

## Lecture 1: Introduction to demographic methods and mark-recapture statistics

### Why study demography of plants and animals?

Of interest in two arenas of ecology:

1. Evolutionary ecology (a basic science). Main goal is to try and understand variation in life history traits among organisms. Examples of some questions include: what is the adaptive significance of latitudinal variation in clutch size of birds, why are some organisms semelparous and others iteroparous, what determines the growth form of plants?
2. Conservation biology and wildlife management (applied sciences). Main goal is to determine population status and to identify demographic rates that influence population growth rates.

### Overview of Biol 823 Demographic Methods

We will cover two major topics in this course:

1. Estimation of demographic rates and their variance. We will focus primarily on transition rates such as survival, probability of changing state and population growth rates. The main software will be Program Mark.
2. Synthesis of demographic rates into matrix population models. We will emphasize matrix methods and use of deterministic population models. The main software will be Program Matlab.

There is no textbook for the course, but I recommend the following books for students interested in learning more about demographic methods.

- Ebert, T.A. 1999. Plant and animal populations: methods in demography. Academic Press, San Diego, CA. Nice basic introduction to life tables and other demographic methods, drawback is that most of the examples are programmed in Basic.
- Caswell, H. 2001. Matrix population models, 2<sup>nd</sup> edition. Sinauer Associates Inc., Sunderland, MA. An excellent reference for all forms of matrix models but writing can be dense and impenetrable for a new graduate student, snippets of Matlab code are provided for some problems.
- Morris, W.F. and D.F. Doak. 2002. Quantitative conservation biology: theory and practice of population viability analysis. Sinauer Associates Inc., Sunderland, MA. Perhaps the best book of the bunch, written at a basic level, extensive Matlab examples.
- Williams, B.L., J.D. Nichols and M.J. Conroy. 2002. Analysis and management of animal populations. Academic Press, San Diego, CA. Also a good reference that covers a lot of problems but presents only the statistical formulae and not the software tools for tackling the problems.

### Four components of demography

Components	Plants/Sessile animals	Vagile animals
Fecundity	Hard (small dispersed seeds)	Easy (clutch/litter size)
Survival	Easy (no dispersal)	Hard (mortality events rare)
Age at maturity	Easy (no dispersal)	V. hard (largely unknown)
Age or stage specific variation	Possible with long-term study	Possible with long-term study

### Why emphasize survival rates?

1. Methodological challenges in estimation – timing and causes of mortality events are usually unknown in population studies of free-living animals. Dead animals are rarely recovered by the observer.
2. Survival rates are often the demographic rate that are predicted to have the greatest impact on population growth rates (high ‘elasticity’ values). In long-lived organisms and in declining populations, survival of adults often has the highest elasticity. In short-lived organisms and in growing populations, survival of juveniles or fecundity rates often have the highest elasticity.

### Three sources of data for estimation of survival rates

1. Dead recovery data. Mark and release large sample of individuals, rely on public to recover and report bands or tags. Works well for game species, including some migratory organisms (fish, waterfowl etc.) but is dismal for nongame species. Emigration is less of a concern because recoveries come from a large geographic area.
2. Radio-telemetry data. Radio-tag individuals and continuously monitor to determine timing and location of mortality events. At the simplest level, the daily survival rate (*DSR*) can then be calculated as:

$$DSR = 1 - \left( \frac{\text{mortality events}}{\text{total days}} \right)$$

and the period survival is then:

$$\text{Period survival} = DSR^{(\text{Duration of period})}$$

Issues regarding use of radio-telemetry include the cost of transmitters and receivers, the limitations of transmitter size and battery life, and potential impacts of attachment method.

3. Live encounter data. Requires that individuals are uniquely marked, either by numbered tags or combinations of colored leg bands (small mammals and birds), or by variation in natural markings (striping on zebra rumps, patterns on the margins of tail flukes of whales). Individuals can then be physically recaptured, resighted without handling or a combination of the two.

### Metrics of survival

1. Maximum longevity. Individually mark a large sample of organisms and determine the oldest surviving individual. The Bird Banding Lab at Patuxent keeps records for North American birds, the oldest birds in the data base include 50+-year old albatrosses and other seabirds. Maximum longevity is biased by sampling effort and is based on extreme outliers, which ignores timing of mortality for most of the population.
2. Age-ratios. It is possible to estimate survival from age-ratios from both dead recovery and live encounter data as:

$$S_a = \frac{A}{(Y + A)}$$

where adult survival ( $S_a$ ) is estimated as the proportion of adults in the population. This metric assumes that the population is stable and that adults and yearlings are sampled with equal probability of capture.

3. Life-table approaches. It is also possible to use the standing age distribution of a population to calculate age-specific survival rates. This method assumes constant annual conditions and a stable population

## Mark-recapture techniques for live encounter data

Early mark-recapture indices were developed to estimate population size. Problem: The precision and bias of estimates of population size can be bad unless underlying assumptions are met. Estimates of survival rates tend to be better. First step was to use models to estimate survival rates, now development is aimed at formal comparisons of survival rates among groups. New models can be used to estimate other useful demographic parameters like probability of moving to a new area, probability of first breeding, and population growth rate.

### Return Rates

Method: Mark a sample of animals at  $t_1$ , recapture a percentage at  $t_2$  (or  $t_2$  to  $t_n$ ).

Assumptions: Population is open. The probability of an animal being recaptured on two consecutive occasions is the product of four independent rates:

1. true survival rate ( $S$ ) = the probability the individual survives across the interval. The complement of  $F$  includes losses due to mortality.
2. site-fidelity rate ( $F$ ) = the probability that an individual returns to the same site if it survives. The complement of  $F$  includes losses due to permanent emigration.
3. site-propensity rate ( $\gamma^*$ ) = the probability that an individual returns the following year, if it survives and returns to the same site. The complement of  $\gamma^*$  includes absences due to temporary emigration ( $\gamma$ ), and,
4. true encounter rate ( $p^*$ ) = the probability that an individual is detected by the observer if present on the study area. The complement of  $p^*$  includes absences due to failure of the observer to detect the individual, which can be due to sampling effort or other issues.

### Cormack-Jolly-Seber Model (1960s):

Method: Mark and recapture individuals at multiple sample times

Assumptions: Population is open (exchange possible), sampling is instantaneous (e.g., 2-4 d sampling for 1 month apart in voles, 3-4 m for 1 yr apart for most breeding animals), equal intervals

The CJS model yields two parameters:

1. 'Local' or 'apparent' survival ( $\phi$  or 'phi') which is the product of the first two probabilities:  $\phi = SF$ .
2. Encounter rate or 'resighting' or 'recapture' rate ( $p$ ) which is the product of the second two probabilities:  $p = \gamma^* p^*$ .

A high return rate indicates that all of these probabilities are high. For example, consider seabirds breeding on a remote oceanic islands where the return rate  $> 95\%$ . This must be due to high true survival (low fecundity in predator refugia), strong site-fidelity (less chance of dispersal), strong site propensity (breeders rarely skip years), and a high resighting rate (ease of detection in an open environment). Problems arise in interpreting low return rates (e.g.,  $< 50\%$ ) because they could be due to low values for any possible combination of the four probabilities.

### **The problem of emigration**

The advantage of CJS and other mark-recapture models is that they separate  $\phi$  from  $p$ . If encounter rates are close to one, mark-recapture methods are unnecessary. Mark-recapture methods are also of little use if a return rate or a local survival rate is  $< 0.20$ . Phi is sometimes just called 'survival', but remember it is not true survival. Local survival is the product of true

survival and philopatry/site-fidelity and losses could be due to mortality, permanent emigration or both. These possibilities cannot be distinguished without corollary data on animal movements. Sex and age differences are common and specific to taxonomic groups. In mammals and waterfowl, young females are more philopatric than males. The opposite is true in most other birds: females disperse and males return. Adults tend to show greater site-fidelity than young.

Dispersal distances are best measured by telemetry or staggered study plots. Not always feasible. Measurements of dispersal are often confounded by study size. In a circular study area, the mean detectability is proportional to the radius. Most study sites are irregular, but it is possible to calculate detectability by digitizing the study area and surroundings and determining possible distances for all suitable habitats. The key is to compare apparent dispersal to detectability rates, being aware that underestimation increases with distance from core of area. Great help for interpreting differences in local survival, one advantage is that the relative biases will be same for two groups in study.

### Constructing capture histories for input

Formatting of data and decision rules (remove the few animals marked in a preliminary year, the few animals recaptured off of the study site or outside of the main season, marks likely to be lost, marks read incorrectly 2 partials = 1 good sighting, handling of first capture event, drop first record for animals marked as young, ) \*\*\*Goal is to strive for homogeneity

Transpose vertical file to a horizontal file (one record per sampling period)

Binary coding (1=detected, 0=not observed). E.g. 1011011100. \*\*\* note that zeroes inside capture histories indicate that animals were missed. If capture histories are 011111000, 001111000 etc., don't need mark-recapture statistics.

Considerations: Recapture vs. resighting information (trap effects less likely with resighting information, older birds may avoid traps also resightings may be biased by activity patterns (sandpiper displays vs. on the nest), breeders vs. nonbreeders.

### Notation of capture histories

Example of study with five years or *occasions* gives four *intervals*. Occasions and intervals can be on any time-step, usually years for vertebrates and long-lived plants, months for small mammals, or weeks to days for invertebrates. The following individual was marked on the first occasion and resighted on the 4<sup>th</sup> and 5<sup>th</sup> occasions. The CJS model has seven apparent survival ( $\phi$ ) and recapture *parameters* ( $p$ ).

<b>t<sub>1</sub></b>		<b>t<sub>2</sub></b>		<b>t<sub>3</sub></b>		<b>t<sub>4</sub></b>		<b>t<sub>5</sub></b>
1	$\phi_1$	0	$\phi_2$	0	$\phi_3$	1	$\phi_4$	1
		$p_2$		$p_3$		$p_4$		$p_5$

Several issues arise:

1. Can't estimate  $p_1$  because all individuals are newly marked at the first occasion  $t_1$ .
2. If there is time-dependence in  $p$ , can't estimate  $p_5$  without subsequent information, and the last two parameters form an inestimable beta term ( $\phi_4 * p_5$ )
3. Number of survival estimates (n-1 or n-2), more needed to model annual covariates
4. Animals newly banded on the last occasion  $t_5$  do not contribute to any of the parameter estimates.

### Basis of Parameter Index Matrices (or PIMs)

Consider an example with five occasions and four transitions for a time-dependent model ( $\phi_t, p_t$ ).

$t_1$	$\phi_1$	$t_2$	$\phi_2$	$t_3$	$\phi_3$	$t_4$	$\phi_4$	$t_5$
		$p_2$		$p_3$		$p_4$		$p_5$

In reality, you are not just going to follow one cohort of animals through time, you are going to capture and mark animals on each occasion. In that case, the above table should be expanded as:

	$t_1$		$t_2$		$t_3$		$t_4$		$t_5$
1		$\phi_1$		$\phi_2$		$\phi_3$		$\phi_4$	
			$p_2$		$p_3$		$p_4$		$p_5$
2				$\phi_2$		$\phi_3$		$\phi_4$	
					$p_3$		$p_4$		$p_5$
3						$\phi_3$		$\phi_4$	
							$p_4$		$p_5$
4								$\phi_4$	
									$p_5$

In MARK, the subscripts on these parameters are simplified to a *Parameter Index Matrix*:

There are four estimates of local survival ( $\phi_1 - \phi_4$ ), hence:

1	2	3	4
	2	3	4
		3	4
			4

There are also four estimates of recapture rate ( $p_2 - p_5$ ) but to avoid confusion, the recapture rates are sequentially renumbered to indicate that they are different:

5	6	7	8
	6	7	8
		7	8
			8