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S34-5 How to study departure decisions of migrants from stopover sites using capture-recapture data

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Abstract Environmental factors (weather conditions, predation risk, competition) as well as intrinsic factors (innate rhythm, fuel deposition rate, body mass) have been shown to be taken into account by birds when they decide to depart from a stopover site on the next flight bout. Only a few empirical studies, however, have evaluated more than one of these factors simultaneously. The relative importance of these factors, as well as possible interactions among them, are therefore largely unknown. The reason for this is the difficulty of observing birds and knowing their condition at departure. Here I present a methodological framework for circumventing these problems when capture-recapture data are available from a stopover site. It shows how multi-state capture-recapture models can be used to test which factors are the most important for departure decisions.

Key words Migration, Stopover, Departure, Capture-recapture, Statistics

1 Introduction

Migrating birds usually divide their journeys into several flight steps with intermittent stopovers. At stopover sites, fuel for flight is accumulated and during flight it is used up. During their journeys, migrants are faced with two main challenges that determine the spatiotemporal pattern, and hence the overall success, of their migrations. The first is when the bird should end the stopover period (departure decision), and the second is when and where the bird should end the flight bout (landing decision). The focus of this paper is on the departure decision.

The decision to depart from a stopover site on the next flight bout may be governed by environmental factors (weather conditions, competition, predation risk) and by intrinsic factors (fuel accumulated, fuel deposition rate, time program). Theory-based predictions about how birds should react to variation in each of these factors already exist (Liechti and Bruderer, 1998; Weber, 1999). Moreover, their effects on departure decision have been studied empirically by a number of workers. Jenni and Schaub (2002) recently reviewed results of empirical studies. The main conclusions were that departure readiness was higher on days/nights when weather was favorable, when food was scarce and hence fuel deposition rate low or negative, and when the risk of predator attack was high. The influence of actual fuel stores was not always clear: some studies found that birds with low fuel stores stayed longer at the stopover site and others did not. To my knowledge, no empirical study that relates departure decision to competition has yet been carried out.

Such results came from studies that used different methods (laboratory or field experiments, observational field studies), and which were sometimes conducted at special stopover sites such as oases. They are therefore difficult to compare, and cannot be extrapolated readily to situations at more typical stopover locations. Some conclusions were even based on the restrictive assumption that birds departed immediately after the last observation.

What is needed for the next step are studies that overcome these shortcomings,, and which use the same methods to investigate several factors affecting departure decision in order to rank their importance. My main objective here is to offer methodological solutions for achieving this goal using capture-recapture data obtained in the field. I will not discuss experiments and telemetry studies. It is assumed that the reader has some basic knowledge about open population capture-recapture statistical methods (Lebreton et al., 1992; Cooch and White, 2001).

2 Capture-recapture and departure decision

Standardized ringing (Bairlein, 1995) is a common method for gathering data to study various aspects of stopover ecology (Kaiser, 1996; Schaub and Jenni, 2000, 2001). Each time a bird is captured, its condition (body mass, fat score) is recorded and it is ringed or its ring number noted. Such data can be stored in an $n \times m$ matrix of individual capture histories, where m is the number of capture days and n is the number of birds caught. An element $I_{n,m}$ of the matrix is either 0 if the nth bird was not caught at the mth day, and 1 if it was caught. Additional information about the condition of the bird at the capture event may be stored as well. These capture histories contain information about the times when the birds leave stopover sites, even though departure may not have been observed directly.

A typical capture history is {1 0 1 1 0}: the bird was caught on days 1, 3 and 4, and not on days 2 and 5. Traditionally, this would infer that the bird left the site on the night between day 4 and 5. However, the bird was not caught at day 2 even though it was there. Recapture probability thus was not 1, and the bird may well have been still present at day 5 but was not detected. What is needed from such data is a method that estimates recapture probability and the probability that the bird remained at the site for one more unit of time. The Cormack-Jolly-Seber model (Lebreton et al., 1992), originally developed to estimate survival rates, is such a method. If it is assumed that mortality during stopover is negligible, estimated local survival probability (ϕ) is the probability of remaining at the site. The complement to one is the probability that the bird has left the site (emigration probability, $\varepsilon = 1 - \phi$). Emigration probability is thus the focus parameter for investigating the departure decision.

Estimated emigration probability is the probability that the bird has left the area covered by the trapping program. It does not necessarily mean that the bird has actually begun its next flight — the bird may just have moved to an adjacent area. The position and number of traps (mist-nets) within the stopover site should be optimized such that birds remaining at the stopover site are readily detected (Chernetsov and Titov, 2000). Additional information on the movement of the birds that stop over (Titov, 1999) helps with the design and the interpretation of the results. The violation of the assumption that there is no mortality during stopover is not a serious problem because daily mortality probabilities are usually an order of magnitude lower than daily emigration probabilities. Other assumptions that apply to these methods are the same as those for the ordinary capture-recapture statistical methods, and some of them can be tested statistically (Lebreton et al., 1992). All models that I will describe can be fitted with program MARK (White and Burnham, 1999) that is freely available at www.phidot.org/software/mark.

3 How to study single factors

3.1 Environmental factors

If weather conditions, predation risk and competition are taken into account by departing birds, they can be expected to affect the departure decision in all individuals in the same way. Temporal variation of emigration probability then becomes the focus. Whether this variation can be explained by temporal variation in the environmental factor requires evaluation. Different models have to be fitted in which emigration probability is either a function of the environmental factor (ε_{env}; i.e., ultrastructural model, Lebreton et al., 1992) and varies independently of it (ε_t: emigration probability is different each day), or is constant over time (ε). Each of these models represents a working hypothesis, and information-theoretic approaches can be used to rank them according to their support in the data (Burnham and Anderson, 1998).

Environmental factors can be categorical or continuous. Examples are daily measures of wind speed, cloud cover, or rain at time of takeoff, daily estimates of predator density (daily count of raptors), and daily estimates of the number of competitors.

The number of competitors can be estimated with capture-recapture methods as well (Jolly-Seber model; Schwarz and Seber, 1999). The Jolly-Seber model estimates population size (number of competitors) and local survival rate. A significant negative process covariance between local survival probability and population size, which needs to be extracted from the total covariance and sampling covariance (Burnham and White, 2002), is an indication that emigration is higher when population size — and thus competition — is high.

3.2 Intrinsic factors

Different approaches have to be used to test whether birds take their actual condition (innate rhythm, fuel deposition rate, amount of fuel stores) into account for departure. If they do, emigration probability is not the same in all birds at a given time, but it is the same in all birds for a particular condition irrespective of time. Each intrinsic factor requires a different testing approach.

Innate rhythm The innate rhythm hypothesis (regular phases of flights and stopovers) is difficult to test. If it is real, we would expect that all birds have the same stopover duration and hence also emigration probability. In principle, models in which emigration probability is constant over time (ε) represent this hypothesis. However, as birds usually arrive in waves at stopover sites, emigration probability may still appear to be time-dependent if all birds stay for exactly the same time at the site. On the other hand, if the constant emigration model turns out to be the best fit, it does not yet give proof of the innate rhythm hypothesis. The power to detect variation in emigration probability may have simply been low. High sample size protects against low power here.

A different, but perhaps more appropriate approach is to estimate stopover duration for birds in different conditions and at different times of the migratory season (Schaub et al., 2001). There is strong evidence that innate rhythm is important for regulating stopover duration if stopover duration is the same under different conditions.

Fuel deposition rate Fuel deposition rate (FDR) is estimated as the difference in body mass between first and last capture divided by the number of days between the captures. In capture-recapture analysis a difficulty arises here: FDR can only be estimated for birds caught at least twice, whereas for capture-recapture statistics, all birds, even those caught only once, must be included. There exists, nevertheless, a simple practical solution to this problem: just delete the first capture (i.e., replace the 1 by a 0) of *all* birds in the input file. The new file then comprises only birds that were caught at least twice. Now emigration probability assesses only birds that stayed at least one day at the stopover site against the non-transients (Pradel et al., 1997). As our aim is to examine the emigration of that fraction of birds that really stops over at the study site, this is not a constraint but a benefit. A more serious problem is the reduction in the sample size, and thus precision of the parameter estimates and test power.

The birds must be allocated into groups according to their FDR. The hypothesis that departure depends on FDR is translated into a model in which the emigration probability of each group is different (ε_{fdr}). The alternative hypothesis is that emigration is the same in each of these groups (ε).

Fuel stores (*body mass*) Body mass, fat scores and other indicators of the amount of fuel stored are all considered together here because their significance for departure is tested with the same models. I will use "body mass" for all indicators of the quantity of fuel stores. For capture-recapture analysis, a further problem emerges. Birds change body mass from day to day, and hence also from capture to capture. If emigration probability is related to body mass at one particular (e.g., first or last) capture, we do not really test whether *actual* body mass is decisive for departure decisions — rather we test whether body mass at first or at last capture is decisive. As the body mass of each bird at each capture event is known, capture histories can be adapted to contain this information.

It is necessary to define classes of body mass, and each bird at each capture event is then assigned to a specific class. An original individual capture history of {1 0 1 1 0} may then be replaced by the following {low 0 high high 0}, that is, the bird had low body mass at first capture and high body mass at second and third. Multi-state capture-recapture models (Hestbeck et al., 1991) are suited to estimate emigration probability for each class from such data. Compared to the one-state models presented so far, multi-state capture-recapture models contain an additional parameter type, the daily probability of change in body mass class. This can be interpreted as an estimation of fuel deposition rate. The hypothesis that departure decision depends on actual body mass is translated into a model where state (class)-specific emigration probabilities differ (ε_{mass}). This model may be compared to a model in which the state-specific emigration probabilities are constrained to be the same (ε).

4 How to study multiple factors

As shown above, the study of single factors requires different models: one-state models with or without groups and multi-state models. I now propose a framework within which all these different factors can be tested simultaneously. First I describe the preparation of the data and secondly the statistical analysis.

First, FDR over the time interval previous-actual capture event is estimated and allocated to the actual capture event. (Alternatively, individual FDR may also be estimated over time interval first-last capture, as shown above, and its value allocated to each capture event. It depends on the focus of the study whether *actual* or *overall* FDR is used.) The first capture in all capture-histories is then deleted (1 replaced by 0) in the capture-recapture data file such that only birds that were recaptured at least once remain. Next, a suitable number of classes (not too many) representing combinations of FDR and body mass at actual capture is created, and allocated to each capture event. The result is a matrix of multi-state capture histories. The procedure is summarized in Table 1.

The states represent different combinations of body mass and FDR, so specific hypotheses about their relationship to departure can be tested by appropriate constraints of state-specific emigration probabilities. With estimates of the unconstrained model ($\varepsilon_1 \neq \varepsilon_2 \neq \varepsilon_3 \neq \varepsilon_4$, where ε_r is the emigration probability of state r, see Table 1), interaction between FDR and body mass can be evaluated. To test whether the interaction is significant, we compare the former model with models where emigration is only a function of FDR ($\varepsilon_1 = \varepsilon_2$)$\neq$($\varepsilon_3 = \varepsilon_4$), only a function of body mass ($\varepsilon_1 = \varepsilon_3$)$\neq$($\varepsilon_2 = \varepsilon_4$), or dependent on neither FDR nor body mass ($\varepsilon_1 = \varepsilon_2 = \varepsilon_3 = \varepsilon_4$). By allowing for temporal variation of state-specific emigration probabilities, it can be assessed whether an environmental factor is taken into account in the departure decision. Models in which state-specific emigration probabilities are time-dependent need to be compared with models in which time-specific emigration probabilities are a function of an environmental factor. If the state-specific emigration probabilities are different functions of environmental factors, it is an indication of interaction between environmental and intrinsic factors. Appropriate model selection can become quite complicated when all aspects are considered, in particular because the recapture and the transition probabilities need to be modeled as well. Burnham and Anderson (1998) describe how model selection is done most efficiently. They emphasize the importance of creating a small list of working hypotheses prior to data analysis based on results from former studies.

5 Recommendations

The price of this framework is a large number of recaptured birds. Although ringing under standardized conditions has been carried out for years and will continue, problems may arise from sample sizes. If data are insufficient, there is a risk that some parameters in the models cannot be estimated, that the iteration process does not find the maximum of likelihood function (Lebreton and Pradel, 2002), or that parameter estimates are imprecise. Solutions to the problem of sample size may be either to analyze only one factor at once, or to analyze all factors except FDR. If FDR is excluded, all birds, not just those recaptured, can be used without reducing the sample size. As the sample size from one migration season may be too small, data for several years can then be pooled in a single analysis.

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Table 1 An example of how to prepare a capture history needed to test simultaneously the significance of environmental and intrinsic factors that regulate departure

1. Original capture history	0 10 0 11 12 0 12 0 0		
2. Calculate fuel deposition rate	0.5 1.0 0.0		
3. Delete first capture	0 0 0 $\binom{0.5}{11}$ $\binom{1.0}{12}$ 0 $\binom{0.0}{12}$ 0 0		
4. FER-body mass states	FDR/mass	<11.5	>11.5
	≤ 0	1	2
	> 0	3	4
5. Final capture history	0 0 0 3 4 0 2 0 0		

In the original capture history, capture is indicated by the body mass of the individual at time of capture, i.e., 10 = 10 g. FDR = fuel deposition rate.

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