Pradel Models

The original epiphany was symmetry under time reversal, hence the realization that one could easily model events before the first capture, i.e. the leading zeros, just as one can model trailing zeros given preceding captures and releases. For example with the encounter history

00011010010

we already can model the part that is 1010010 (i.e., conditioning on the leading 0001), given that first “1," i.e. given first capture occurred at occasion 4. Can we model the initial 0001 part? Yes, but a new parameter class is needed: either recruitment (f), seniority (γ), or population finite rate of change (λ). There is not a unique way to represent this new parameter class although the only easy and intuitive parameterization is in terms of the seniority probability γ which is the “reverse time" equivalent of survival probability (in forward time). Thus, seniority is the converse of survival:

$\phi_i =$ probability the animal is alive and in the population at risk of capture at occasion $i+1$ given it was alive and in the population at risk of capture at occasion i (survival).

$\gamma_{i+1} =$ probability the animal was alive, and in the population at risk of capture, at occasion i given it is alive and in the population at risk of capture on occasion $i+1$ (seniority).

All individuals at risk of capture at occasion $i+1$ were either in the population at occasion i, or entered the population during interval i and survived to occasion $i+1$.

Let population sizes (at risk of capture) at these two occasions be N_i and N_{i+1}. A subset, of these two sets of animals, is the set of all animals that are alive in the population at both times. At time $i+1$ the size of that set can be given as $N_i \times \phi_i$. At time i the size of that set can be given as $\gamma_{i+1} \times N_{i+1}$. Both formulae are for the size of the same set, hence

$$\boxed{N_i\,\phi_i = \gamma_{i+1} N_{i+1}}$$

Moreover, the (estimated) finite population rate of change from time i to $i+1$ is

$$\boxed{\lambda_i = \frac{N_{i+1}}{N_i}}$$

Therefore, $\boxed{\phi_i = \gamma_{i+1}\lambda_i}$ or $\boxed{\lambda_i = \frac{\phi_i}{\gamma_{i+1}}}$ or $\boxed{\gamma_{i+1} = \frac{\phi_i}{\lambda_i}}$.

To look at this parameterization from a different view point considered the original Jolly-Seber parameters:

	p_1	p_2	p_3	p_4	(and so forth)
and					
	ϕ_1	ϕ_2	ϕ_3	ϕ_4	
	N_1	N_2	N_3	N_4	(population size at occasion *i*)
	B_0	B_1	B_2	B_3	(recruitment at occasion *i*+1)

The above three parameter types constitute only 2 mathematically independent parameters because of the relationship

$$N_i \times \phi_i + B_i = N_{i+1}.$$

Thus, given any two sets of the three, the other set can be computed. In the classical Jolly-Seber model $\hat{N}_i = n_i / \hat{p}_i$ and $\hat{B}_i = \hat{N}_{i+1} - \hat{N}_i \hat{\phi}_i$. However, N and B are derived parameters; they are not placed into any actual likelihood function so their estimates are not obtained directly. If we model the complete encounter history (i.e., model also leading zeros and the first "1") we can construct a likelihood that is a function of the ϕ_i, p_i and the γ_i (or λ_i, or a fecundity-recruitment type parameter, denoted below as f_i).

Reiterating that $\lambda_i = \frac{N_{i+1}}{N_i}$ we obtain from the above equation

$$\phi_i + \frac{B_i}{N_i} = \lambda_i \equiv \phi_i + f_i$$

where we define

$$f_i = \frac{B_i}{N_i} ,$$

which is really a recruitment parameter, but has been denoted *f* for "fecundity" by Pradel). It is not a probability: $f_i > 1$ is possible (just as is $\lambda_i > 1$).

Alternatively divide as

$$\frac{N_i}{N_{i+1}} \times \phi_i + \frac{B_i}{N_{i+1}} = 1 ,$$

hence,

$$\frac{1}{\lambda_i} \times \phi_\text{i} = 1 - \frac{B_i}{N_{i+1}} \quad \equiv \quad \frac{1}{\lambda_i} \times \phi_i = \gamma_{i+1}$$

So we have seniority as

$$\boxed{\gamma_{i+1} = 1 - \frac{B_i}{N_{i+1}}}\ ;$$

this seniority parameter is a probability. Finally, a big deal is that

$$\boxed{\frac{\phi_i}{\gamma_{i+1}} = \lambda_i}\ .$$

The Jolly-Seber model can, essentially, be created by fully modelling (i.e., a likelihood) each complete capture history in terms of p_i, ϕ_i and γ_i probability parameters for any animal ever captured; the all-0s history is not included in the Pradel likelihood.

(some theory below)   ------

Consider the history $01\cdots$ with regard to modelling the 01 part (given the animal was the population at or before occasion 2). Either the animal was in the population at risk of capture on occasion 1, or it was not, but recruited at occasion 2. These two case are mutually exclusive with probabilities γ_2 and $1-\gamma_2$. In the first case it also had to be not captured on occasion 1 and survival to occasion 2. Thus the needed term is

$$\Pr\{01\} = \gamma_2(1\text{-}p_1)\phi_1 p_2 \ + (1-\gamma_2)p_2 = [\gamma_2(1\text{-}p_1)\phi_1 + (1-\gamma_2)]\, p_2\ .$$

Then the probability element for the full history is just

$\Pr\{01\} \times \Pr\{$capture history after occasion 2 given it was captured at occasion 2$\}$.

The needed terms for pr{001}, or Pr{0001} are built-up recursively. For example

$$\Pr\{001\} = \left\{[\gamma_2(1\text{-}p_1)\phi_1 + (1-\gamma_2)]\gamma_3(1-p_2)\phi_2 + (1-\gamma_3)\right\}p_3\ .$$

Let $\Pr\{1\} = \psi_1 p_1$ with boundary condition $\psi_1 = \gamma_1 = 1$. For $i > 1$ let

$$\psi_i = \gamma_i(1\text{-}p_{i\text{-}1})\phi_{i\text{-}1} + (1-\gamma_i)\ ,$$

then

$$\psi_{i+1} = \psi_i\gamma_{i+1}(1-p_i\,)\phi_i + (1-\gamma_{i+1})\,,\quad i \geq 1,\ \ \psi_1 = 1\ .$$

Now for first capture being on occasion i we have

$$\Pr\{0\cdots01\} = \psi_i\, p_i\ .$$

(Maybe I'll add more someday to complete that - esp. that one must condition on seeing an animal at least once and problems with loss on capture; KPB, Feb. 2004).