Lecture 9

Survival estimation

WILD3810 (Spring 2019)

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	1.0000	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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What types of data can be used for known fate analyses?

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

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

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

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

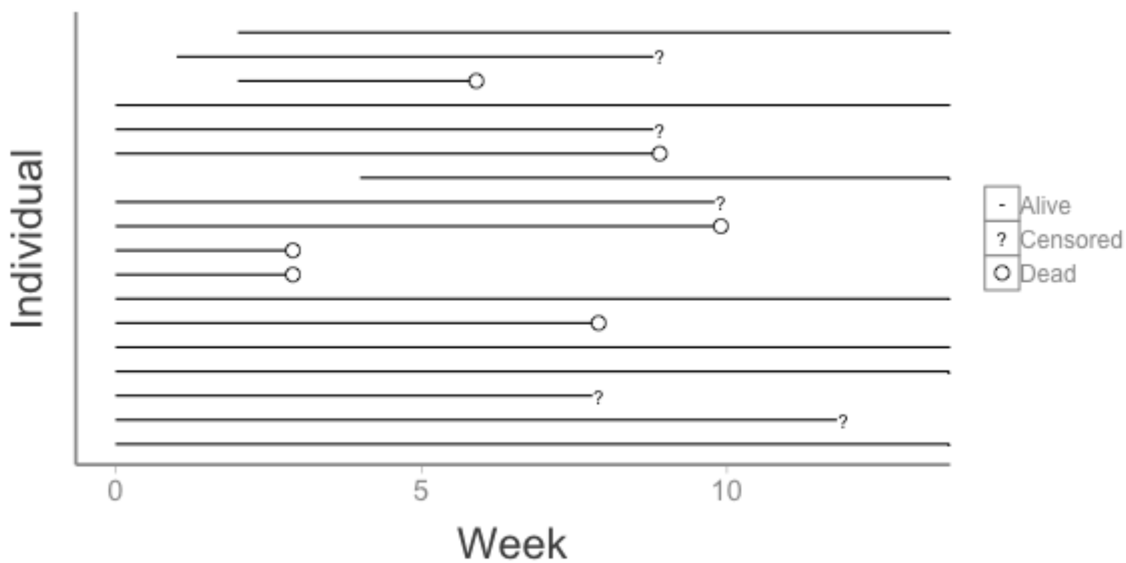
$$S_T = \prod_{t=1}^{T} s_t$$

Who is at risk of dying?

Known fate

Who is at risk of dying?

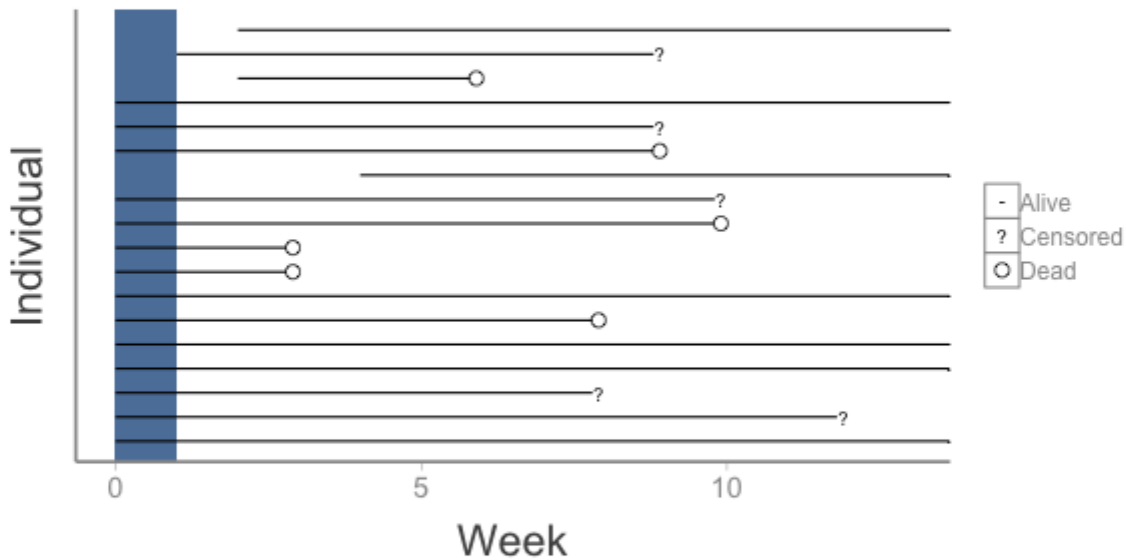
- Individuals who are **known** alive at the beginning of the interval
  - Does not include individuals not yet marked (*staggered entry*)
  - Does not include individuals who's fates are unknown (*censoring*)



Known fate

Estimating survival

Who is at risk of dying?

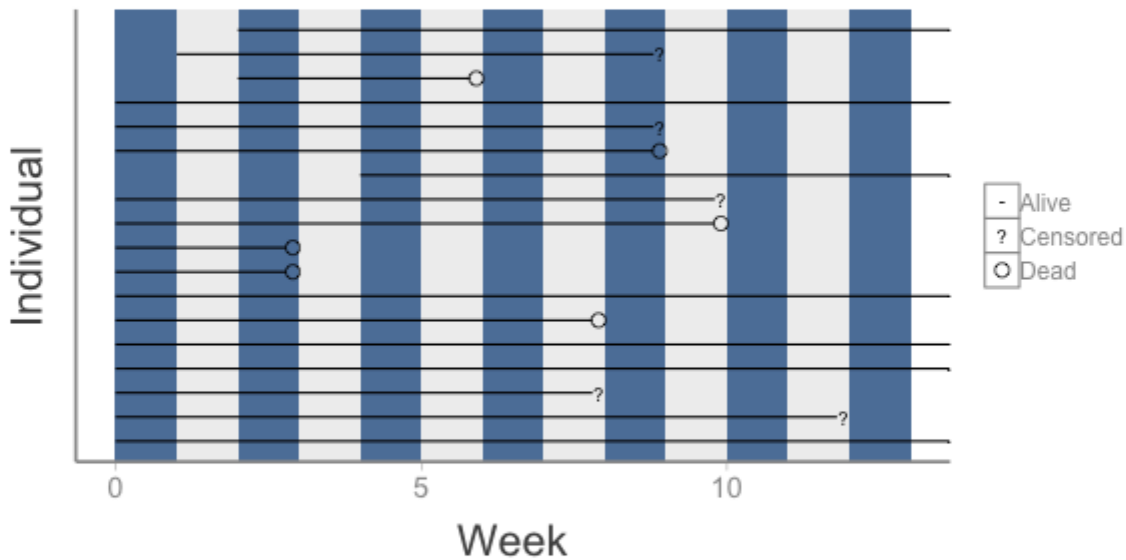


- $n_1 = 14, d_1 = 0$
- $s_1 = 1.00$

Known fate

Estimating survival

Who is at risk of dying?

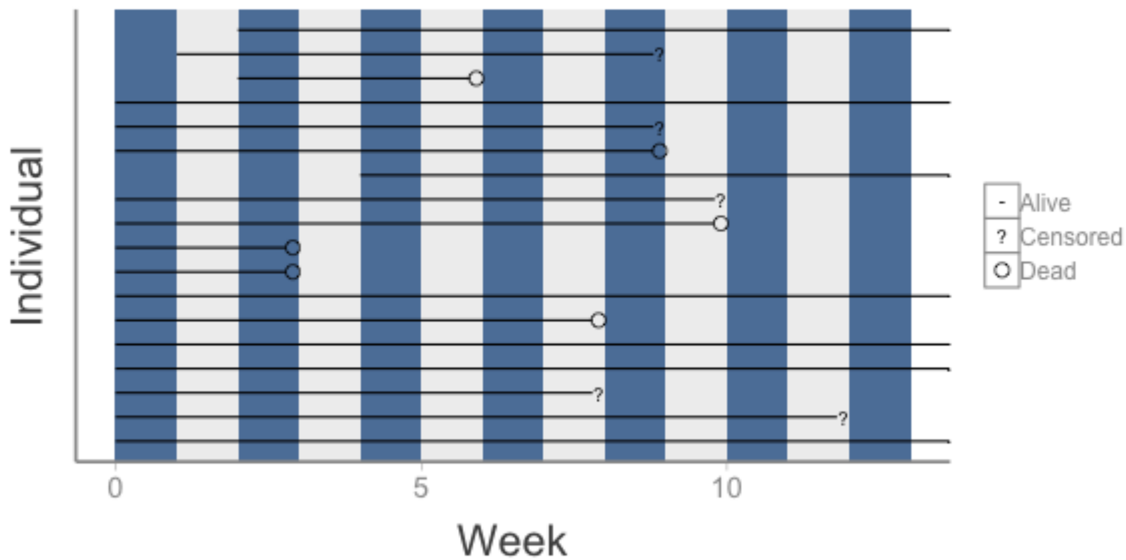


- $n_3 = 17, d_3 = 2$
- $s_3 = 0.88$

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, it's 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 occassion 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`)

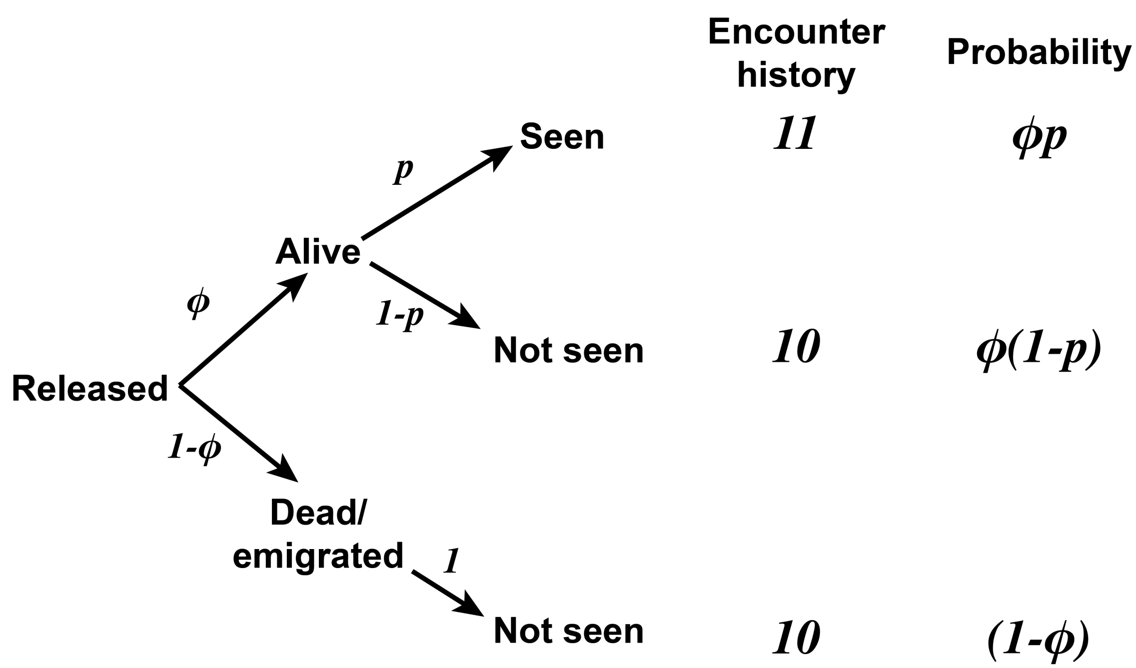
Not possible to distuingish between scenarios 3 & 4 without additional data

- $\phi_t = s_t \times (1 - \epsilon_t)$
- ϕ_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



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 (ϕ_1), recaptured on occasion 2 (p_2), survived occasion 2 (ϕ_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 (ϕ_1), not recaptured on occasion 2 $(1 - p_2)$, survived occasion 2 (ϕ_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 (ϕ_1), recaptured on occasion 2 (p_2)
    - survived occasion 2 (ϕ_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 (ϕ_1), not recaptured on occasion 2 $(1-p_2)$, died during occasion 2 $(1-\phi_2)$; **or**
- survived occasion 1 (ϕ_1), not recaptured on occasion 2 $(1-p_2)$, survived occasion 2 (ϕ_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

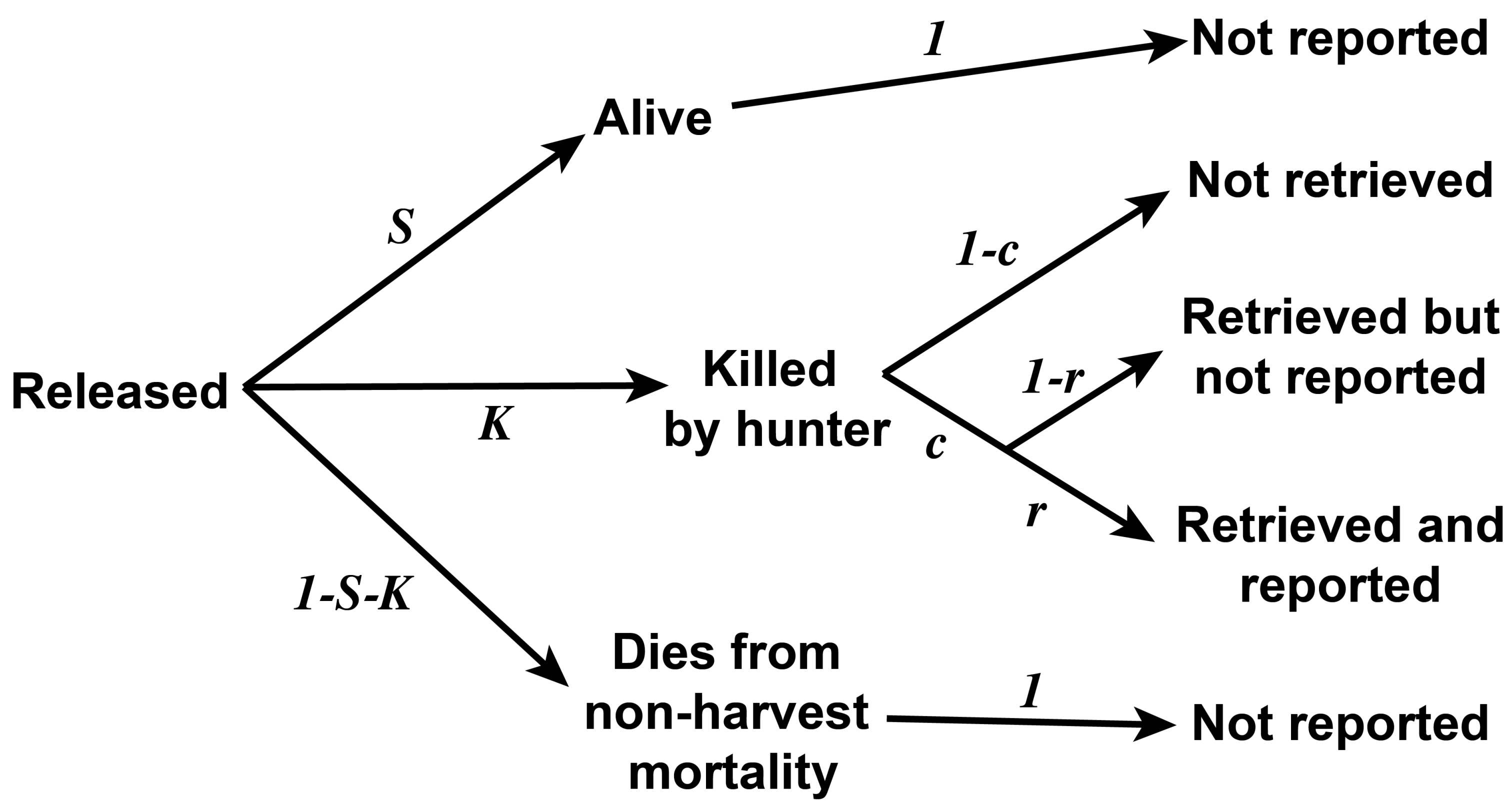
- every individual has the same recapture probability p *
- every individual has the same apparent survival probability ϕ *
- tags are not lost
- all emigration is permanent

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 ϕ 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
- $l_0 = 1, l_{x+1} = 1_x P_x$
- $q_x = 1 - P_x$

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			