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Estimating stop over duration in the presence of trap-effects

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ABSTRACT

Detection probability of individuals is increasingly taken into account during field monitoring schemes and in demographic models. Conversely, it is often taken for granted that trappability of animals will remain fairly constant and broadly similar between individuals present in a given area. However, animals may change their behaviour after being trapped. In this paper, we introduce a new hidden Markovian model to estimate stop over duration in the presence of trap-effects. This model combines nonhomogeneous Markovian states with semi-Markovian states in the non-observable state process, and simple distributions with first-order Markov chains as observation models. This model generalizes previously proposed models and enables the joint modeling of the time of residence and the trap effect. Two cases are considered, depending on whether or not emigration is time-dependent since arrival. We illustrate the latter with teal *Anas crecca* wintering in Camargue, Southern France and we demonstrate the importance of handling trap-effects.

1. Introduction

Bird land and depart at various times on intermediate stop over areas (Schaub et al., 2001) but also from their wintering grounds (Pradel et al., 1997b; Caizergues et al., 2011). It is important to measure stop over duration (SOD) because the onset of departures marking the end of the staying period can then be estimated with greater precision and the number of bird days at a given site can be predicted more accurately. Both types of information are of primary interest for the management of migratory bird populations. For instance, determining the onset of spring migration of game species is crucial as it is used to determine when the hunting season should close (after the 2009/147/EC Council Directive on the conservation of wild birds).

The migratory movements of birds have long been used by man as seasonal landmarks within the annual cycle, suggesting general and simultaneous movements of the birds, hence that migration movement dates can be identified easily. Pradel et al. (1997c) conversely demonstrated progressive departure from the wintering grounds, which has since been backed up by ringing (or banding) data (Guillemain et al., 2006). SOD models should therefore be able to handle various scenarios for arrival and departure dates. SOD models should thus deal with the fact that individual detection at a site is always not certain. A convenient and flexible way to study departures from observations is to use capture–mark–recapture (CMR) data. While detection probability of individuals is increasingly taken into account during field monitoring schemes and in demographic models (e.g. Defos du Rau et al., 2003), it is often taken for granted that trappability of animals will remain fairly constant and broadly similar between individuals present in a given area, which may be strongly misleading.

Several methods have been developed to study stop-over-duration of migratory birds through the analysis of CMR data. The first method estimates a minimum SOD by calculating the mean over individuals of the time between the first and the last observation. This method provides underestimation of the SOD since individuals could have been on the site before their first capture and still be on the site after their last capture. This is especially true if capture probability is low. The second method calculates the equivalent of the life expectancy from the emigration probabilities (Kaiser, 1999; Pradel et al., 1997c), thus correcting for the presence beyond the last observation. However the length of presence before the first capture is still ignored. Indeed the date of first capture is not necessarily similar to the arrival date. To deal with the problem of the first date of arrival, Schaub et al. (2001) assimilated the arrival with recruitment and performed a separate analysis for emigration and recruitment to estimate SOD. This approach assumes that departure only depends on the current time. It does not handle cases where departures depend on

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the date of arrival. Recently, three papers independently proposed time elapsed since arrival (TSA)-dependent modelling approaches (Pradel, 2009; Pledger et al., 2009; Fewster and Patenaude, 2009). TSA approaches are important because they consider that the likelihood of an individual departing depends on the time it has already spent at the site. It allows to model a SOD of fixed length whatever the date of arrival. For instance, for birds that need refueling, the time spent on the stop-over site may be identical whatever the date of arrival and may be only determined by the number of days needed for food provisioning.

Authors however generally assumed homogeneity of capture rate among the individuals, although this assumption is often violated. For example, trap-effects can occur when individual behaviour is affected by the trap itself (Pradel, 1993) as can frequently happen with baited traps. Neglecting trap-effects generates bias in survival analysis for classical CR models and can potentially generate bias in the probability to stay at the refueling site.

Because traditional approaches may therefore provide unreliable results in presence of trap effect, we here develop new models to estimate SOD in presence of such immediate trap-effects. We consider two cases. In the first case, we develop a hidden non-homogenous Markov model in which the residence probability (probability to stay at a site) depends on time (the capture occasion). In the second case, the residence probability depends on the past, specifically on the TSA. For that purpose, we propose a hybrid Markov/semi-Markov model (Guédon, 2005) where the TSA was explicitly modeled by a sojourn time (state occupancy) distribution.

Several general softwares or packages exist to deal with hidden semi-Markov models, for example V-Plants, the successor of AMAPmod (Godin and Guédon, 2001) or MHSMM (O'Connell and Hojsgaard, 2011), but our model requires a specific conditionning since we aimed at taking into account the fact that not all individuals present at the site are seen. So if $P(h)$ is the probability of individual history h then $P(h)$ must be considered conditional on the set H of individuals seen at least once (Pradel, 2009):

$$P(h|H) = \frac{P(h)}{1 - P(h_{\emptyset})},$$

where $P(h_{\emptyset}) = 1 - P(H)$ is the probability that an individual is present but nonetheless never captured. This type of conditioning is easily handled by software E-SURGE (Choquet et al., 2009b).

2. Methodologies for estimating stop over duration

Assume that we have T capture occasions and N individuals captured at least once. The set of observations is $O_t = \{0 \text{ for "notcaptured"}, 1 \text{ for "captured"}\}$. Let the encounter history for individual i be $h_i = (o_{i1}, \ldots, o_{iT})$ where o_{it} denotes whether individual i is observed ($o_{it} = 1$) or not ($o_{it} = 0$) at occasion t. Let e_i be the occasion when individual i is captured for the first time, l_i the last occasion when individual i is recaptured. The usual assumption of independence among individuals is used here. As a consequence, the likelihood L is the product of each individual contribution $L = \prod_{i=1}^{N} P(h_i|H)$.

For the expression of $P(h)$, we consider 4 main cases of increasing complexity:

Case 1: joint modelling of arrival and time-dependent only residence,
Case 2: joint modelling of arrival and time-dependent only residence with trap-effects,
Case 3: joint modelling of arrival and TSA-dependent only residence,
Case 4: joint modelling of arrival and TSA-dependent only residence with trap-effects.

Cases 1 and 3 are sub-cases for cases 2 and 4, respectively, i.e. without trap-effects and are used here to introduce the latter. Case 1 is the joint modelling of Schaub et al. (2001). Case 3 is equivalent to models presented in Pradel (2009), Pledger et al. (2009) and Fewster and Patenaude (2009). To our knowledge, cases 2 and 4 are fully new. For all cases we assumed that there are no individuals at the site at time 1, which is a standard assumption for this kind of study.

To deal with TSA residence, it is not sufficient to condition on the past state as in a classical first-order Markov chain: we also need to know for how long the animal has been present. Pradel (2009) handled the TSA question by considering the following hidden states: "not yet arrived", "just arrived", "arrived one occasion earlier", "arrived two occasions earlier", and "departed". This approach is not adequate when many occasions and/or trap-effects or heterogeneity have to be considered, because of the large number of states this generates. So, we therefore reformulated this model in a more appropriate framework. One convenient way to represent SOD is to introduce semi-Markovian states where the time spent in these states is explicitly modeled by appropriate sojourn time distributions. In the next section, we set a single statistical modeling framework that combines non-homogeneous Markovian states with semi-Markovian states in the non-observable state process, and simple distributions with first-order Markov chains as observation models. This framework encompasses cases 1–4 as particular cases.

2.1. Definition of a hidden hybrid Markov/semi-Markov model

Let $\{S_t\}$ be a hybrid Markov/semi-Markov model with finite state space $\{1, \ldots, J\}$; see Kulkarni (1995) for a general reference about Markov and semi-Markov models. This J-state hybrid Markov/semi-Markov model is defined by the following parameters:

- initial probabilities $\pi_j = P(S_1 = j)$ with $\sum_j \pi_j = 1$,
- transition probabilities
- semi-Markovian state j: for each $k \neq j$, $\phi_{jk} = P(S_{t+1} = k|S_{t+1} \neq j, S_t = j)$ with $\sum_{k \neq j} \phi_{jk} = 1$ and $\phi_{jj} = 0$,
- Markovian state j: $\phi_{jk} = P(S_{t+1} = k|S_t = j)$ with $\sum_k \phi_{jk} = 1$.

An explicit sojourn time distribution is attached to each semi-Markovian state

$$d_j(u) = P(S_{t+u+1} \neq j, S_{t+u-v} = j, v = 0, \ldots, u-2|S_{t+1} = j, S_t \neq j),$$
$$u = 1, \ldots, M_j,$$

where M_j denotes the upper bound to the time spent in state j. Hence, we assume that the sojourn time distributions are concentrated on finite sets of time points.

The output process $\{O_t\}$ is related to the hybrid Markov/semi-Markov chain $\{S_t\}$ by the observation (or emission) models. In our case, we consider both zero-order Markov chains (i.e. simple observation distributions) and first-order Markov chains as possible observation models

$$b_j(y) = P(O_t = y|S_t = j) \text{ with } \sum_y b_j(y) = 1 \qquad \text{zero-order},$$

$$b_{j,x}(y) = P(O_t = y|O_{t-1} = x, S_t = j) \text{ with } \sum_y b_{j,x}(y) = 1 \quad \text{first-order}.$$

Markov chains as observation models within hidden Markov models (HMM) were introduced by Churchil (1989) for analyzing DNA sequences. We assume that some transition or observation distributions are function of the index parameter t introducing some non-homogeneity in the model definition.