



# Lecture 8

Survival estimation

WILD3810 (Spring 2020)

# Readings

Powell & Gale 103-122; 123-138

# Life tables

If detection probability is  $< 1$

- $N_x$  will be biased low
- All other life table statistics will be biased as well
  - Survival biased low, mortality biased high



TABLE 1  
LIFE TABLE FOR *Phlox drummondii* AT NIXON, TEXAS

Age Interval (days) $x - x'$	Length of Interval (days) $D_x$	No. Surviving to Day $x$ $N_x$	Survivorship $l_x$	No. Dying During Interval $d_x$	Average Mortality Rate Per Day $q_x$	Mean Expectation of Life (days) $E_x$
0- 63 .....	63	996	1.000	328	.0052	122.87
63-124 .....	61	668	.6707	373	.0092	104.73
124-184 .....	60	295	.2962	105	.0059	137.59
184-215 .....	31	190	.1908	14	.0024	137.05
215-231 .....	16	176	.1767	2	.0007	115.72
231-247 .....	16	174	.1747	1	.0004	100.96
247-264 .....	17	173	.1737	1	.0003	85.49
264-271 .....	7	172	.1727	2	.0017	68.94
271-278 .....	7	170	.1707	3	.0025	62.71
278-285 .....	7	167	.1677	2	.0017	56.78
285-292 .....	7	165	.1657	6	.0052	50.42
292-299 .....	7	159	.1596	1	.0009	45.19
299-306 .....	7	158	.1586	4	.0036	38.46
306-313 .....	7	154	.1546	3	.0028	32.36
313-320 .....	7	151	.1516	4	.0038	25.94
320-327 .....	7	147	.1476	11	.0107	19.55
327-334 .....	7	136	.1365	31	.0325	13.85
334-341 .....	7	105	.1054	31	.0422	9.90
341-348 .....	7	74	.0743	52	.1004	5.58
348-355 .....	7	22	.0221	22	.1428	3.50
355-362 .....	7	0	.0000			

# Survival estimation

# Survival estimation

Methods used to estimate plant and animal survival generally fall into three categories:

- 1) Known fate
- 2) Capture-mark-recapture
- 3) Recovery models

# Known fate

# Known fate

Location and fate (alive or dead) of every marked individual is known at each sampling occasion

- $P_{det} = 1$

What types of data can be used for known fate analyses?



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# Known fate

## Data

Individual	Capture history	Probability
Indv 1	111	$s_1 \times s_2$
Indv 2	110	
Indv 3	100	

## Individual 1

- Captured on occasion 1
- Resighted **alive** on occasion 2
- Resighted **alive** on occasion 3

# Known fate

## Data

Individual	Capture history	Probability
Indv 1	111	$s_1 \times s_2$
Indv 2	110	$s_1 \times (1 - s_2)$
Indv 3	100	

## Individual 2

- Captured on occasion 1
- Resighted **alive** on occasion 2
- Resighted **dead** on occasion 3

# Known fate

## Data

Individual	Capture history	Probability
Indv 1	111	$s_1 \times s_2$
Indv 2	110	$s_1 \times (1 - s_2)$
Indv 3	100	$1 - s_1$

## Individual 3

- Captured on occasion 1
- Resighted **dead** on occasion 2
- Known **dead** on occasion 3

# Known fate

Kaplan-Meier model

$$s_t = \frac{n_t - d_t}{n_t}$$

$$\text{var}(s_t) = \frac{s_t^2(1 - s_t)}{n_t}$$

- $n_t$ : Number of individuals at risk of dying during interval  $t$
- $d_t$ : Number of individuals that died during interval  $t$

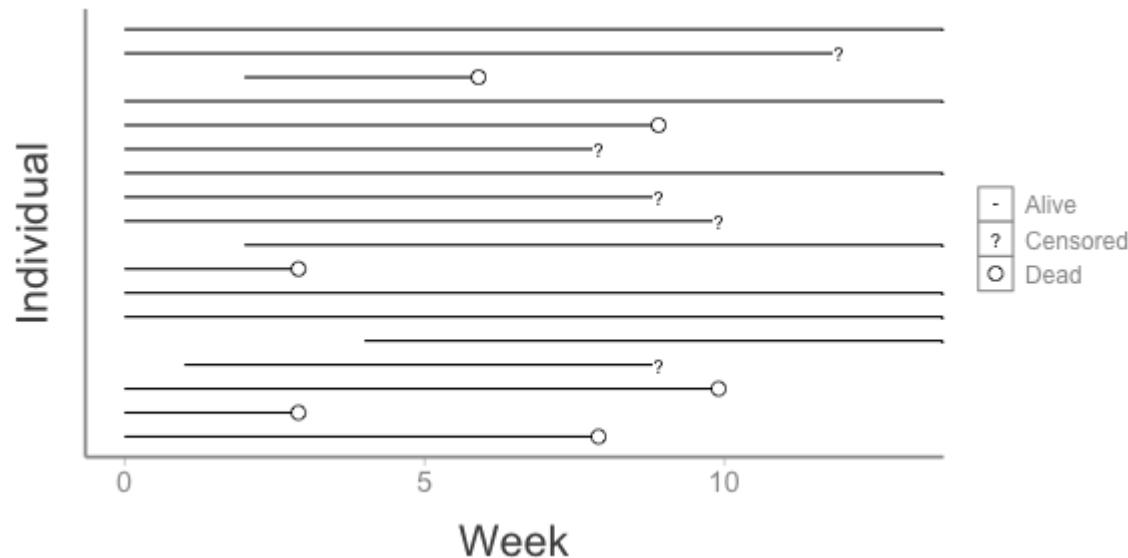
$$S_T = \prod_{t=1}^T s_t$$

Who is at risk of dying?

# Known fate

Who is at risk of dying?

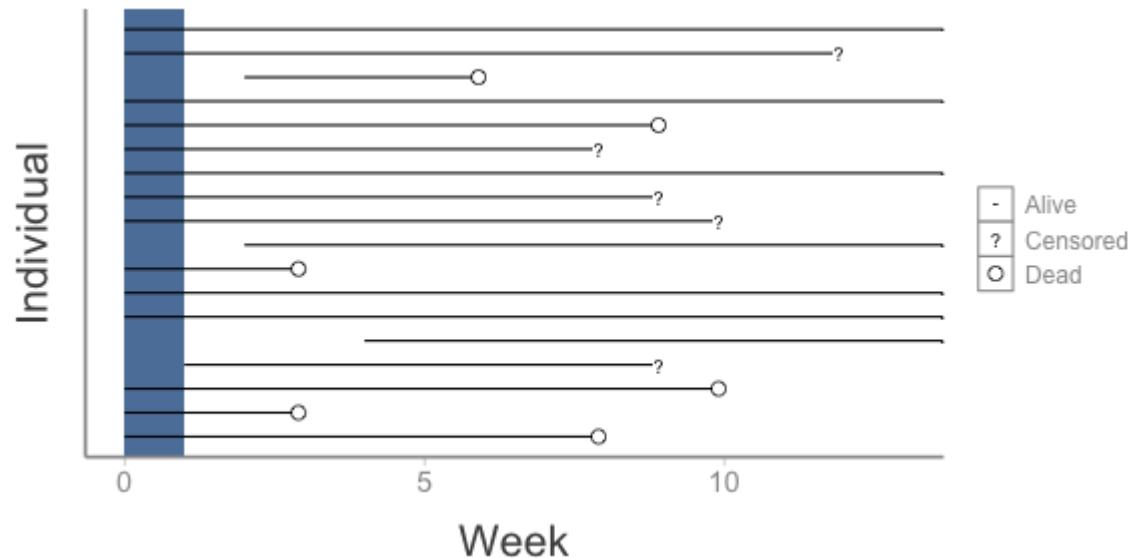
- Individuals who are **known** alive at the beginning of the interval
  - Does not include individuals not yet marked (*staggered entry*)
  - Does not include individuals whose fates are unknown (*censoring*)



# Known fate

Estimating survival

Who is at risk of dying?

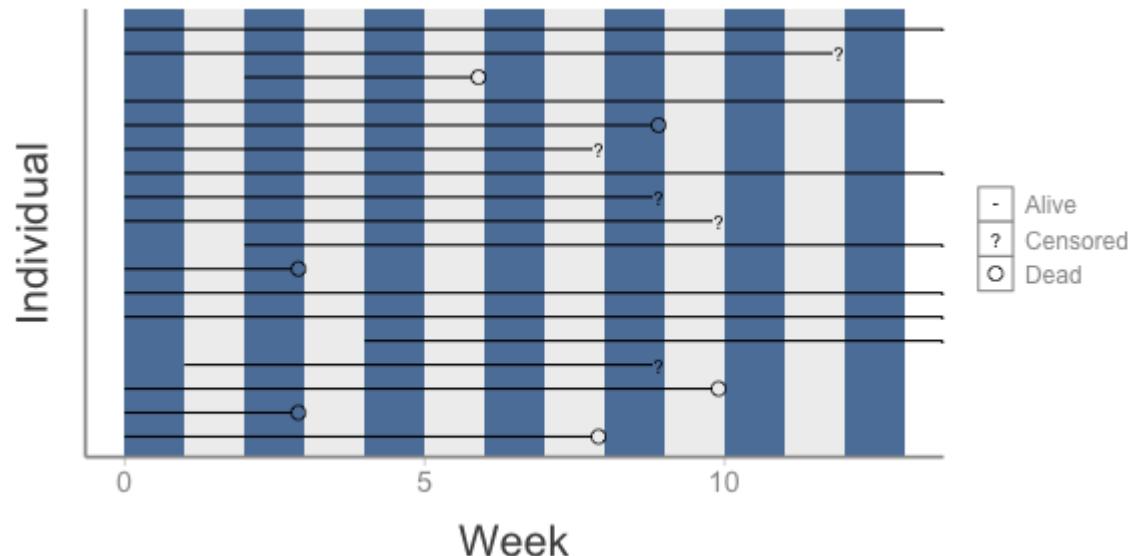


- $n_1 = 14, d_1 = 0$
- $s_1 = 1.00$

# Known fate

Estimating survival

Who is at risk of dying?

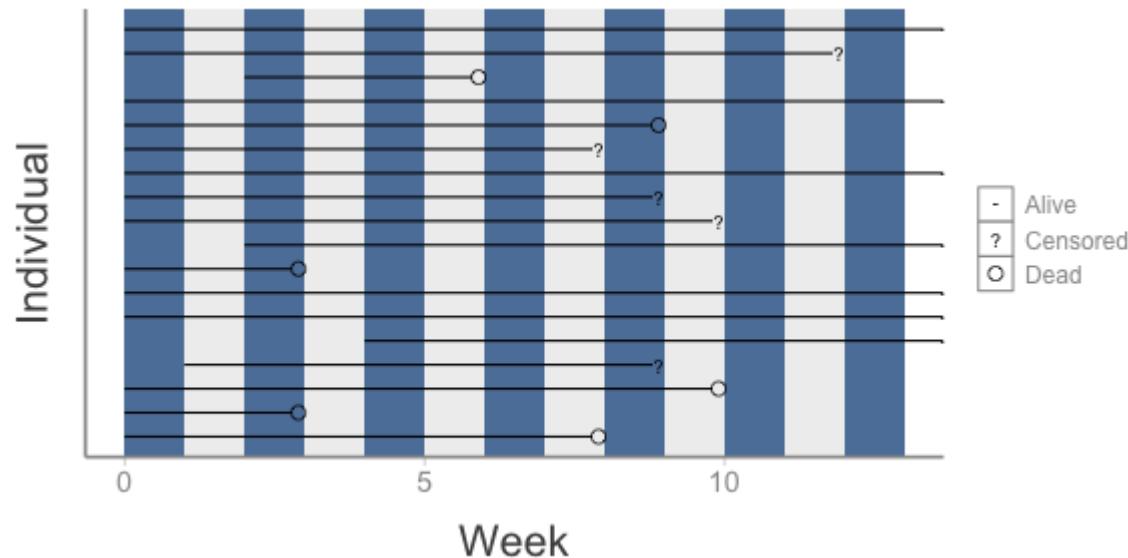


- $n_3 = 17, d_3 = 2$
- $s_3 = 0.88$

# Known fate

Estimating survival

Who is at risk of dying?



- $n_9 = 13 - 2 = 11, d_9 = 1$
- $s_9 = 0.91$

# Known fate

Week (t)	# at risk	# deaths	# censored	# added	s(t)	S(t)
1	14	0	0	1	1.0000	1.0000
2	15	0	0	2	1.0000	1.0000
3	17	2	0	0	0.8824	0.8824
4	15	0	0	1	1.0000	0.8824
5	16	0	0	0	1.0000	0.8824
6	16	1	0	0	0.9375	0.8272
7	15	0	0	0	1.0000	0.8272
8	15	1	1	0	0.9286	0.7681
9	13	1	2	0	0.9091	0.6983
10	10	1	1	0	0.8889	0.6207
11	8	0	0	0	1.0000	0.6207
12	8	0	1	0	1.0000	0.6207
13	7	0	0	0	1.0000	0.6207

# Assumptions of Kaplan-Meier

- 1) Animal at risk if **known** alive at the start of the interval
- 2) Survival is constant within each interval
- 3) Newly tagged individuals have the same survival probability as previously tagged individuals
- 4) Tagged animals are a random sample of the population
- 5) Animals are independent
- 6) Working tags are always located
- 7) Censoring is a random event/independent of mortality
- 8) Tagging method does not impact survival

# Capture-recapture

# Capture-recapture

When using known-fate methods,  $P_{det} = 1$

When using mark-recapture,  $P_{det} < 1$

- if an individual is not detected, its fate (alive or dead) cannot be known with certainty
- in closed population models (Lincoln-Peterson), we assumed no deaths occurred between sampling occasions

**Open population** models relax this assumption

During each sampling occasion

- individuals are captured
- marked or identified
- released alive



# Capture-recapture

On the occasion after release, 4 possible scenarios:

- 1) Individual survives and is re-captured (capture history = **11**)
- 2) Individual survives but is not recaptured (capture history = **10**)
- 3) Individual dies and is **not available** for recapture (capture history = **10**)
- 4) Individual survives but leaves the study area and is **not available** for recapture (capture history = **10**)

Not possible to distinguish between scenarios 3 & 4 without additional data

- $\phi_t = s_t \times (1 - \epsilon_t)$
- $\phi_t$ : **Apparent survival** (prob. individual survives *and* remains within study area)

# Capture-recapture

How do we distinguish between scenarios 2 & 3/4?

## Cormack-Jolly-Seber model

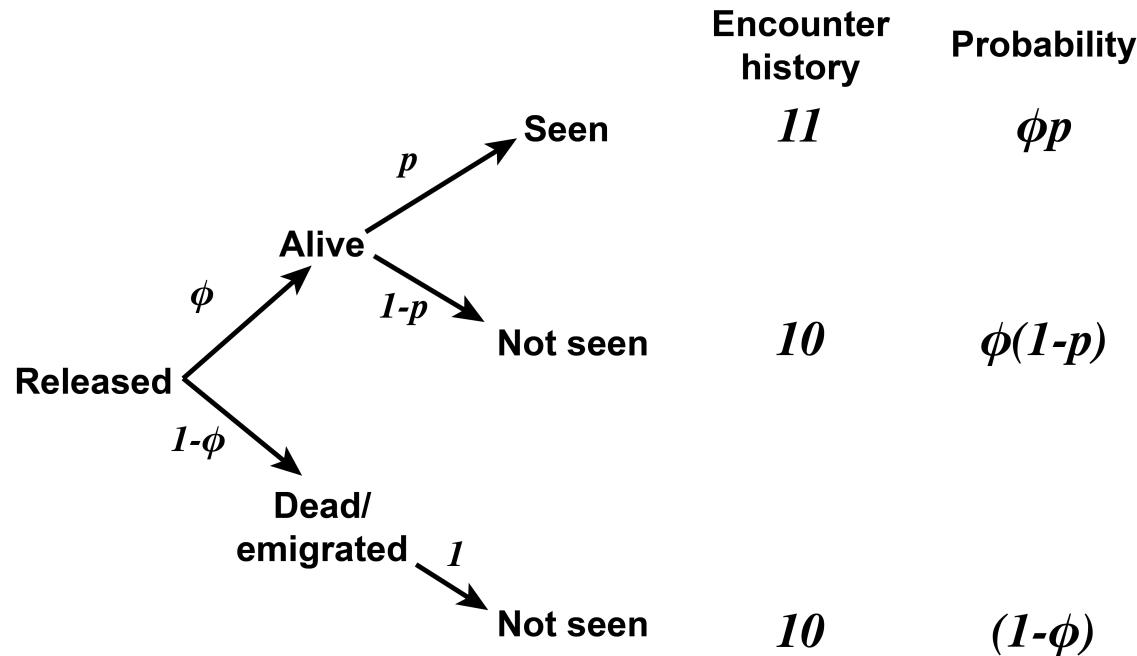
Parameters

- $\phi$ : Apparent survival probability
- $p$ : Recapture probability

# Capture-recapture

How do we distinguish between scenarios 2 & 3/4?

## Cormack-Jolly-Seber model



# Capture-recapture

## Cormack-Jolly-Seber model

Individual	Capture history	Probability
Indv 1	111	$\phi_1 p_2 \phi_2 p_3$
Indv 2	101	
Indv 3	110	
Indv 4	100	

### Individual 1

- survived interval 1 ( $\phi_1$ ), recaptured on occasion 2 ( $p_2$ ), survived occasion 2 ( $\phi_2$ ), recapture on occasion 3 ( $p_3$ )

# Capture-recapture

## Cormack-Jolly-Seber model

Individual	Capture history	Probability
Indv 1	111	$\phi_1 p_2 \phi_2 p_3$
Indv 2	101	$\phi_1 (1 - p_2) \phi_2 p_3$
Indv 3	110	
Indv 4	100	

### Individual 2

- survived interval 1 ( $\phi_1$ ), not recaptured on occasion 2 ( $1 - p_2$ ), survived occasion 2 ( $\phi_2$ ), recapture on occasion 3 ( $p_3$ )

# Capture-recapture

## Cormack-Jolly-Seber model

Individual	Capture history	Probability
Indv 1	111	$\phi_1 p_2 \phi_2 p_3$
Indv 2	101	$\phi_1 (1 - p_2) \phi_2 p_3$
Indv 3	110	$\phi_1 p_2 \phi_2 (1 - p_3) + (1 - \phi_2)$
Indv 4	100	

### Individual 3

- survived interval 1 ( $\phi_1$ ), recaptured on occasion 2 ( $p_2$ )

# Capture-recapture

## Cormack-Jolly-Seber model

Individual	Capture history	Probability
Indv 1	111	$\phi_1 p_2 \phi_2 p_3$
Indv 2	101	$\phi_1 (1 - p_2) \phi_2 p_3$
Indv 3	110	$\phi_1 p_2 \phi_2 (1 - p_3) + (1 - \phi_2)$
Indv 4	100	

### Individual 3

- survived interval 1 ( $\phi_1$ ), recaptured on occasion 2 ( $p_2$ )
  - survived occasion 2 ( $\phi_2$ ), not recaptured on occasion 3 ( $1 - p_3$ ); **or**
  - died during occasion 2 ( $1 - \phi_2$ )

# Capture-recapture

## Cormack-Jolly-Seber model

Individual	Capture history	Probability
Indv 1	111	$\phi_1 p_2 \phi_2 p_3$
Indv 2	101	$\phi_1 (1 - p_2) \phi_2 p_3$
Indv 3	110	$\phi_1 p_2 \phi_2 (1 - p_3) + (1 - \phi_2)$
Indv 4	100	$(1 - \phi_1) + \phi_1 (1 - p_2) (1 - \phi_2 p_3)$

### Individual 4

- died during interval 1 ( $1 - \phi_1$ ); or
- survived occasion 1 ( $\phi_1$ ), not recaptured on occasion 2 ( $1 - p_2$ ), died during occasion 2 ( $1 - \phi_2$ ); or
- survived occasion 1 ( $\phi_1$ ), not recaptured on occasion 2 ( $1 - p_2$ ), survived occasion 2 ( $\phi_2$ ), not recaptured on occasion 3 ( $1 - p_3$ )

# Capture-recapture

## Advantages

- inexpensive (relative to telemetry)
- possible to mark many individuals
  - often more precise than known-fate
- can use natural marks
- possible to measure effects of age, stage, environment, habitat, management actions, etc.

## Assumptions

- every individual has the same recapture probability  $p^*$
- every individual has the same apparent survival probability  $\phi^*$
- tags are not lost
- all emigration is permanent

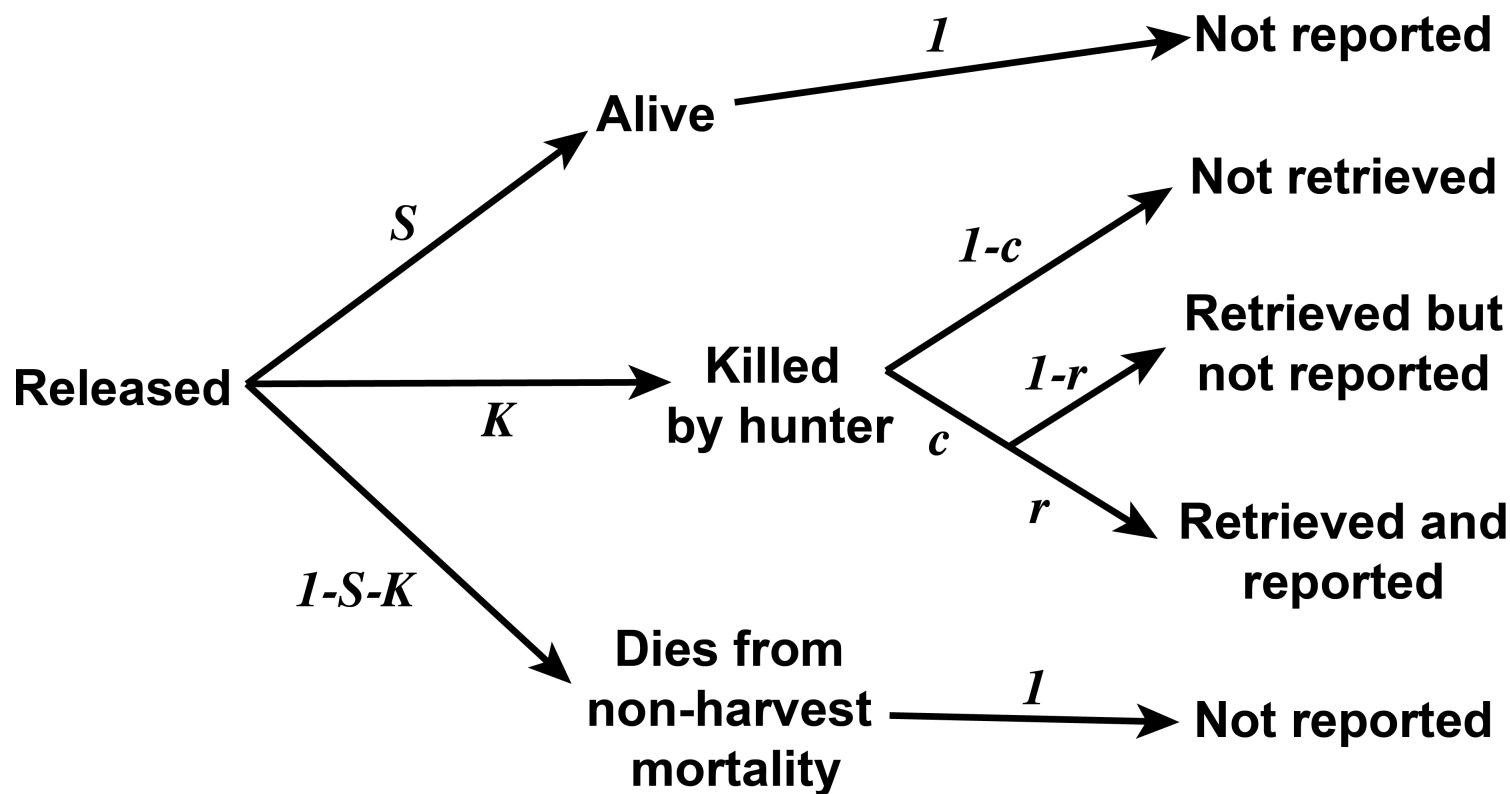
# Recovery models

# Recovery models

In some cases, marked individuals may be recovered dead



# Recovery models



# Life tables

# Life tables

- Ages-specific estimates of  $S$  or  $\phi$  are equivalent to  $P_x$

$x$	$P_x$
0	0.7
1	0.86
2	0.67
3	0
4	

# Life tables

- With unbiased estimates of  $P_x$ , can obtain unbiased estimates of  $l_x$  and  $q_x$
- $l_0 = 1, l_{x+1} = l_x P_x$
- $q_x = 1 - P_x$

$x$		$l_x$	$P_x$	$q_x$	
0		1.0	0.7	0.3	
1		0.7	0.86	0.14	
2		0.6	0.67	0.33	
3		0.4	0	1	
4		0.0			