Life Tables:
Like projection matrices, another way to account for age/stage specific survivorship patterns in a population. When paired with fecundity data estimation of growth rates, stable stage distribution, and lifetime reproduction possible.

174 PART THREE The Problem of Abundance: Populations

TABLE 11.2 Stage-based life table and fecundity table for the loggerhead sea turtle.[a]

Stage number	Class	Size (carapace length) (cm)	Approximate age (yr)	Annual survivorship	Fecundity (eggs/yr)
1	Eggs, hatchlings	<10	<1	0.6747	0
2	Small juveniles	10.1–58.0	1–7	0.7857	0
3	Large juveniles	58.1–80.0	8–15	0.6758	0
4	Subadults	80.1–87.0	16–21	0.7425	0
5	Novice breeders	>87.0	22	0.8091	127
6	First-year remigrants	>87.0	23	0.8091	4
7	Mature breeders	>87.0	24–54	0.8091	80

[a]These values assume a population declining at 3% per year.
Source: Data from Crouse et al. (1987).

TABLE 11.3 Stage-class population matrix for the loggerhead sea turtles.[a]

0	0	0	0	127	4	80
0.6747	0.7370	0	0	0	0	0
0	0.0486	0.6610	0	0	0	0
0	0	0.0147	0.6907	0	0	0
0	0	0	0.0518	0	0	0
0	0	0	0	0.8091	0	0
0	0	0	0	0	0.8091	0.8089

[a]Estimates based on the life table presented in Table 11.2, with the survival estimates broken down into survival within the same stage and survival and movement into the next stage.
Source: Data from Crouse et al. (1987).

Table 16. Life table based on age distribution of female white-tailed deer found dead (data from Eberhardt 1969:488).

Age (years)$_x$	$\hat{n}_x$	d_x	$\hat{q}_x$
0–1	198	106	0.535
1–2	92	18	0.196
2–3	74	14	0.189
3–4	60	18	0.300
4–5	42	9	0.214
5–6	33	5	0.152
6–7	28	6	0.214
7–8	22	8	0.364
8–9	14	4	0.286
9–10	10	2	0.200
>10	8	8	1.000

Estimated number of age class alive

Number of age class found dead

Finite rate of mortality during interval

Table 14. Stable age distribution calculated from survival and reproduction data for white-tailed deer in central Michigan, USA (from Eberhardt 1969).

Age (x)	Survival to age (l_x)	Fraction in age (C_x)
0	1.0000	0.3214
1	0.5800	0.1913
2	0.4060	0.1375
3	0.2842	0.0988
4	0.1989	0.0709
5	0.1392	0.0510
6	0.0974	0.0366
7	0.0682	0.0263
8	0.0478	0.0189
9	0.0334	0.0136
>9	$0.58(0.70)^{x-1}$	0.0337

Proportion of individuals surviving at start of interval

Proportion of individuals in each stage/age at ssd/ssa distribution (must have fecundity data to estimate lambda)

Types of Life Tables

Cohort or **age-specific** or **dynamic** life tables: data are collected by following a cohort throughout its life. This is rarely possible with natural populations of animals. Note: a cohort is a group of individuals all born during the same time interval.

Static or **time-specific** life tables: age-distribution data are collected from a cross-section of the population at one particular time or during a short *segment* of time, such as through mortality data. Resulting age-specific data are treated *as if* a cohort was followed through time (i.e., the number of animals alive in age class *x* must be less than alive in age class *x*-1). Because of variation caused by small samples, data-smoothing techniques may be required (see Caughley 1977).

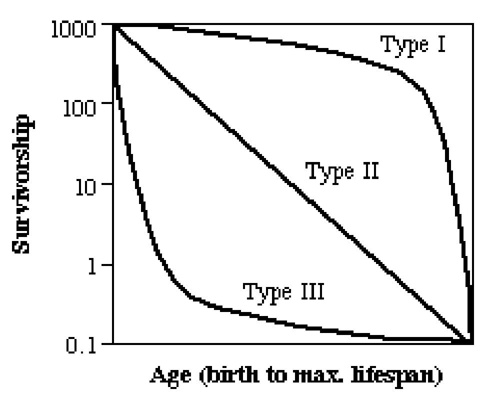
Composite - data are gathered over a number of years and generations using cohort **or** time-specific techniques. This method allows the natural variability in rates of survival to be monitored and assessed (Begon and Mortimer 1986).

Life Tables:

Survivorship curves are often created from life table data, plotting the proportion of a cohorts individuals alive (l_x) over time.

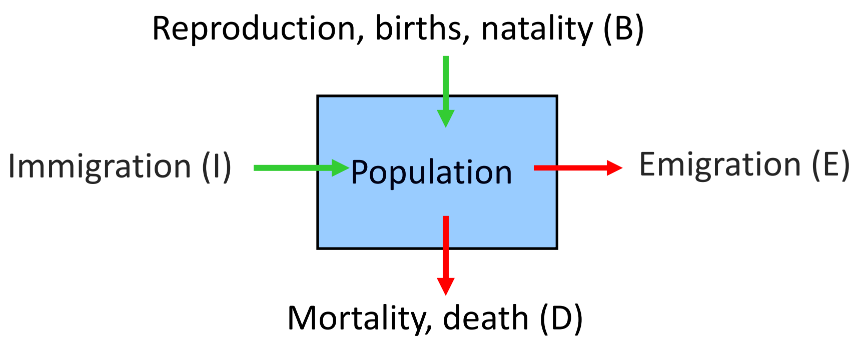
Three common patterns of survivorship are seen in populations (but others exist).

Description/example of each?



Begon and Mortimer (1996)

Measuring/Estimating Demographic Parameters:



Births / Fecundity

Natality: Average number of live offspring born to individuals that reproduce

Fecundity: Average number of offspring (usually female) born per individual (usually female)

Fecundity = Natality x proportion of population that gives birth

How do we measure this for different taxa?

Estimating fecundity

Field methods:

Direct counts of young observed

in utero: ultra sound, placental scars

after birth: in dens, nests, schools, etc

Indirect

Number of young inferred from some component(s) of reproduction (clutch size, nest/hatching success, etc)

Landscape specific fecundity estimates:

From spot-mapping data and nest monitoring

Territory success rates

Number of fledglings/ successful nest

These numbers used to estimate fecundity

	Reserves	Changing	Developed
Song Sparrow			
% Successful	61.2	70.6	64.4
% 2^{nd} Brood	7.5	16.4	16
Fledglings/nest attempt	1.56	2.00	2.14
Fledgling/female	0.54	.87	.86

(Oleyar & Marzluff unpub data)

Fecundity = (% successful * mn fledglings) + (% 2^{nd} brood * mn fledglings)/2

Estimating fecundity

Analytical methods (mark-recapture):

Jolly-Seber open population (Program MARK) :

estimates number of individuals added to population (if assume no immigration then that number is births)

Ratios of juveniles to adults:

gives an index of yearly reproduction and if stable age/stage distribution is assumed/known, then can be used to calculate numbers in each class and estimate fecundity

Mortality / Survival

Survival rate = (1 - Mortality rate)
****Survival estimators generally arise from 3 types of data:**

1) All animals can be relocated (known fate) and determined to have survived or died

2) Only survivors are encountered (e.g., capture-mark-recapture)

3) Only deaths are recorded (e.g., band recovery)

Mortality / Survival

Known-fate Model

Kaplan-Meier method:
Individuals in the population are monitored (e.g., via telemetry) over time

Accommodates 'staggered' entry into the known population

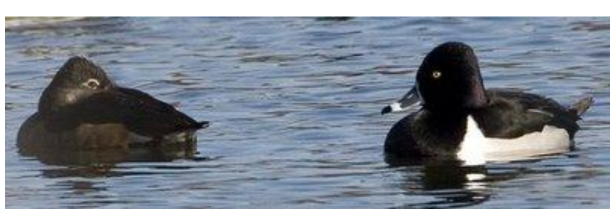
Animals may be 'censored' (i.e., leave the known population)

Survival can change over time (due to harvest, seasons, etc.)

Kaplan-Meier Survival:

$$S(t_j) = \prod_{t_j \le t}\left(1 - \frac{d_i}{n_i}\right)$$

Time Period	At Risk	Became Unavailable (Censored)	Died	Survived	Kaplan-Meier Survival Probability Estimate
Year 1	100	3	5	95	
Year 2	92	3	10	82	
Year 3	79	3	15	64	
Year 4	61	3	20	41	
Year 5	38	3	25	13	



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Time Period	At Risk	Became Unavailable (Censored)	Died	Survived	Kaplan-Meier Survival Probability Estimate
Year 1	100	3	5	95	(95/100)=0.95
Year 2	92	3	10	82	
Year 3	79	3	15	64	
Year 4	61	3	20	41	
Year 5	38	3	25	13	

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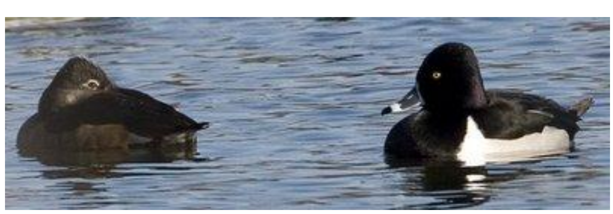
Time Period	At Risk	Became Unavailable (Censored)	Died	Survived	Kaplan-Meier Survival Probability Estimate
Year 1	100	3	5	95	(95/100)=0.95
Year 2	92	3	10	82	(95/100)x(82/92) =0.8467
Year 3	79	3	15	64	
Year 4	61	3	20	41	
Year 5	38	3	25	13	



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$$S(t_i) = \prod_{t_i \le t}\left(1 - \frac{d_i}{n_i}\right)$$

Time Period	At Risk	Became Unavailable (Censored)	Died	Survived	Kaplan-Meier Survival Probability Estimate
Year 1	100	3	5	95	(95/100)=0.95
Year 2	92	3	10	82	(95/100)x(82/92) =0.8467
Year 3	79	3	15	64	(95/100)x(82/92) x(64/79)=0.70
Year 4	61	3	20	41	(95/100)x(82/92) x(64/79)x(41/61) =0.4611
Year 5	38	3	25	13	(95/100)x(82/92) x(64/79)x(41/61) x(13/38)=0.1577

Mark-recapture

Cormack-Jolly-Seber method:

•Open population model
•Use Program MARK to run analyses
•Accommodates 'staggered' entry into the known population
•Animals may be 'censored' (i.e., leave the known population)
•Survival can change over time (due to harvest, seasons, etc.)
•Assume NO emigration...

Underlying concept:

Recapturing/resighting a marked animal is a product of 2 probabilities:

1) The probability that the animal is alive and still in the study area
   apparent survival vs true survival

2) The probability of capturing/encountering the animal during a sample period

Mark-recapture

Cormack-Jolly-Seber method:

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- Survival can change over time (due to harvest, seasons, etc.)
- Assume NO emigration...

$$\hat{S}_1 = \frac{\hat{M}_2}{\hat{M}_1 - m_1 + R_1}$$

Where:

$$\hat{M}_1 = m_1 + \frac{R_1 z_1}{r_1}$$

Where:

M-hat $_i$ = size of marked population at time i

m $_i$ = number marked at time i (recaps)

R $_i$ = number of marked individuals released at i

r $_i$ = number released at i that are captured again

z $_i$ = number captured prior to i and caught again later, but not caught during i

Table 6. Mark–recapture statistics for a population of meadow voles trapped in 1981, Maryland, USA (Pollock et al. 1990:29).[a]

Period	Dates	n_i	m_i	R_i	r_i	z_i	$\hat{S}_i$	SE
1	27 Jun–1 Jul	108	0	105	87	0	0.88	0.039
2	1 Aug–5 Aug	127	84	121	76	5	0.66	0.048
3	29 Aug–2 Sep	102	73	101	68	8	0.69	0.049
4	3 Oct–7 Oct	103	73	102	63	3	0.63	0.049
5	31 Oct–4 Nov	102	61	100	84	5		
6	4 Dec–8 Dec	149	89	148				

[a] For the ith occasion, n_i animals are captured, of which m_i were already marked; R_i is the number of n_i animals released after the ith sampling occasion; r_i is the number of R_i animals released at i that are captured again; z_i is the number of animals that were captured before i, not captured at i, but captured again later; and $\hat{S}_i$ is the estimated survival rate.

$$\hat{M}_1 = m_1 + \frac{R_1 z_1}{r_1}$$

$$\hat{M}_2 = m_2 + \frac{R_2 z_2}{r_2}$$

$$\hat{S}_1 = \frac{\hat{M}_2}{\hat{M}_1 - m_1 + R_1}$$

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$$= 0 + 105\left(\frac{0}{87}\right)$$

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$$= 0 + 105\left(\frac{0}{87}\right)$$

$$= 0$$

$$\hat{M}_2 = m_2 + \frac{R_2 z_2}{r_2}$$

$$= 84 + 121\left(\frac{5}{76}\right)$$

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$$\hat{M}_1 = m_1 + \frac{R_1 z_1}{r_1} = 0 + 105\left(\frac{0}{87}\right) = 0$$

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$$\hat{S}_1 = \frac{\hat{M}_2}{\hat{M}_1 - m_1 + R_1} = \frac{91.96}{0 - 0 + 105} = 0.88,$$

Band Recovery

Based on Mark-Recapture Methods

Recoveries are only dead individuals