					
10					
11					
12					
>12					

Follow cohort through life

f_x (or n_x) is number of individuals entering that age class

Age class	# Alive at start of year	Survival	Mortality	Mortality rate	Survival rate
x	f_x	l_x	d_x	q_x	p_x
0	205				
1	96				
2	94				
3	89				
4	79				
5	68				
6	55				
7	43				
8	32				
9	22				
10	15				
11	10				
12	6				
>12	0				

Survival: $l_x = f_x / f_0$

Proportion of initial population surviving to any given age;
sometimes expressed as # surviving to a given age
from a standardized population size (e.g., 1000)

Age class	# Alive at start of year	Survival	Mortality	Mortality rate	Survival rate
x	f_x	l_x	d_x	q_x	p_x
0	205	1.000			
1	96	0.468			
2	94	0.459			
3	89	0.434			
4	79	0.385			
5	68	0.332			
6	55	0.268			
7	43	0.210			
8	32	0.156			
9	22	0.107			
10	15	0.073			
11	10	0.049			
12	0	0.000			

or

Age class	# Alive at start of year	Survival	Mortality	Mortality rate	Survival rate
x	f_x	l_x	d_x	q_x	p_x
0	205	1000			
1	96	468			
2	94	459			
3	89	434			
4	79	385			
5	68	332			
6	55	268			
7	43	210			
8	32	156			
9	22	107			
10	15	73			
11	10	49			
12	0	0			

Mortality: $d_x = l_x - l_{x+1}$

Proportion of initial population (f_0) dying in any given time interval

Sometimes expressed as # dying [$(l_x - l_{x+1})*f_0$ or $f_{x+1} - f_x$]

Age class	# Alive at start of year	Survival	Mortality	Mortality rate	Survival rate
x	f_x	l_x	d_x	q_x	p_x
0	205	1.000	0.532		
1	96	0.468	0.010		
2	94	0.459	0.024		
3	89	0.434	0.049		
4	79	0.385	0.054		
5	68	0.332	0.063		
6	55	0.268	0.059		
7	43	0.210	0.054		
8	32	0.156	0.049		
9	22	0.107	0.034		
10	15	0.073	0.024		
11	10	0.049	0.049		
12	0	0.000			

or

Age class	# Alive at start of year	Survival	Mortality	Mortality rate	Survival rate
x	f_x	l_x	d_x	q_x	p_x
0	205	1000	532		
1	96	468	10		
2	94	459	24		
3	89	434	49		
4	79	385	54		
5	68	332	63		
6	55	268	59		
7	43	210	54		
8	32	156	49		
9	22	107	34		
10	15	73	24		
11	10	49	49		
12	0	0			

Mortality rate: $q_x = d_x / l_x$

Proportion of individuals entering age class X
that will die before entering the next age class

Age class	# Alive at start of year	Survival	Mortality	Mortality rate	Survival rate
x	f_x	l_x	d_x	q_x	p_x
0	205	1.000	0.532	0.532	
1	96	0.468	0.010	0.021	
2	94	0.459	0.024	0.053	
3	89	0.434	0.049	0.112	
4	79	0.385	0.054	0.139	
5	68	0.332	0.063	0.191	
6	55	0.268	0.059	0.218	
7	43	0.210	0.054	0.256	
8	32	0.156	0.049	0.313	
9	22	0.107	0.034	0.318	
10	15	0.073	0.024	0.333	
11	10	0.049	0.049	1.000	
12	0	0.000			

or

Age class	# Alive at start of year	Survival	Mortality	Mortality rate	Survival rate
x	f_x	l_x	d_x	q_x	p_x
0	205	1000	532	0.532	
1	96	468	10	0.021	
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5	68	332	63	0.191	
6	55	268	59	0.218	
7	43	210	54	0.256	
8	32	156	49	0.313	
9	22	107	34	0.318	
10	15	73	24	0.333	
11	10	49	49	1.000	
12	0	0			

Survival rate: $p_x = 1 - q_x$

Proportion of individuals entering age class X
that will survive to enter the next age class

Age class	# Alive at start of year	Survival	Mortality	Mortality rate	Survival rate
x	f_x	l_x	d_x	q_x	p_x
0	205	1.000	0.532	0.532	0.468
1	96	0.468	0.010	0.021	0.979
2	94	0.459	0.024	0.053	0.947
3	89	0.434	0.049	0.112	0.888
4	79	0.385	0.054	0.139	0.861
5	68	0.332	0.063	0.191	0.809
6	55	0.268	0.059	0.218	0.782
7	43	0.210	0.054	0.256	0.744
8	32	0.156	0.049	0.313	0.688
9	22	0.107	0.034	0.318	0.682
10	15	0.073	0.024	0.333	0.667
11	10	0.049	0.049	1.000	0.000
12	0	0.000			

or

Age class	# Alive at start of year	Survival	Mortality	Mortality rate	Survival rate
x	f_x	l_x	d_x	q_x	p_x
0	205	1000	532	0.532	0.468
1	96	468	10	0.021	0.979
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8	32	156	49	0.313	0.688
9	22	107	34	0.318	0.682
10	15	73	24	0.333	0.667
11	10	49	49	1.000	0.000
12	0	0			

Table 8.2. Interrelationship of life table statistics

In terms of	l_x	d_x	q_x	p_x
l_x	l_x	$l_x - l_{x+1}$	$1 - (l_{x+1}/l_x)$	l_{x+1}/l_x
d_x	$\sum_{y=x}^{\infty} d_y$	d_x	$d_x \Big/ \sum_{y=x}^{\infty} d_y$	$1 - \left(d_x \Big/ \sum_{y=x}^{\infty} d_y\right)$
q_x	$\prod_{y=0}^{x-1} (1 - q_y)$	$q_x \prod_{y=0}^{x-1} (1 - q_y)$	q_x	$1 - q_x$
p_x	$\prod_{y=0}^{x-1} p_y$	$(1 - p_x) \prod_{y=0}^{x-1} p_y$	$1 - p_x$	p_x

$\sum$ = summation, $\prod$ = multiplication

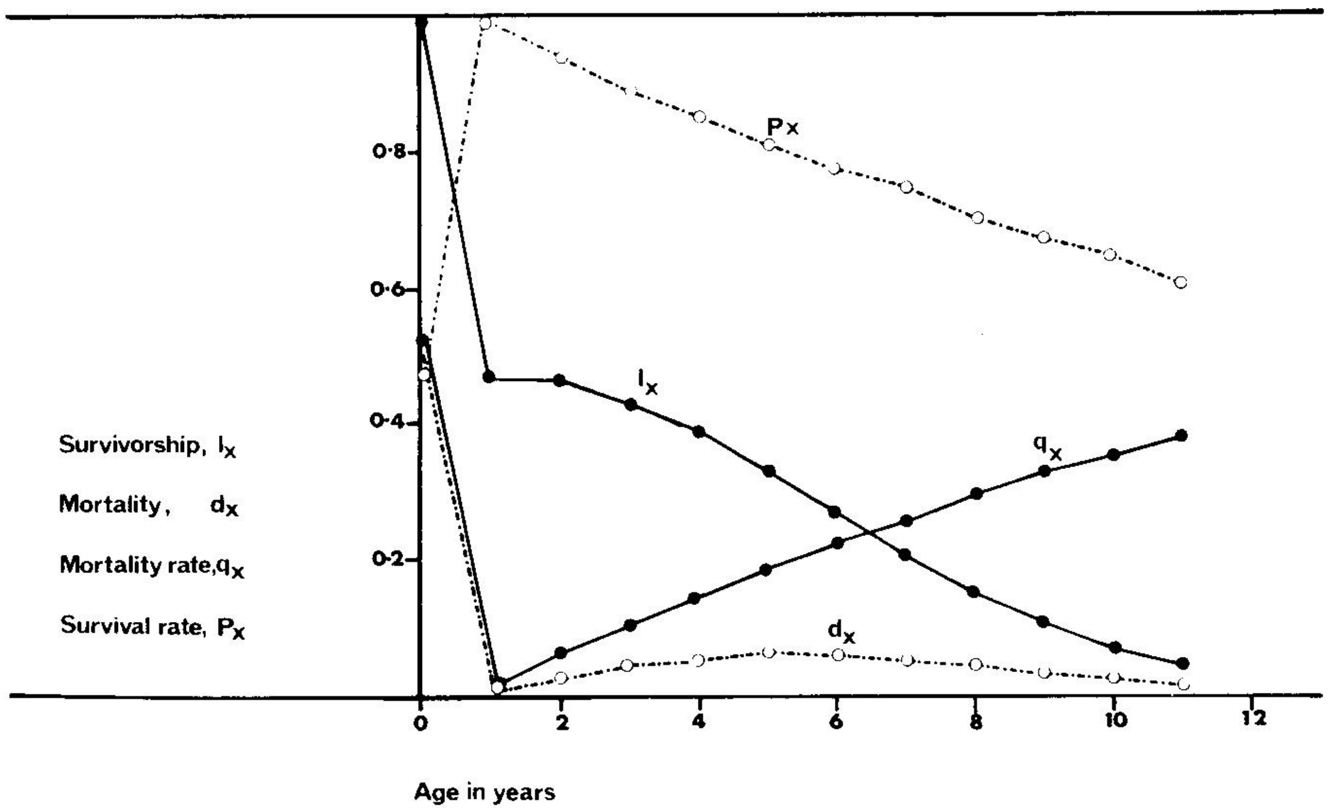


Figure 8.1. Graphic representation of the four life table schedules of female Himalayan thar (Caughley 1966).

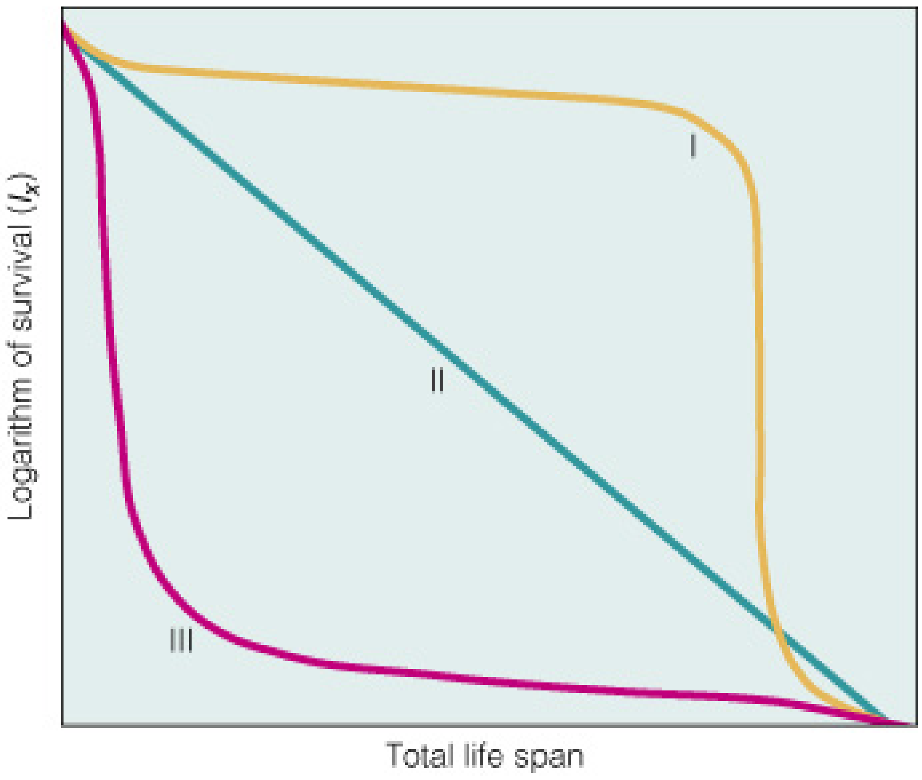
Survivorship curves

- *Survivorship curve* (l_x vs time)
  - -really a snapshot in time
  - -good for comparing times, areas, or sexes
  - -GIGO

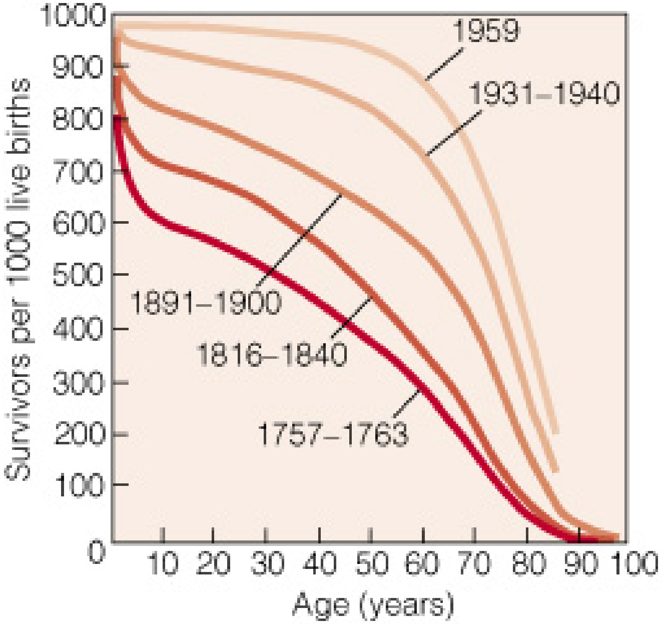
- Low mortality during life, then high mortality late in life (**I**)
  - -humans, some plants

- Constant mortality (**II**)
  - -adult birds, rodents, plants

- High mortality early in life (**III**)
  - -fish, invertebrates, some plants

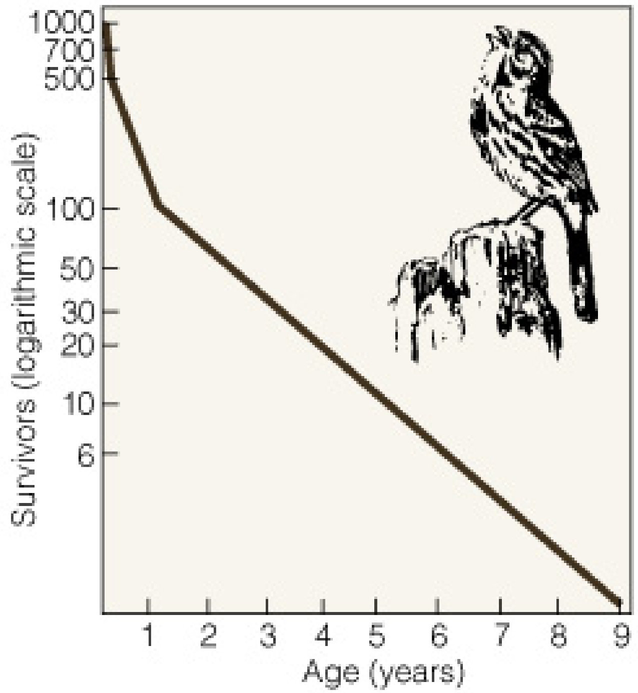


Survivorship curves for animals



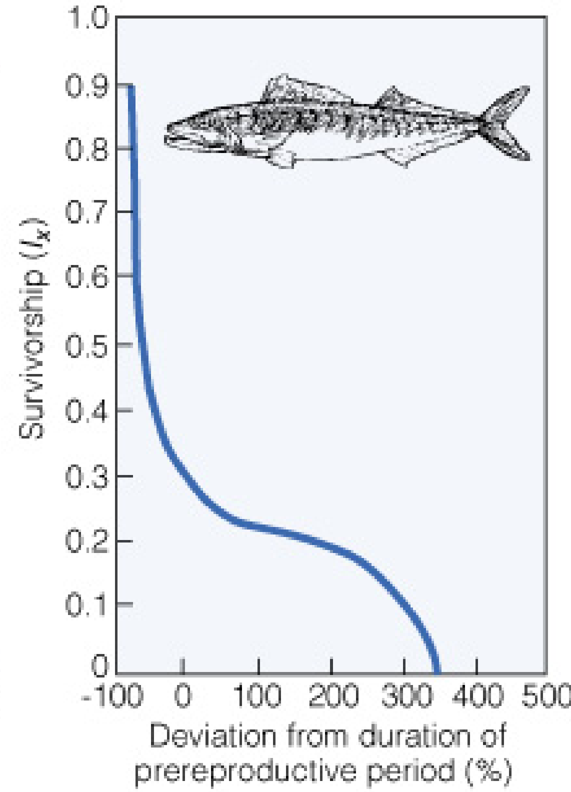
(a)

Humans in Sweden
Type(s) = ?



(b)

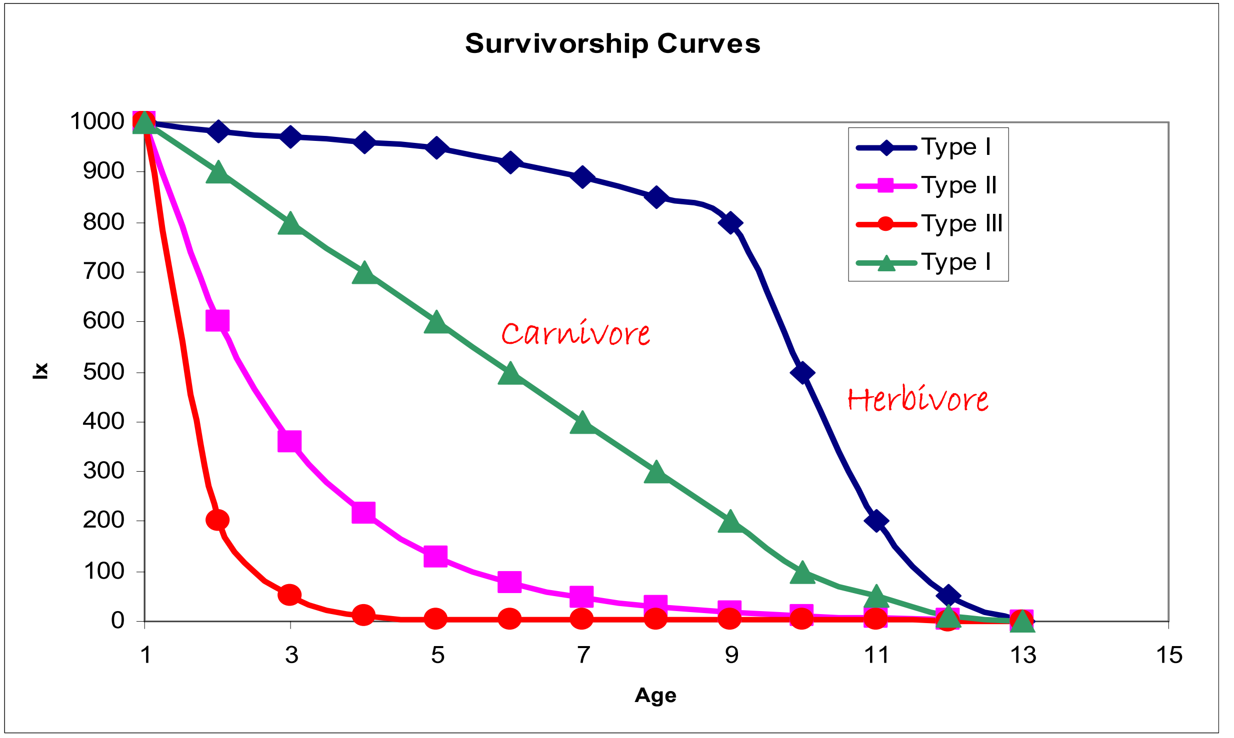
Song sparrow
Type(s) = ?



(c)

Atlantic mackerel
Type(s) = ?

Arithmetic



Be careful about
the scale of the Y-axis!!

Logarithmic

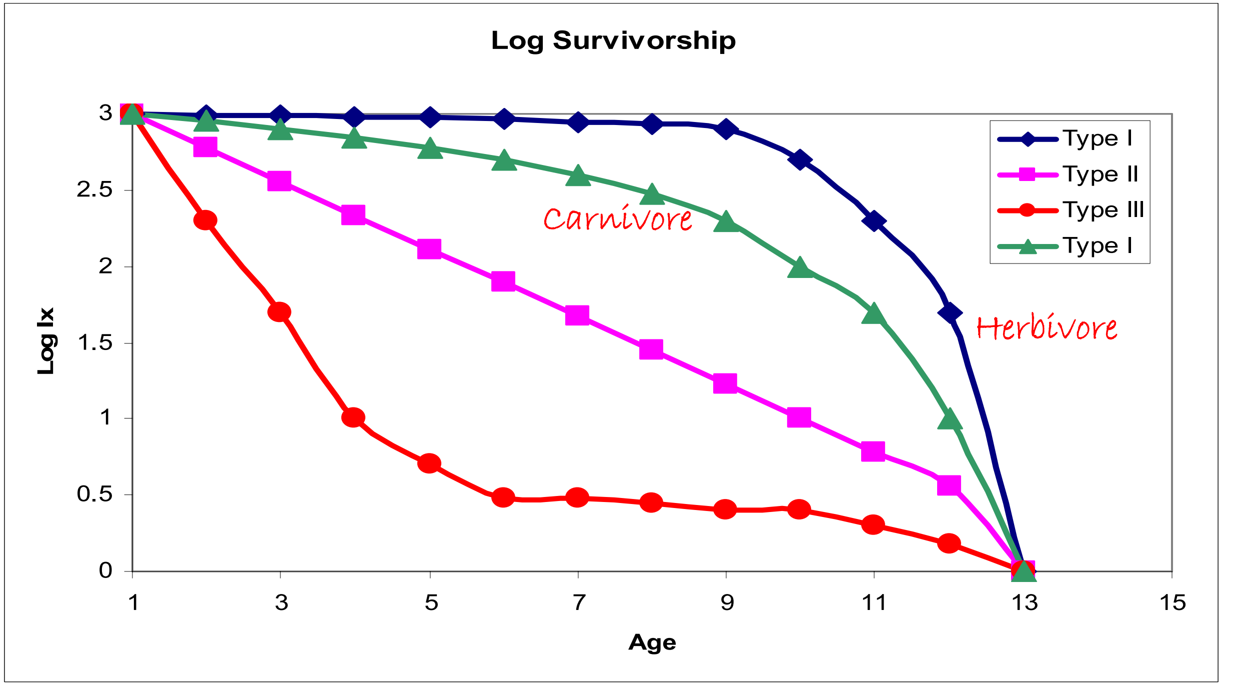
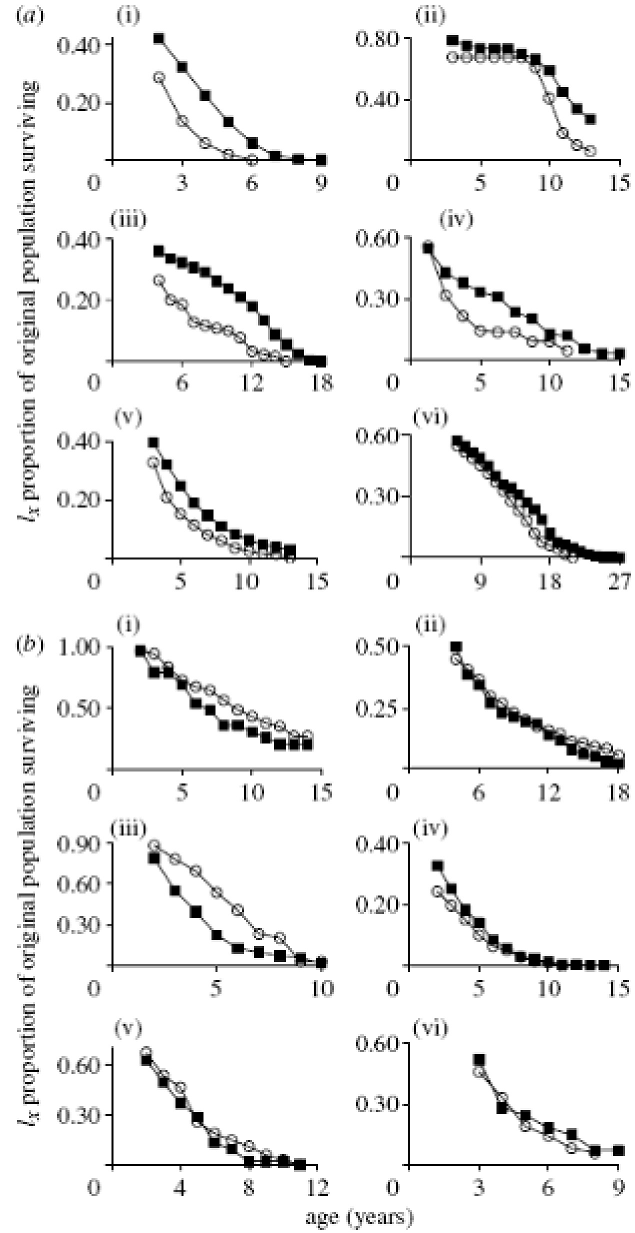


Figure 2. Survivorship curves (proportion of original population remaining) for females (filled squares) and males (open circles) in (*a*) six socially polygynous ((i) black-tailed prairie dog, *Cynomys ludovicianus*; (ii) red deer, *Cervus elaphus*; (iii) African lion, *Panthera leo*; (iv) Soay sheep, *Ovis aries*; (v) southern elephant seal, *Mirounga leonina*; and (vi) savannah baboon, *Papio cynocephalus*) and (*b*) six socially monogamous ((i) barnacle goose, *Branta leucopsis*; (ii) Bewicks's swan, *Cygnus columbianus*; (iii) Arabian babbler, *Turdoides squamiceps*; (iv) dwarf mongoose, *Helogale parvula*; (v) African wild dog, *Lycaon pictus* and (vi) American beaver, *Castor canadensis*), long-lived vertebrates from studies of marked or recognizable individuals. Survivorship values are shown from the beginning of adulthood (see §2 for details; data sources are given in the electronic supplementary material 1).



Polygynous

Monogamous

open circles = ♂♂
closed squares = ♀♀

Proc. Royal Soc. London (2007) 274:3097-3104.

Life expectancy: $e_x = T_x / l_x$

of years of remaining life expected for each individual entering age class *x*

Computational statistic: $L_x = (l_x + l_{x+1})/2$

Computational statistic: $T_x = \Sigma L_x$ (from *x* to oldest)

Age class	# Alive at start of year	Survival	Mortality	Mortality rate	Survival rate			Life expectancy
x	f_x	l_x	d_x	q_x	p_x	L_x	T_x	e_x
0	205	1.000	0.532	0.532	0.468	0.734	3.471	3.471
1	96	0.468	0.010	0.021	0.979	0.463	2.737	5.844
2	94	0.459	0.024	0.053	0.947	0.446	2.273	4.957
3	89	0.434	0.049	0.112	0.888	0.410	1.827	4.208
4	79	0.385	0.054	0.139	0.861	0.359	1.417	3.677
5	68	0.332	0.063	0.191	0.809	0.300	1.059	3.191
6	55	0.268	0.059	0.218	0.782	0.239	0.759	2.827
7	43	0.210	0.054	0.256	0.744	0.183	0.520	2.477
8	32	0.156	0.049	0.313	0.688	0.132	0.337	2.156
9	22	0.107	0.034	0.318	0.682	0.090	0.205	1.909
10	15	0.073	0.024	0.333	0.667	0.061	0.115	1.567
11	10	0.049	0.020	0.400	0.600	0.039	0.054	1.100
12	6	0.029	0.029	1.000	0.000	0.015	0.015	0.500
>12	0	0.000						

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11	10	0.049	0.020	0.400	0.600	0.039	0.054	1.100
12	6	0.029	0.029	1.000	0.000	0.015	0.015	0.500
>12	0	0.000						

Net reproductive rate (R_0)= $\Sigma l_x m_x$

Average # female offspring produced per lifetime per female born

(requires females-only life table)

♀♀ born per female (measured from population)

Age class	# ♀♀alive at start of year	Survival	Mortality	Mortality rate	Survival rate	Fecundity	
x	f_x	l_x	d_x	q_x	p_x	m_x	$l_x m_x$
0	110	1.000	0.545	0.545	0.455	0.000	0.000
1	50	0.455	0.018	0.040	0.960	0.010	0.005
2	48	0.436	0.018	0.042	0.958	0.500	0.218
3	46	0.418	0.018	0.043	0.957	0.500	0.209
4	44	0.400	0.082	0.205	0.795	0.500	0.200
5	35	0.318	0.009	0.029	0.971	0.400	0.127
6	34	0.309	0.036	0.118	0.882	0.400	0.124
7	30	0.273	0.091	0.333	0.667	0.350	0.095
8	20	0.182	0.045	0.250	0.750	0.300	0.055
9	15	0.136	0.045	0.333	0.667	0.100	0.014
10	10	0.091	0.045	0.500	0.500	0.100	0.009
11	5	0.045	0.009	0.200	0.800	0.000	0.000
12	4	0.036					
>12	0					R_0 =	1.055

Generation time (T) = $(\Sigma x l_x m_x)/R_0$

(Average age of female at birth of all of her offspring)

Age class	# ♀♀alive at start of year	Survival	Mortality	Mortality rate	Survival rate	Fecundity		
x	f_x	l_x	d_x	q_x	p_x	m_x	$l_x m_x$	$x l_x m_x$
0	110	1.000	0.545	0.545	0.455	0.000	0.000	0.000
1	50	0.455	0.018	0.040	0.960	0.010	0.005	0.005
2	48	0.436	0.018	0.042	0.958	0.500	0.218	0.436
3	46	0.418	0.018	0.043	0.957	0.500	0.209	0.627
4	44	0.400	0.082	0.205	0.795	0.500	0.200	0.800
5	35	0.318	0.009	0.029	0.971	0.400	0.127	0.636
6	34	0.309	0.036	0.118	0.882	0.400	0.124	0.742
7	30	0.273	0.091	0.333	0.667	0.350	0.095	0.668
8	20	0.182	0.045	0.250	0.750	0.300	0.055	0.436
9	15	0.136	0.045	0.333	0.667	0.100	0.014	0.123
10	10	0.091	0.045	0.500	0.500	0.100	0.009	0.091
11	5	0.045	0.009	0.200	0.800	0.000	0.000	0.000
12	4	0.036					T =	4.325
>12	0					R_0 =	1.055	

Generation time (T) = $(\Sigma x l_x m_x)/R_0$

(Average age of female at birth of all of her offspring)

Age class	# ♀♀alive at start of year	Survival	Mortality	Mortality rate	Survival rate	Fecundity		
x	f_x	l_x	d_x	q_x	p_x	m_x	$l_x m_x$	$x l_x m_x$
0	110	1.000	0.545	0.545	0.455	0.000	0.000	0.000
1	50	0.455	0.018	0.040	0.960	0.010	0.005	0.005
2	48	0.436	0.018	0.042	0.958	0.500	0.218	0.436
3	46	0.418	0.018	0.043	0.957	0.500	0.209	0.627
4	44	0.400	0.082	0.205	0.795	0.500	0.200	0.800
5	35	0.318	0.009	0.029	0.971	0.500	0.159	0.795
6	34	0.309	0.036	0.118	0.882	0.500	0.155	0.927
7	30	0.273	0.091	0.333	0.667	0.500	0.136	0.955
8	20	0.182	0.045	0.250	0.750	0.300	0.055	0.436
9	15	0.136	0.045	0.333	0.667	0.300	0.041	0.368
10	10	0.091	0.045	0.500	0.500	0.300	0.027	0.273
11	5	0.045	0.009	0.200	0.800	0.000	0.000	0.000
12	4	0.036					T =	4.668
>12	0					R_0 =	1.205	

Generation time (T) = $(\Sigma x l_x m_x)/R_0$

(Average age of female at birth of all of her offspring)

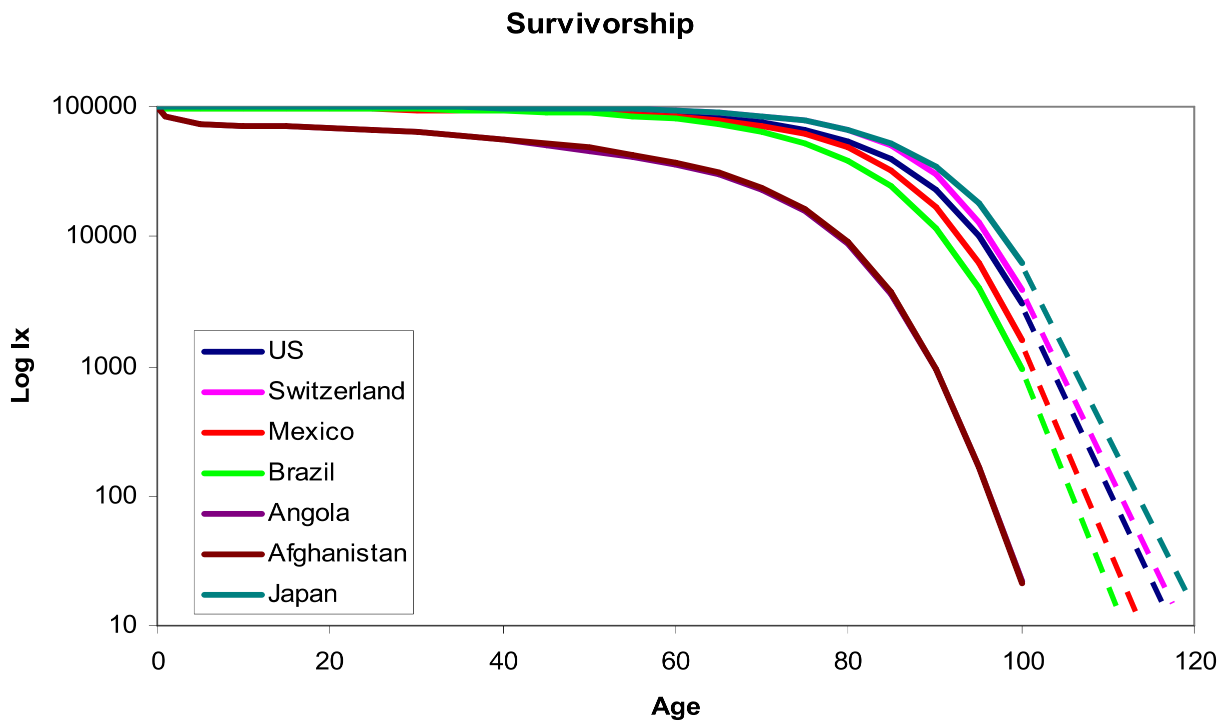
Age class	# ♀♀alive at start of year	Survival	Mortality	Mortality rate	Survival rate	Fecundity		
x	f_x	l_x	d_x	q_x	p_x	m_x	$l_x m_x$	$x l_x m_x$
0	110	1.000	0.545	0.545	0.455	0.000	0.000	0.000
1	50	0.455	0.018	0.040	0.960	0.010	0.005	0.005
2	48	0.436	0.018	0.042	0.958	0.500	0.218	0.436
3	46	0.418	0.018	0.043	0.957	0.500	0.209	0.627
4	44	0.400	0.082	0.205	0.795	0.500	0.200	0.800
5	35	0.318	0.009	0.029	0.971	0.500	0.159	0.795
6	34	0.309	0.036	0.118	0.882	0.500	0.155	0.927
7	30	0.273	0.091	0.333	0.667	0.500	0.136	0.955
8	20	0.182	0.045	0.250	0.750	0.300	0.055	0.436
9	15	0.136	0.045	0.333	0.667	0.300	0.041	0.368
10	10	0.091	0.045	0.500	0.500	0.300	0.027	0.273
11	5	0.045	0.009	0.200	0.800	0.000	0.000	0.000
12	4	0.036					T =	4.668
>12	0					R_0 =	1.205	

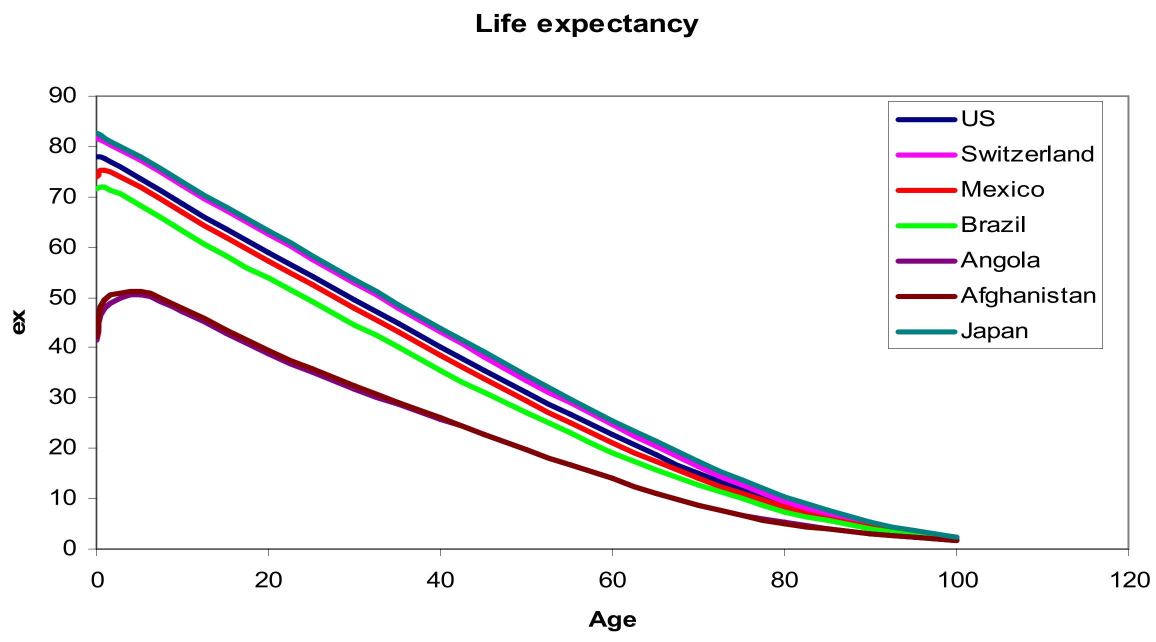
Generation time (T) = $(\Sigma x l_x m_x)/R_0$

(Average age of female at birth of all of her offspring)

Age class	# ♀♀alive at start of year	Survival	Mortality	Mortality rate	Survival rate	Fecundity		
x	f_x	l_x	d_x	q_x	p_x	m_x	$l_x m_x$	$x l_x m_x$
0	110	1.000	0.545	0.545	0.455	0.000	0.000	0.000
1	50	0.455	0.018	0.040	0.960	0.000	0.000	0.000
2	48	0.436	0.018	0.042	0.958	0.000	0.000	0.000
3	46	0.418	0.018	0.043	0.957	0.500	0.209	0.627
4	44	0.400	0.082	0.205	0.795	0.500	0.200	0.800
5	35	0.318	0.009	0.029	0.971	0.500	0.159	0.795
6	34	0.309	0.036	0.118	0.882	0.500	0.155	0.927
7	30	0.273	0.091	0.333	0.667	0.500	0.136	0.955
8	20	0.182	0.045	0.250	0.750	0.300	0.055	0.436
9	15	0.136	0.045	0.333	0.667	0.300	0.041	0.368
10	10	0.091	0.045	0.500	0.500	0.300	0.027	0.273
11	5	0.045	0.009	0.200	0.800	0.000	0.000	0.000
12	4	0.036					T =	5.278
>12	0					R_0 =	0.982	

Human survivorship in 7 countries based on 2006 data





Source: World Health Organization (www.who.int)

Static life table

also called ‘time-specific’ or vertical’

- Created from collection of data from animals at time of death
- Do not follow a single cohort—rather take a snapshot of all cohorts living at the time
- Example: moose on Isle Royale—collect skulls of all mortalities and determine age
- Should result in the same life table statistics if . . .

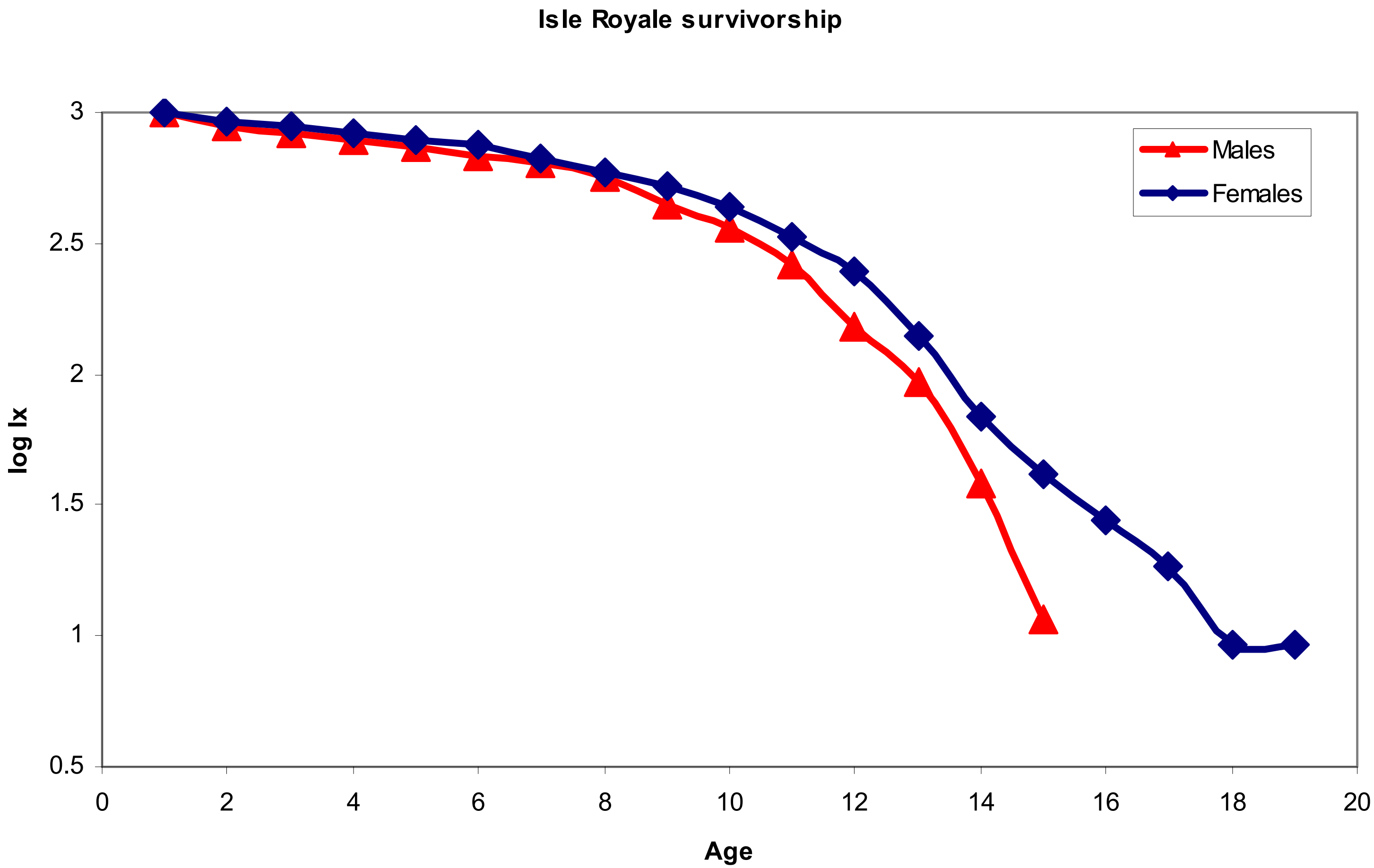
Assumptions of life tables

- Stable age distribution!!!
  - Consistent proportions in each age group over time
  - Recruitment into each age class balanced by mortality within that age class
- Populations with a stable age distribution can increase in size as long as l_x and m_x schedules don't change
- Population with a stable age distribution that is not growing is a special case—stationary age distribution

Isle Royale Moose
static life table

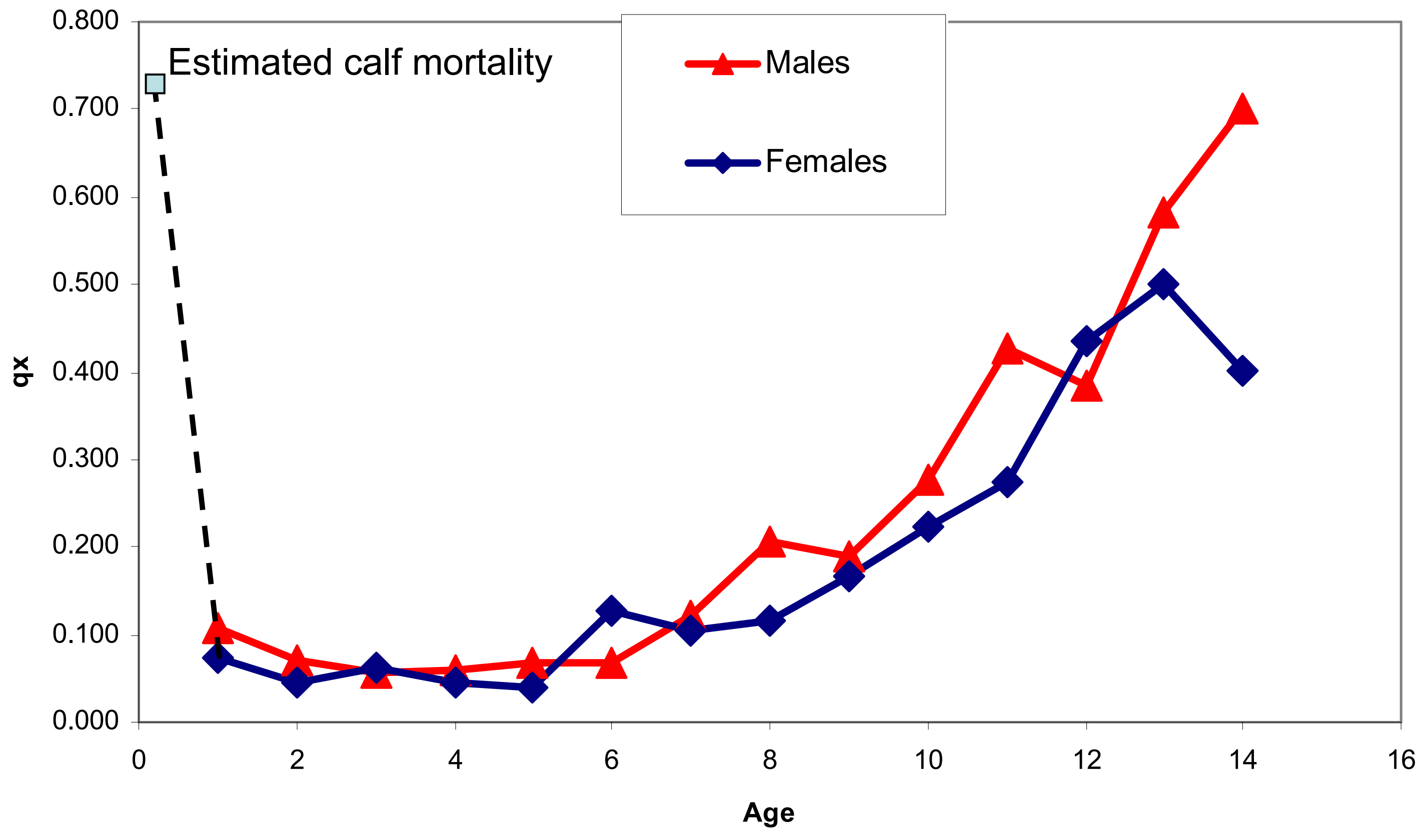
	Males						Females						All				
Age	# remains	dx	lx	qx	Lx		# remains	dx	lx	qx	Lx		# remains	dx	lx	qx	Lx
1	28	108	1000	0.108	946		16	74	1000	0.074	963		47	88	1000	0.088	956
2	16	62	892	0.069	861		9	42	926	0.045	905		27	51	912	0.056	886
3	12	46	830	0.056	807		12	56	884	0.063	856		29	55	861	0.063	834
4	12	46	784	0.059	761		8	37	829	0.045	810		22	41	806	0.051	786
5	13	50	737	0.068	712		7	32	792	0.041	775		26	49	765	0.064	741
6	12	46	687	0.067	664		21	97	759	0.128	711		37	70	716	0.097	681
7	20	77	641	0.120	602		15	69	662	0.105	627		45	85	647	0.131	604
8	30	116	564	0.205	506		15	69	593	0.117	558		50	94	562	0.167	515
9	22	85	448	0.190	405		19	88	523	0.168	479		46	86	468	0.185	425
10	26	100	363	0.277	313		21	97	435	0.223	387		54	102	382	0.266	331
11	29	112	263	0.426	207		20	93	338	0.274	292		52	98	280	0.349	231
12	15	58	151	0.385	122		23	106	245	0.434	192		39	73	182	0.402	146
13	14	54	93	0.583	66		15	69	139	0.500	104		30	56	109	0.517	81
14	7	27	39	0.700	25		6	28	69	0.400	56		15	28	53	0.536	39
15	3	12	12	1.000	6		3	14	42	0.333	35		7	13	24	0.538	18
16	0	0	0	0.000	0		2	9	28	0.333	23		2	4	11	0.333	9
17	0	0	0	0.000	0		2	9	19	0.500	14		2	4	8	0.500	6
18	0	0	0	0.000	0		0	0	9	0.000	9		0	0	4	0.000	4
19	0	0	0	0.000	0		2	9	9	1.000	5		2	4	4	1.000	2
Total	259						216						532				

Source: Peterson, RO. 1977. Wolf Ecology and Prey Relationships on Isle Royale. USDI, NPS, Scientific Monograph Series 11. http:/www.nps.gov/history/online_books/science/11/index.htm



Source: Peterson, RO. 1977. Wolf Ecology and Prey Relationships on Isle Royale. USDI, NPS, Scientific Monograph Series 11. http:/www.nps.gov/history/online_books/science/11/index.htm

Age-specific mortality rate



Source: Peterson, RO. 1977. Wolf Ecology and Prey Relationships on Isle Royale. USDI, NPS, Scientific Monograph Series 11. http:/www.nps.gov/history/online_books/science/11/index.htm

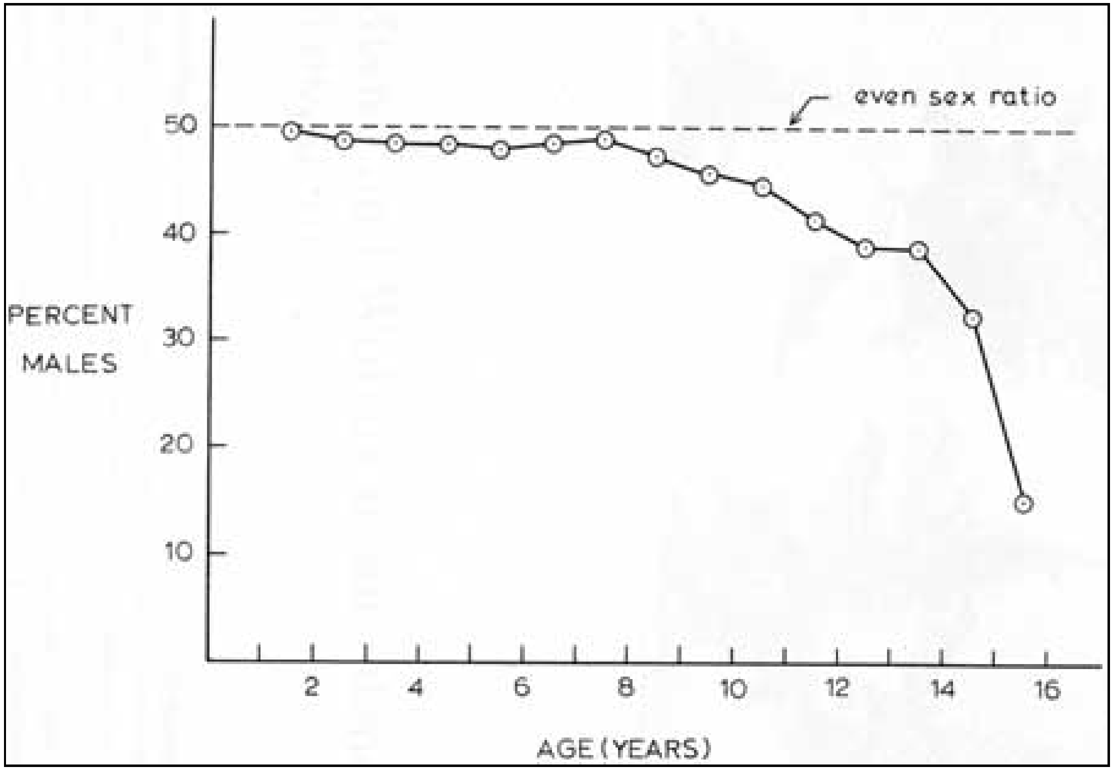


Fig. 108. Calculated proportion of males alive in each age interval, based on a hypothetical age distribution for adult moose on Isle Royale.

Source: Peterson, RO. 1977. Wolf Ecology and Prey Relationships on Isle Royale. USDI, NPS, Scientific Monograph Series 11. http:/www.nps.gov/history/online_books/science/11/index.htm

Problems with life-table analysis
(Caughley)

- Populations commonly fail to have a stable age distribution
- Sample size considerations
  - in a static life table you can have zeros in age classes because of sampling error (or the age distribution is not stable)
  - l_x schedule cannot handle zeros in any but the last age class
- The zero-age class is usually underrepresented
- Confusion concerning how to treat data
  - d_x or l_x series?
    - **d_x** ages at death of a large number of animals born at the same time
    - **l_x** the numbers of animals of a single cohort still alive at various ages
    - **d_x** ages at death of animals from different chorts
    - **d_x** ages of carcasses
    - **l_x** individuals killed by a catastrophe (flood, avalanche)
    - **l_x** individuals collected by non-selective killing (trapping, shooting)