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Analyzing movement behavior and dynamic space-use strategies among habitats using multi-event capture–recapture modeling

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Abstract

1. The environment of most species is heterogeneous at different spatial and temporal scales; this heterogeneity can have a direct effect on various components of fitness. As a consequence, individual space-use and movement strategies are central issues in ecology and conservation and receive considerable attention from researchers.
2. In the last 30 years, this issue has led to the development of capture–recapture models that allow movement between sites to be quantified, while handling imperfect

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detection. For studies involving numerous recapture sites in which the emphasis is on dispersal or migration rather than movement between particular sites, Lagrange et al. recently proposed a parsimonious CR multi-event model that contrasts individuals that move and individuals that stay in place, irrespective of the sites involved.

3. In this study, we developed a generalized version of this model to allow survival probability and movement probability to differ for different types of habitat to which the individual sites may be assigned. We investigated the potential of this new parameterization by studying the movements of an amphibian, the yellow-bellied toad (*Bombina variegata*), in a set of breeding and resting/foraging ponds.
4. Our capture-recapture multi-event model provides a highly flexible tool allowing users to model movements within and between several habitats. This approach can be potentially used to study movement behavior and space-use strategies of a wide range of taxa.

Key-words: capture–recapture, habitat selection, movement, dispersal, multi-event model, amphibian

Authors' contribution

Hugo Cayuela collected the data, performed the analyses and wrote the article. Roger Pradel supervised the analyses and wrote the article. Pierre Joly helped to collect the data. Aurélien Besnard supervised the analyses and wrote the article.

Introduction

The environment of most species is heterogeneous at different spatial and temporal scales; this heterogeneity can have a direct effect on a range of aspects concerning the fitness of organisms. Habitat selection, a complex, hierarchical behavioral process, is thus likely to be influenced by strong selective pressures (Cody 1985). Johnson (1980) identified four hierarchical levels of habitat selection: distribution range, home range in the distribution area, patch within a home range, and site (e.g. nest) or item (e.g. food) within a patch. As habitat selection takes place on a continuum from very coarse to very fine spatial scales, it involves a diverse range of strategies for space use and movement between locations, both between and within species (Bowler & Benton 2005; Sanz-Aguilar et al. 2005).

At interspecific level, a wide array of movement types occur in nature, varying from the daily vertical displacement of zooplankton and fish (Zaret & Suffern 1976; Scheuerell & Schindler 2003) and the routine inter-habitat movement of insects (Van Dyck & Baguette 2005) to the intercontinental seasonal migration of birds (Newton 2010) and the long-distance oceanic travels of sea turtles (Luschi 2003). At intraspecific scale, space-use and movement strategies between sites can vary according to age or ontogenetic stage (Mittelbach 1981). For instance, in many animals with a complex lifecycle (e.g. fish and aquatic invertebrates), juveniles grow up in nursery habitats with certain characteristics and then undertake rapid, directional movements to completely different habitats in adulthood (Beck et al. 2001). Individual space-use and movement strategies can also depend on gender and/or social state (Chapman et al. 2011). For example, males and females can differ in their habitat requirements, leading to gender-specific patterns of foraging and movement (Weissburg 1993; Gros et al. 2008). Intraspecific competition for limited food resources and social fences can also lead to heterogeneity in space use between subordinates and dominants (Gauthreaux 1982; Mysterud et al. 2011).

Direct and indirect methods exist to analyze individual space-use and movement strategies in heterogeneous environments. Indirect methods, such as biogeochemical markers, have received considerable attention from researchers (Post 2002). In particular, stable isotope measurements in animal tissues provide useful information about diet and the location of foraging areas (Rubenstein & Hobson 2004). Molecular approaches also provide useful tools for evaluating the likelihood that an individual originates from a given population among a set of putative sources (Berry et al. 2004). Although these methods allow movement patterns within coarse regions or populations to be studied, they cannot be used to infer relationships between landscape heterogeneity and individual space-use strategies on a fine scale. Direct methods, such as Global Positioning Systems (GPS) and other tracking devices, are also available for analyzing an animal's space use and movement with a high spatial resolution in real time (Patterson et al. 2008). However, despite continuous progress in the miniaturization of these devices, many animals are still too small to carry them without potential deleterious effects. These methods also remain expensive, limiting the number of individuals that can be surveyed and thus generating weakly generalizable results. Another set of methods, so-called capture–recapture (CR) methods (Nichols 1992), involve direct and repeated observations of an animal through individual recognition using various marking techniques (e.g. bands or tags) or an individual's natural markings (e.g. color pattern, visible scars). These CR methods allow a large number of individuals to be studied in order to estimate demographic parameters, including dispersal or migration between sites, but they require the use of specific models to take into account the fact that not all individuals are observed on a given resighting/recapture occasion.

Two main approaches have been used to model CR data in the context of movement (defined here as dispersion, migration or routine displacement of individuals between sites). Schwarz et al. (1993) and Brownie et al. (1993) first developed multisite CR models that

allow survival, recapture and transition probabilities between different localities to be modeled simultaneously while assuming first-order and second-order Markovian transitions respectively. However, these models involve estimating movement probability between all pairs of sites, which limits their use in practice to a small number of resighting locations (Lebreton et al. 2009).

Alternatively, Ovaskainen (2004) proposed a movement model for capture-recapture data based on diffusion equations that describe the actual path followed by an individual during dispersal or migration. By comparison, the multisite model of Arnason (1973) is a cruder model concerned only with the realized dispersal, that is, with the arrival site given a particular site of departure. Yet, when studying movements such as migration or dispersal among habitats, the actual path followed by individuals is often of no particular interest, and thus the diffusion model proposed by Ovaskainen (2004) may be unnecessarily complicated for the task. Indeed, it requires detailed data (especially precise locations of the individuals, a data that is not always available) and above all is very computationally intensive. On the other hand, an advantage of Ovaskainen's diffusion model over the classical multisite models was parsimony: when there are numerous sites involved, being at its core a diffusion model, the model requires a number of parameters proportional to the number of different habitats; conversely, the general multisite model includes a number of transition parameters proportional to the number of pairs of sites. As a consequence, when the number of sites is large, the multisite approach becomes rapidly intractable because the number of transitions between sites rapidly increases (as the square of the number of sites). However, Lagrange et al. (2014) have shown recently that the number of parameters of multisite models can be curtailed drastically by an appropriate parameterization when the specific sites are of no particular interest, nullifying the advantage of Ovaskainen's approach in terms of parsimony. Yet, Lagrange's model only allows homogenous habitats to be studied as all sites are

considered as strictly equivalent. In order to study movement among sites pertaining to different habitats, corresponding for instance to different requirements such as breeding, staging or wintering, the Lagrange's model must be adapted.

We hereby present a generalized version of the CR multi-event model proposed by Lagrange et al. (2014). By expanding the parameters' state-space, this extended version allows survival and movement probabilities to differ for the different types of habitats found in several recapture sites within the study area. Following a presentation of our CR multi-event model (in the next section), we illustrate its efficacy and interest by applying it to CR data collected on the yellow-bellied toad (*Bombina variegata*), an amphibian that breeds in small temporary ponds. Field observations suggest that differing aquatic habitat requirements during ontogenesis could lead to an age- or sex-biased pattern of space use and movement within yellow-bellied toad populations (Gyöngyvér 2011). In our empirical study, we examine how age and sex influence movement patterns between and within foraging/resting ponds and breeding ponds.

Materials and methods

MODEL DESCRIPTION: DEFINITION OF STATES AND EVENTS

In multievent models, a distinction is made between events and states (Pradel 2005). An event is what is observed in the field and thus coded in the individual capture history. This observation is related to the latent state of the individuals. Yet observations can come with a certain degree of uncertainty regarding the latent state. Multievent models aim at modeling this uncertainty in observation process using hidden Markov chains. The Lagrange et al. (2014) CR multi-event model is based on seven states that combine information about

whether or not an individual occupies the same site as on the previous capture occasion and information about whether or not the individual was/is captured at the previous and current occasions. The previous capture status determines whether the information about movement is available at the current occasion: if an individual was not captured at the previous occasion, there is no possibility of knowing whether it has moved or not; conversely, if it was captured, we have some chance (if we capture it again) to know what it did. Thus, because it determines the set of potential events at t , the capture status at $t-1$ must be incorporated into the codification of the individual's state.

We developed a generalized version of the Lagrange et al. (2014) CR multi-event model by allowing individuals to move between different habitats in addition to moving among sites within the same habitat. The states considered include the movement status, the previous and current capture statuses, and the current habitat occupied, which is a novelty relative to Lagrange et al. (2014). These elements are coded in the state designation in the following way. Individuals that occupy the same site as in the previous occasion are coded S for 'stayed'; else, they are coded M for 'moved'. These codes are prefixed by the previous capture status and suffixed by the current capture status (+ for 'captured', o for 'not captured'). Additionally, the state designation includes the current habitat. Without loss of generality, we assume in what follows that there are only two habitats, A and B. As an example, an individual +MA+ is an individual that was captured at $t-1$, has changed site (movement status M), and was captured at t in habitat A; note that this individual may have moved between two sites belonging to habitat A or between sites of different habitats (from habitat B to A). An individual +SB+ was captured both at $t-1$ and at t in the same site of habitat B. An individual oMA+ was not captured at $t-1$, and has moved to a new site in habitat A where it is captured at t ; at $t-1$, this individual may have been in a habitat B site or in another habitat A site. As in Lagrange et al. (2014), when an individual is not captured at t ,

information about its capture at $t-1$ becomes useless and we relinquish the distinction of states based on the capture status at $t-1$. With these rules, two habitats lead to the consideration of 13 states, 'dead' state included (see Table 1). Because the events coded in the capture histories reflect the information available to the observer at the time of capture, there are fewer events than states (seven vs. 13 in the two-habitat case), principally because the movement status is not attainable when the individual was not captured at the previous occasion (Fig. 1 and Table 2). For individuals captured at t and $t-1$, we attribute a code of 1 or 4 if they did not change sites and are in habitat A or B respectively, and 2 or 5 if they changed sites and are in habitat A or B respectively (whether they were in the other habitat or in another site of the same habitat at $t-1$ is unimportant). For individuals that were not captured at $t-1$ and are captured at t in habitat A or B, we attribute a code of 3 or 6 respectively, and individuals not captured at t are given a code of 0. Fig. 1 provides an example of a capture history for an individual captured at several sites within habitats A and B, and the corresponding encoding of events and potential states.

MODEL PARAMETERIZATION

Basic movement model

When an individual is captured for the first time, we know which habitat it occupies (A or B), but its movement status is unknown: if it is in A, its state is $oSA+$ or $oMA+$; if in B, $oSB+$ or $oMB+$. The simplest model will assume that successive movements are independent, i.e. the fact that an individual has just moved does not influence its probability of moving again. Then, the model is unable to determine whether an individual captured for the first time has just moved or not. Hence, the probability of $oSA+$ (resp. $oSB+$) as initial state cannot be

estimated separately from the probability of oMA+ (resp. oMB+) as initial state. Only their sum is estimable. To avoid overparameterization, we may arbitrarily pick one of the two undistinguishable states, say oSA+ (resp. oSB+), to represent the partially indeterminate state (as regards movement status) of an individual captured for the first time in habitat A (resp. B). As the movement status has no influence on the transitions that follow, this choice has no influence on the model.

In the transition from the state at time $t-1$ to that at time t , we distinguish four successive steps: (1) survival, (2) movement between habitats, (3) movement between sites within habitats, and finally (4) recapture or not. Each step is conditional on all previous steps. In keeping with the established presentation of multievent models (Pradel 2005), we use a matrix presentation where the rows correspond to time $t-1$, the columns to time t . Also, abiding by the convention set in Souchay et al. (2014), whenever a status element in the state descriptor is updated to its situation at t , it becomes bold (and stays bold throughout the following steps) (Fig. 2).

Step 1: Survival – Individuals survive with a probability ϕ , or die with a probability $1-\phi$ (ϕ may depend on the movement status) (Fig. 2). At this step, we can drop the information about whether or not the individual was captured at $t-2$ as this will not be used at time t . Thus from a possible departure point of 13 initial states, individuals can transit to one of 5 arrival intermediate states. For instance, individuals in states +SA+ and oSA+ at $t-1$ move to the same intermediate state A+ if they survive.

Step 2: Movement between habitats – Individuals that have survived between $t-1$ and t can change habitat with probability ψ or may stay in the same habitat with a probability $1-\psi$ (Fig. 2). For instance, an individual that was in habitat B at $t-1$ can stay in habitat B or move to habitat A. In this latter situation, we update as well the movement status since moving from B to A implies movement (in this case, the intermediate state designation includes an

M, either **MA** or **MB**, depending on the habitat occupied at t). This results in a transition matrix with 5 departure and 9 arrival intermediate states. For instance, individuals in the departure intermediate states **A+** and **Ao** will attain respectively the arrival intermediate states **+A** and **oA** if they stay in habitat A or else the arrival intermediate states **+MB** and **oMB** if they move to habitat B.

Step 3: Movement among sites within habitats – This step updates the movement status of individuals that survived and remained in the same habitat from $t-1$ to t (Fig. 2). These individuals may have stayed in the same site with a probability $1-\alpha$ or moved to another site in the same habitat with a probability α . If they stayed in the same site, their movement status is updated to **S**, either **SA** or **SB**, depending on the habitat occupied. Alternatively, if they changed site, their status is updated to **M**, either **MA** or **MB**, depending on the habitat occupied. This results in a transition matrix with 9 departure and 9 arrival intermediate states. For example, individuals in the intermediate states **+A** and **oA** will then be respectively in the intermediate states **+SA** and **oSA** if they stayed in the same site or else be in the states **+MA** and **oMA** if they moved to another site in habitat A.

Step 4: Recapture or not – This step is an update of the recapture status (Fig. 2). Dead individuals are unobservable and thus have a capture probability of 0. For all other situations, individuals can either be captured with a probability p or not captured with a probability $1-p$ and their capture probability may depend on their movement status, on the habitat they occupy, and whether or not they were captured at $t-1$ (trap-dependence, see Pradel & Sanz-Aguilar 2012). This results in a transition matrix with 9 departure intermediate states and 13 arrival states at time t . For example, individuals in the departure intermediate states **+SA** and **oSA** will then be respectively in the intermediate states **+SA+** and **oSA+** if they are captured at t or else in the same state **SAo** if they are not captured.

The last component of the model links events to states. In this specific situation, each state corresponds to only one possible event (Fig. 2).

It is easy to generalize to more than two habitats. For illustration, an extended version of this model including four habitat types is presented in Appendix A.

Model with correlated successive movements

Analyzing how past dispersal or migration status of individuals may affect their current movement behavior is of critical interest for biologists. For that purpose, we propose an extension of the model described above that keeps track of the previous movement status along the first transition steps in order to allow to apply different movement parameters to individuals that moved and to individuals that stayed. The basic data are unchanged and the same 13 states and 7 events remain (see Table 1 and Fig. 3). Yet, along transition steps 1 to 3, we will consider a richer set of intermediate states.

Step 1: Survival – Contrary to the previous model, the arrival intermediate states must retain the movement status as it will be relevant in the subsequent steps. As a consequence, the number of arrival intermediate states increases to 9 (Table 1 and Fig. 3).

Step 2: Movement between habitats – For individuals that change habitat, the movement status is updated as in the previous model. However, for those that remain in the same habitat, the previous movement status is now retained as it may influence movement among sites within the habitat in the next step. The matrix has 9 states of departure and 13 states of arrival (Fig. 3). Movement behavior is made dependent on the individual's previous movement status ('stayed' vs 'moved') by forcing different ψ values for the rows 1, 3, 5, and 7 (resident) and for the rows 2, 4, 6, and 8 (disperser).

Step 3: Movement among sites within habitats – This is the last time the information about the previous movement will be used. Thus, we no longer need to retain it in the arrival intermediate states, which consequently include only the *current* movement status (in bold) as in the previous model. The matrix for this step has 13 states of departure and 13 states of arrival (Fig. 3). To account for the correlation of the current movement with the previous movement, the α values of rows 1, 4, 7, and 10 (previously residents) are allowed to differ from those of rows 3, 6, 9, and 12 (previously dispersers).

The recapture (Step 4) and event matrices are similar to those of the previous model.

CASE STUDY: USING THE MODEL ON THE YELLOW-BELLIED TOAD

Yellow-bellied toad data

The yellow-bellied toad (*Bombina variegata*) is an anuran that during the breeding season occupies both breeding ponds (water bodies exposed to the sun with little aquatic vegetation) and non-breeding ponds (more densely vegetated water bodies in shaded areas), where individuals may forage or take shelter during periods of drought (Cayuela et al. 2011; Gyöngyvér 2011). The data was collected in a population located along a 300-m segment of river in Ardèche in southern France where toads occupy a set of 187 rocky pools used either for reproduction activities (male calling, mating and egg deposition) or for non-breeding activities (resting, foraging). The toads were intensively surveyed using the CR method over a three-year period (2010–2012). Each year, three sets (each set is considered a ‘primary period’) of three capture sessions (each capture session is considered a ‘secondary session’) were carried out during the breeding season. Within a primary period, the time separating two secondary capture sessions was 24 hours, while the time between each primary period was

one month (one in April, one in May and one in June). At each capture session, we sampled all the ponds located along the surveyed river segment. Toads were caught, stored for less than 10 minutes for measurement and then released back to their pond of origin. An individual was identified by the unique pattern of black and yellow mottles on its belly, which was recorded by photographs (see Cayuela et al. 2014). We considered three ontogenetic stages: juveniles (captured after their first overwintering), subadults (captured after their second overwintering), and sexually mature adults (captured after at least three overwinterings); individuals only changed age class between years (see Cayuela et al. 2016). Details concerning the number of toads captured during the study period are provided in Appendix C.

Building biological scenarios

The two models described above were implemented in the E-SURGE program (Choquet et al. 2009) and applied to the yellow-bellied toad dataset. We present the outputs of two parsimonious versions, one of each type, in Appendix B, as well as a detailed description of their implementation in E-SURGE. It appears that successive movements are positively correlated as individuals that moved are more likely to move again. Yet, these models do not describe correctly the yellow-bellied toad system which has an additional terrestrial habitat where toads are not capturable and thus unobservable. We take this opportunity to show how the proposed framework can be adapted to closely fit the ecology of a particular system (the matrices of this specific model are provided in Appendix C). To account for the possibility that toads may reach terrestrial sites where capture cannot occur, we allowed individuals to move between monitored (i.e. ponds) and unmonitored sites (i.e. terrestrial habitats). For the use of unobservable sites in capture-recapture framework, see for instance Cayuela et al.

(2014) or Sanz-Aguilar et al. (2016). We also considered movements between aquatic sites (occupied during the activity period), including two categories of ponds: breeding ponds where mating and oviposition occur (type A); non-breeding ponds where individuals may forage or take shelter (type B). Movement can therefore occur among ponds of the same category (i.e. supplementation movement) or among ponds that differ in their biological functions (i.e. complementation movement). The movement probabilities between the different types of sites followed a nested process: first, individuals may move between aquatic sites (i.e. either non-breeding or breeding) and terrestrial sites; second, when staying in aquatic sites, individuals may move between resting and breeding sites; third, when staying in the same aquatic habitat, individuals may move to a different site. We modeled monthly (between primary periods) and daily (between secondary sessions) movements between and within habitats on an intra-season scale only. The data recorded over the successive years were not treated longitudinally: the three years of the study were 'aligned' and analyzed simultaneously. The encounter histories of the individuals captured at at least one of the nine primary periods during the three years of study were pooled in a single one-year long dataset and a year effect was integrated in the model as a group effect to account for potential year-specific variations (noted Y). For instance, an individual captured during the three years of the study has led to the consideration of three different CR histories in our dataset.

We built a model, $[\phi(\text{AS} + \text{Y}), \gamma(\text{AS} + \text{Y}), \psi(\text{AS} + \text{Y}), P(\text{AS})]$, where all the parameters (except recapture) depended on year (Y) as well as age and sex (AS), which was coded as a group effect in the model including four modalities: unsexed juvenile, unsexed subadult, adult female and adult male. Note that, between secondary sessions (daily scale), survival and movements between terrestrial and aquatic sites was held constant. Furthermore, because identifiability issues are a well-known problem in CR models including ghost sites

(see for instance Sanz-Aguilar et al. 2016), we therefore checked parameter identifiability using E-SURGE diagnostic (Choquet et al. 2009).

Results

First, two models with a reduced number of parameters were run to show the efficiency of the basic model and of the model including a memory of the past movement status of individuals.

The model outputs provided in Appendix B (Tables B1 and B2) show that all the parameters (i.e. survival, between-habitats movements, within-habitat movements and recapture) are correctly estimated and identifiable.

Second, our empirical case well illustrates the flexibility of the modeling system (see model outputs in Fig. 4). E-SURGE diagnostic indicated the absence of parameter identifiability issues. Monthly survival ϕ (Appendix C, Fig.C1, STEP 1) slightly varied between years and increased with ontogenetic stages. Concerning movements between water and land (Appendix C, Fig.C1, STEP 2), the probability of movement γ varied between years and was relatively similar between ontogenetic stages (Fig.4). Nevertheless, subadults had a higher probability of moving again in aquatic habitats after being on land. Regarding between-habitats (Appendix C, Fig.C1, STEP 3) and within-habitat movements (Appendix C, Fig.C1, STEP 4), the movement probabilities ψ and α differed between years and ontogenetic stages and depended on the function of the water body (i.e. if the habitat was for reproduction or non-breeding activities) (Fig. 4). Juveniles had the lowest movement probability regardless of the type of pond and more frequently moved to non-breeding than to breeding ponds. Subadults had a higher movement probability and frequently moved between breeding and non-breeding ponds. Adults had the highest movement probability, indicating intense routine movement between breeding and resting/foraging sites and among sites of the same category.

When they were in non-breeding ponds, males more frequently moved to breeding ponds than females did. Conversely, when they occupied a breeding pond, females had a higher probability to move to a non-breeding pond. Moreover, movement probability of adults among ponds of the same category was higher in breeding ponds than in non-breeding ponds.

Discussion

The modeling system described in this paper is designed to estimate survival and movement between and within habitats when recapture probability is below 1. As in the model developed by Lagrange et al. (2014), our approach permits dispersal flow to be modeled among multiple sites while circumventing the computational issue encountered in standard multisite models. Yet while the Lagrange et al. (2014) model estimates dispersal only among homogeneous sites, our model allows movement behavior to be examined between qualitatively heterogeneous sites, which is a parameter of particular interest in ecology.

Our empirical case study is a good illustration of the usefulness of this approach in investigating movement and space-use strategies in heterogeneous environments. We were able to detect sex-, age- and time-specific differences in both intra- and inter-habitat movement probabilities. We found that there is a low probability of juveniles moving between ponds, likely due to their small body size and low vagility (Beshkov & Jameson 1980). They also often remain in non-breeding ponds, suggesting that juvenile anurans may use aquatic nursery zones for feeding and/or sheltering during their post-metamorphosis development, as has been previously shown in other vertebrates (bird: Hockey et al. 2003; fish: Sheaves et al. 2006). Our results also indicate that habitat requirements may vary between genders. We found that females more often move to non-breeding aquatic habitats where they likely forage (Gyöngyvér 2011) in order to continuously produce oocytes

throughout the breeding activity period (Guarino et al. 1998) and where they are presumably less affected by forced copulation and male harassment. In contrast, males more often move to breeding ponds, presumably to increase mating opportunities and to find suitable breeding sites (Wells 2010).

Although our case study deals with amphibians, this approach could be used to investigate the dispersal or migration in heterogeneous and spatially structured environments of any organisms that can be surveyed using CR methods. Furthermore, while our case study focused on intra-annual movements, the approach also allows inter-annual transition probability to be modeled (or both situations together, using a Robust Design approach as we did at an intra-seasonal scale). It should allow the investigation of individual space-use strategies in organisms that use multiple habitats at different stages of their lifecycle. For instance, in large mammals such as the Mediterranean mouflon, female movement patterns between foraging and sheltering areas differ between the lambing period and the remainder of the year (Marchand et al. 2015) as well as differing from those of males. Moreover, our model allows habitat-specific dispersal decisions to be studied. For example, studying how colonial birds use both individual (their own breeding success) and public (conspecific breeding success) information to ‘make the decision’ to disperse (see for instance Serrano et al. 2001). One could also investigate how introduced species may affect dispersal behavior in native organisms (see for instance the case of introduced predators in colonial birds, Igual et al. 2007). Furthermore, our modeling system could help to optimize management policies by allowing conservationists to examine the effects of conservation measures on survival and movement behavior in endangered species (Libois et al. 2012). This model could also be applied to the investigation of dispersal strategies at different spatial levels. While it cannot explicitly include Euclidean distances between recapture sites to improve dispersal estimates, it could allow this issue to be studied by quantifying dispersal while accounting for spatial

structuration (the position and isolation of recapture sites) at a landscape scale. For instance, in colonial sea birds this approach could allow the simultaneous modeling of site fidelity at different nested spatial levels, i.e. a nest site incorporated in a colony on an island, which may itself be embedded in an island archipelago.

In theory, our approach is highly flexible, allowing users to model movements between a large number of habitats. In practice, it should be noted that as the number of habitats increases both dataset coding and model implementation may become technically challenging as the number of states and events dramatically increase with the number of habitats. Yet, the model presented in Appendix A (including four types of habitat) shows that the matrices keep a relatively simple structure even when incorporating additional habitats. Indeed, the 6 states corresponding to a single habitat are simply added in the matrices through copying-pasting entire blocks of the previous matrices, which actually makes model implementation straightforward. Thus, additional habitats can be easily included in the model following this example.

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SUPPORTING INFORMATION

APPENDIX S1. Model including four habitats.

APPENDIX S2. Additional information regarding the model and its implementation in the E-SURGE program

APPENDIX S2. Empirical case using CR data on *Bombina variegata*

Table 1. Description of the 13 states of the two-habitat CR multi-event model. The state formulation includes four pieces of information: ‘S’ for ‘stayed’, ‘M’ for ‘moved’, ‘+’ for ‘captured’ and ‘o’ for not captured.

State	State description
+SA+	Captured at $t-1$ and t in the same site of habitat A
+MA+	Captured at t in a site of habitat A different from the site where captured at $t-1$
+SB+	Captured at $t-1$ and t in the same site of habitat B
+MB+	Captured at t in a site of habitat B different from the site where captured at $t-1$
oSA+	Captured at t in the same site of habitat A occupied at $t-1$ when not captured
oMA+	Captured at t in a site of habitat A different from the site occupied at $t-1$ when not captured
oSB+	Captured at t in the same site of habitat B occupied at $t-1$ when not captured
oMB+	Captured at t in a site of habitat B different from the site occupied at $t-1$ when not captured
SAo	Not captured at t and in the same site of habitat A as at $t-1$
MAo	Not captured at t and in a site of habitat A different from the site occupied at $t-1$
SBo	Not captured at t and in the same site of habitat B as at $t-1$
MBo	Not captured at t and in a site of habitat B different from the site occupied at $t-1$
D	Dead

Table 2. Possible events of the CR two-habitat multi-event model and their codes.

Code	Possible events
0	Not captured
1	Captured in same site of habitat A as at $t-1$
2	Captured in a site of habitat A, captured at $t-1$ in a different site
3	Captured in a site of habitat A, not captured at $t-1$
4	Captured in same site of habitat B as at $t-1$
5	Captured in a site of habitat B, captured at $t-1$ in a different site
6	Captured in a site of habitat B, not captured at $t-1$

Fig. 1. Example of a capture history. The top level lists the sites (A1 and A2 are two sites within habitat A; B1 and B2 are two sites within habitat B) where individuals are captured; a question mark indicates that the individual is not captured at this time. The intermediate level gives the event code of the capture history. The bottom level shows the corresponding set of potential states as identified in Table 1 and Fig. 2.

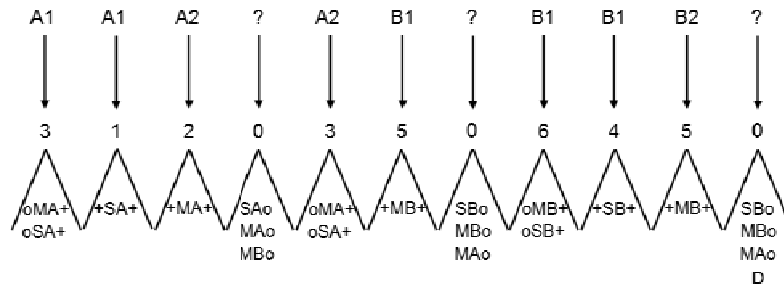


Fig. 2. Simplest model parameterization: matrices of initial states of departure, state–state transitions and events. The definition of the states and events is provided in Table 1 and Table 2 respectively. Four state-state transition steps are considered in the model: survival probability ϕ , between-habitats movement probability ψ , within-habitat movement probability α and recapture probability p are successively considered.

Initial states of departure												
+SA+	+MA+	+SB+	+MB+	oSA+	oMA+	oSB+	oMB+	SAo	MAo	SBo	MBo	
(0 0 0 0 i 0 $1-i$ 0 0 0 0 0)												
Step 1: Survival												
+SA+	+MA+	+SB+	+MB+	oSA+	oMA+	oSB+	oMB+	SAo	MAo	SBo	MBo	
(0 0 0 0 ϕ 0 0 0 0 0 0 0)												
Step 2: Movements between habitats												
+A	+MB	+B	+MA	oA	oMB	oB	oMA	D				
(0 0 0 0 $1-\psi$ ψ 0 0 0 0 0 0)												
Step 3: Movements within habitats												
+A	+MA	+SB	+MB	oSA	oMA	oSB	oMB	D				
(0 0 0 0 $1-\alpha$ α 0 0 0 0 0 0)												
Step 4: Recapture												
+SA	+MA	+SB	+MB	oSA	oMA	oSB	oMB	SAo	MAo	SBo	MBo	D
(0 0 0 0 0 0 0 0 0 0 0 0 $1-p$ 0 0 0 0)												
Events												
+SA+	+MA+	+SB+	+MB+	oSA+	oMA+	oSB+	oMB+	SAo	MAo	SBo	MBo	D
(0 1 0 0 0 0 0 0 0 0 0 0 0)												

Fig. 3. Model parameterization including individual past dispersal status: matrices of initial states of departure, state–state transitions (one for each of the four steps considered in our model) and events. Four transition steps are considered in the model: survival probability ϕ , between-habitats movement probability ψ , within-habitat movement probability α and recapture probability p are successively considered.

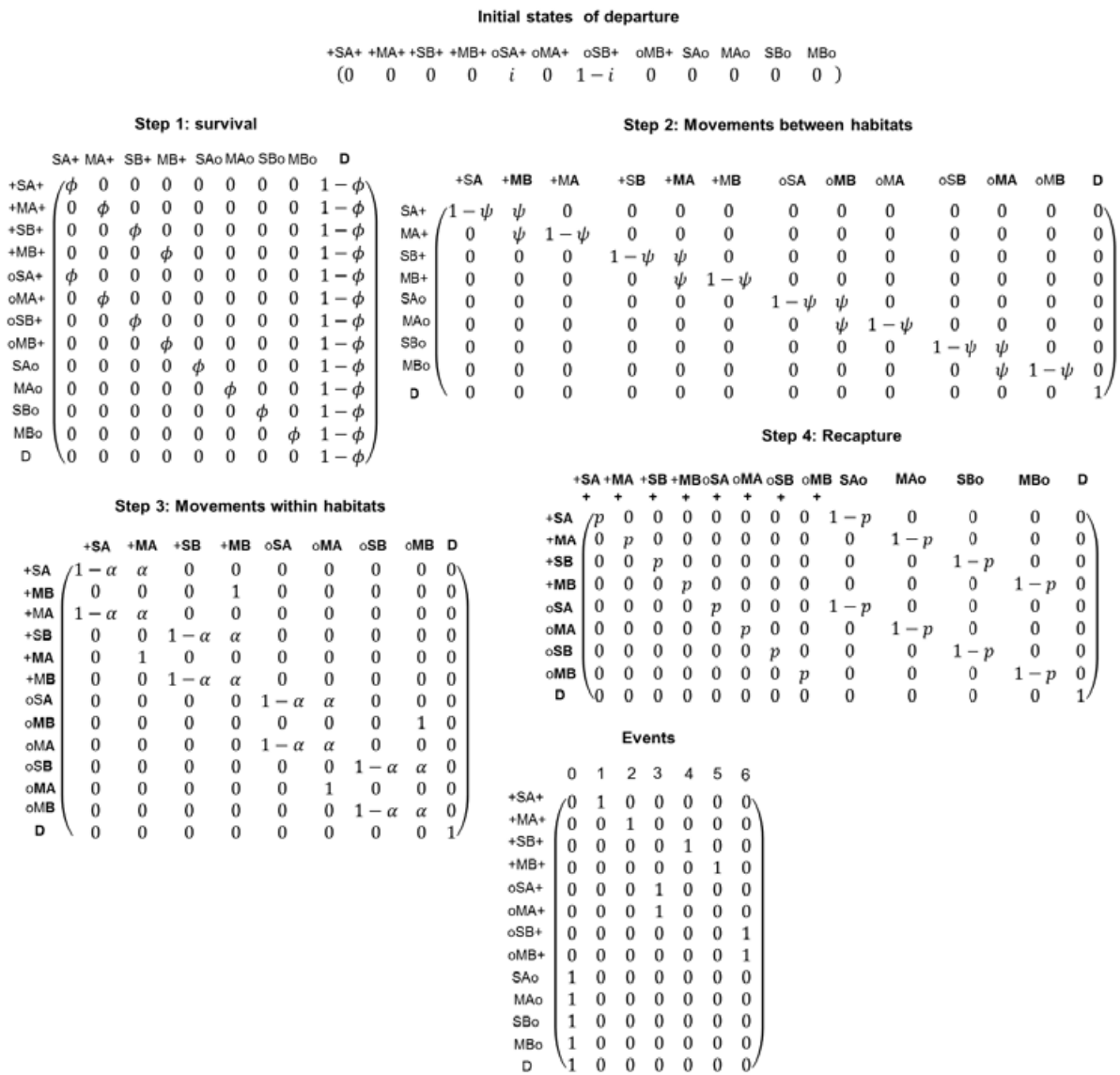


Fig. 4. Empirical case: survival and movement in yellow-bellied toad. Monthly survival (A) and monthly movement between aquatic and terrestrial habitats (B and C) differ between years and ontogenetic stages: juveniles (empty circle), subadults (full circle), sexually mature males (empty square) and sexually mature female (full square). The movement between breeding and non-breeding ponds (daily, D and F; monthly E and G) and the movement among ponds of the same category (daily, H and J; monthly I and K) also vary between years and ontogenetic stages.

