Multievent modeling for the Egyptian Vulture

The multievent framework distinguishes what can be observed in the field (the events coded in the encounter histories) from the underlying biological states of the individuals, which must be inferred (Pradel 2005). Here, the events were ‘0’ (bird not observed on a particular occasion), ‘1’ (vulture observed alive with a functioning radio signal), ‘2’ (vulture resighted alive by means of its PVC mark and without an active radio signal), ‘3’ (vulture recovered recently dead with a functioning radio signal) and ‘4’ (vulture recovered recently dead without an active radio signal). Each occasion comprised a year, considering 1st June (i.e., when chicks fledge) as the beginning of the period. The model included 5 underlying biological states: two states for live individuals, coded AAR (i.e., alive with an active radio signal) and ANR (i.e., alive without an active radio signal); and three states for dead individuals, coded DAR (i.e., recently dead with an active radio signal), DNR (i.e., recently dead with an active radio signal) and LD (i.e., long dead).

Multievent models use three kinds of parameters: the initial state probabilities, which correspond in our model to the proportions of live individuals belonging to the states AAR and ANR; the probabilities of transition between the states (i.e., radio signal functioning and survival probabilities, see below); and the probabilities of the events (i.e., resighting and recovery probabilities). These parameters were estimated simultaneously from the whole encounter histories by maximum likelihood (Choquet et al. 2009b). Matrix representations with departure states in rows and arrival states in columns are commonly used in multievent models (Sanz-Aguilar et al. 2012). The initial state probabilities corresponded to the probability that a newly marked individual
was equipped (AAR) or not equipped (ANR) with a radiotransmitter. Here, the initial state was known for every captured individual and was modeled to vary over time and states. Note that individuals cannot be captured for the first time as dead. We broke down the transition between the state probabilities into two steps: the first step corresponded to the probabilities of radio signal functioning, \( \eta \) and radio signal loss \( (1-\eta) \). Probabilities of radio signal functioning were modeled as a function of radiotransmitter age (i.e., time elapsed since the animal was equipped with the radiotransmitter).

\[
\begin{pmatrix}
AAR & ANR & LD \\
AAR/\eta & 1-\eta & 0 \\
ANR & 0 & 1 & 0 \\
DAR & 0 & 0 & 1 \\
DNR & 0 & 0 & 1 \\
LD & 0 & 0 & 1 \\
\end{pmatrix}
\]

The second step corresponded to survival \( (\phi) \) and mortality \( (1-\phi) \) probabilities (matrix 2). Survival probabilities of individuals of known age were modeled as a function of their age (following different age structures) and survival probabilities of individuals of unknown age (i.e., adults) were modeled to be constant in all models.

\[
\begin{pmatrix}
AAR & ANR & DAR & DNR & LD \\
AAR/\phi & 0 & 1-\phi & 0 & 0 \\
ANR & 0 & \phi & 0 & 1-\phi & 0 \\
LD & 0 & 0 & 0 & 0 & 1 \\
\end{pmatrix}
\]

The event probabilities (matrix 3) corresponded to the resighting probabilities \( (p) \) that were allowed to vary with time for all models (due to annual differences in monitoring
effort) and the recovery probability \((r)\) that was considered constant for all models (due to the low number of individuals recovered). Note that resighting and recovery probabilities of individuals with active radio signals (AAR and DAR) were modeled to be 1 (matrix 3).

\[
\begin{pmatrix}
0 & 1 & 0 & 0 & 0 \\
1 - p & 0 & p & 0 & 0 \\
0 & 0 & 0 & 1 & 0 \\
1 - r & 0 & 0 & 0 & r \\
1 & 0 & 0 & 0 & 0
\end{pmatrix}
\]

matrix 3.