

# Assessing the effect on survival of natal dispersal using multistate capture–recapture models

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**Abstract.** Despite their crucial importance in understanding and modeling of the evolution of natal dispersal, it is still difficult to reliably estimate the costs of natal dispersal. We have developed a multistate capture–recapture model, mixing telemetry and recoveries, to simultaneously estimate natal dispersal probability, survival probability of dispersers vs. philopatric individuals, and the proportions of individuals dying from different causes. By applying this model to the European hare (*Lepus europaeus*), we show that dispersing juveniles suffer from a considerably higher mortality rate during their first post-weaning year compared to philopatric juveniles, due to both hunters and predators. We emphasize the usefulness and reliability of our model in the broader context of studies of natal dispersal costs, as well as the evolutionary and management implications of such a dispersal cost in declining European hare populations.

**Key words:** dispersal costs; European hare; France; *Lepus europaeus*; multistate capture–recapture models; natal dispersal; recoveries; telemetry.

## INTRODUCTION

Dispersal is a crucial parameter in evolutionary biology and ecology due to its influence on individual fitness, gene flow, effective population size and genetic drift, local adaptation, inbreeding, colonization, and long-term persistence of populations and species (for a review, see Clobert et al. 2001). One central assumption of most theoretical models of the evolution of dispersal is that dispersers incur fitness costs and that the relative cost/benefit ratios of dispersal vs. philopatry shape the degree and extent of dispersal (Johnson and Gaines 1990, Gandon and Michalakis 2001). Thus, to understand the evolutionary and proximate causes of dispersal as well as its genetic and demographic consequences, we need to know the fates of dispersers. Emigration and settlement in a new habitat change the social, physical, and genetic environment to which individuals are exposed. Hence, dispersers theoretically face higher mortality risks and lower reproductive success than philopatric individuals for several reasons. Increased predation and human-mediated mortality (e.g., Isbell and Van Vuren 1996), aggression, stress, lack of knowledge of good quality foraging sites and shelters (e.g., Spinks et al. 2000), absence of kin (e.g., Lambin 1994), difficulty in finding a mate, and reduced fecundity (e.g., Alberts and Altmann 1995) are usually invoked as

major dispersal costs due to the movement across and the settlement into an unfamiliar habitat.

Previous studies have attempted to compare survival rates of dispersers and philopatric individuals during transience or after settlement with mixed results (for a review, see Belichon et al. 1996). Unfortunately, quantitative measures of dispersal costs in terms of survival are rare (see VanVuren and Armitage 1994, Alberts and Altmann 1995, Gillis and Krebs 2000, for examples) and suffer from potential biases. Indeed, the comparison of survival rates between dispersers and philopatric individuals born in the same study area has seldom been undertaken because it is difficult to monitor dispersers after they have left their natal area. Therefore, the difference in survival rates between immigrants and residents within a focal study area is often used as a measure of dispersal costs. However, as immigrants and residents do not grow up in the same habitat, such a difference in survival might reflect a difference in natal habitat. In addition, a lack of difference does not mean that dispersal is not costly because the survival of immigrants is investigated after settlement, and thus, dispersal costs due to transience are missed. Tracking individuals during dispersal and settlement, possibly by telemetry, is thus seen as the best way to investigate dispersal costs (McShea and Madisson 1992, Small et al. 1993, Larsen and Boutin 1994, Gillis and Krebs 2000).

We recently took advantage of an intensive telemetry monitoring of a European hare (*Lepus europaeus*; see Plate 1) population to provide a very detailed description of the natal dispersal pattern in this species (Bray et al. 2007). To further our understanding of both the

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evolutionary causes and the management implications of natal dispersal in a given species, it is necessary to investigate the fitness consequences of natal dispersal, the so-called cost/benefit ratio of dispersal. To do so, we built individual multistate capture–recapture histories including dispersal (disperser vs. philopatric) and mortality (hunting, predation, and other causes) states. A juvenile hare is philopatric at birth, and then, during each trapping interval, it may either survive or die. If it survives, it may either disperse or not, and if it dies, it may die from different mortality causes. Multistate capture–recapture (MS-CR) models that combine two different types of competing events in individual history data (Pollock et al. 1995, Lebreton et al. 1999, Lebreton and Pradel 2002) provide an ideal framework to investigate the pattern of variability of transition probabilities within and between the successive states taken by an individual. Here, we develop a MS-CR model to analyze MS capture histories that combine information on telemetry locations and dead recoveries. This formulation allowed us to estimate, simultaneously, the natal dispersal probability, the costs of dispersal on survival, and the proportions of individual that died from different mortality causes. Following on from previous works by Grosbois and Tavecchia (2003) and Schaub and Pradel (2004), this allowed us to assess the effect of dispersal state (philopatric vs. disperser) alone or in combination with factors such as the sex of individuals, the period of the year (hunting vs. nonhunting), or the density of the birth zone, on first-year survival probability.

## METHODS

### *Study site, telemetry, and natal dispersal pattern*

The study area (Chareil-Montord, France, 46°18' N, 3°17' E) is characterized by mixed-cropping–livestock farming (see Bray and Léonard 2000 for details). Two zones differing in hunting pressure and density are delimited within the study area: the hunting zone (HZ, 14 hares/km<sup>2</sup>, 12.3 km<sup>2</sup>) and the nonhunting one (NHZ, 49 hares/km<sup>2</sup>, 2.43 km<sup>2</sup>; Péroux et al. 1997). Hunting is allowed in the HZ only in September, October, and November each year. During 1994–1996 from May to October each year, we trapped juvenile hares using unbaited box traps (Bray and Léonard 2000). The juveniles were then equipped with ear tags (“TIP-TAG” type) and radio transmitters (TXP2, 50 g, 3000-m range, battery life 16 months; Televilt, Lindsberg, Sweden). For each first capture, trap location, sex, body mass (g), and skull length (mm) were recorded. Age (in days) of juveniles at first capture was then estimated using different methods depending on their skull length and body mass (see Bray et al. 2007). Telemetry locations were recorded by triangulation using a hand-held five-element Yagi antenna (Televilt, Lindsberg, Sweden). Additional information on hare presence was recorded visually.

Consistent with expectations in a promiscuous-polygynous mating system (Dobson 1982), we have recently shown that juvenile male European hares dispersed more than females in two zones with different population density (Bray et al. 2007). Both males and females dispersed preferentially when they reached physiological sexual maturity between four and six months of age, thus becoming potential competitors for local resources (mates and food). The dispersal rates increased with decreasing density and were independent of potential disturbance caused by hunting. Finally, females seemed to disperse farther than males and natal dispersal distance was not related to the population density.

### *Data used for analysis*

The three-year monitoring of European hares is summarized in capture–recapture histories including information on their presence and dispersal state (Appendix A) at capture occasions occurring once every two weeks from 1 May to 15 March each year (22 capture occasions). We used the previous results of Bray et al. (2007) to define the dispersal state for each individual at each capture occasion. We used a restricted data set incorporating only philopatric and “one-way” dispersing hares (Bray et al. 2007) that informed us precisely of the time of dispersal. “One-way” dispersing hares are hares that suddenly change their home range by making a one-way and permanent movement to establish in a new home range disjunctive from the previous one (Appendix A). Since dispersal occurs only after hares are 90 days old, the first capture of the individuals was recorded when they were aged between 73 and 90 days, even if their monitoring began earlier. The survival analyses were performed using the capture–recapture histories of 74 juvenile hares (39 females and 35 males). Of those 74 juveniles, 49 and 25 were born in the NHZ and in the HZ, respectively and, 17, 31, and 26 were monitored in 1994, 1995, and 1996, respectively. Over all years, 29 juveniles (15 females, 14 males) were still alive at the end of monitoring in mid-March. We determined the mortality cause for each of the 45 juveniles that died during monitoring. Deaths of 18 juveniles could definitively be attributed to hunting. For 19 other juveniles, predation was the most plausible cause of mortality, as small carnivore bites were found on the corpse. Only eight other juveniles died from other (road, disease) or undefined causes. Finally, 46 were still philopatric at the end of monitoring and 28 had dispersed during their first year of life.

### *Modeling survival of dispersers vs. philopatric hares using MS-CR models*

Multistate capture–recapture (MS-CR) models combining two different types of competing events were used: live relocations and dead relocations or recoveries (Pollock et al. 1995, Lebreton et al. 1999, Lebreton and Pradel 2002). The general parameterization of the Pollock et al. (1995) model can be written as a product

of the matrix of survival–transition probabilities between states from time  $t$  to  $t + 1$  (departure states in rows, arrival states in columns) by the associated vector of state-specific capture probabilities in the multistate framework:

$$A \begin{bmatrix} s\delta & (1-s)\delta & 0 \\ 0 & 0 & 1 \\ 0 & 0 & 1 \end{bmatrix} \begin{bmatrix} p \\ p \\ 0 \end{bmatrix}$$

where  $A$  is the state “alive,” ND is the state “newly dead,” † is the state “dead since more than one time interval,”  $s$  is the survival probability,  $\delta$  is the probability of remaining in the study area, and  $p$  is the probability of detection of a live and of a dead animal (assumed to be equal in the Pollock et al. [1995] parameterization). The state † is an absorbing state, so it is not necessary to include it explicitly in MS models (Lebreton et al. 1999). Note that  $\delta$  was fixed to 1 because all the monitored hares stayed within the study area. This parameter will thus not appear and the matrix of survival–transition probabilities becomes row stochastic, i.e., the sum of the row elements equals to 1, when  $\delta$  equals 1. Note also that the probabilities of detection  $p$  for a live and for a dead animal were all equal to 1 in our study (whatever the mortality cause) because (1) we used telemetry data; (2) we did not lose any signal and we recovered all the dead animals. The simplified version of the Pollock et al. (1995) model is now

$$A \begin{bmatrix} s & 1-s & 0 \\ 0 & 0 & 1 \\ 0 & 0 & 1 \end{bmatrix} \begin{bmatrix} 1 \\ 1 \\ 0 \end{bmatrix}$$

We then extended this general model to several causes of mortality (see Schaub and Pradel 2004 for a similar application for recovery data) acting on two different dispersal states.

Indeed, a marked animal may survive from time  $t$  to time  $t + 1$  with probability  $s$ , or it may die with probability  $(1 - s)$ . Conditional on mortality, it may die either from hunting (H) with probability  $\alpha$ , from predation (P) with probability  $\beta$ , or from other causes of mortality (O) with probability  $(1 - \alpha - \beta)$ . Conditional on survival, it may disperse inside the study area (see Bray et al. 2007) with probability  $d$  or remain philopatric with probability  $(1 - d)$ . Note that in this formulation dispersal occurs only once and that a disperser cannot become philopatric again later.

We adopted the MS-CR framework developed by Grosbois and Tavecchia (2003) to model the transition probabilities between states because dispersal is conditional on survival, and the determination of the mortality cause is conditional on mortality. In such a case, these authors proposed to subdivide the transition probability between states from time  $t$  to  $t + 1$  in a sequence of successive transition matrices incorporating some unobservable intermediate states (Grosbois and Tavecchia 2003). In such models, the transition between

states are modeled as first-order Markov processes, so that the “arrival” state of an individual at time  $t + 1$  depends only on the “departure” state at time  $t$  (i.e., no-memory model). As the probability of detection of any state at time  $t + 1$  depends only on the “arrival” state, the model described thereafter belongs to the Arnason-Schwarz family of models (Arnason 1972).

Here, the fate of any marked individual between time  $t$  and  $t + 1$  can thus be viewed as a three-step process, and the transition probability matrix  $\Phi$  can be written as a product of three successive transition matrices,  $\Phi = \mathbf{DMS}$ , with survival (matrix  $\mathbf{S}$ ) occurring before the attribution of mortality type (matrix  $\mathbf{M}$ ), which occurs before dispersal (matrix  $\mathbf{D}$ ). We chose this three-step formulation because we think that such a formulation is easier to understand at first sight for the reader, but we acknowledge that the above three-step process can be rewritten in a two-step process (survival step, and then dispersal–mortality cause step).

Hence the state vector  $\mathbf{n}_{t+1}$  giving the expected number of individuals in each state at time  $t + 1$  can be computed from the state vector  $\mathbf{n}_t$  at time  $t$  as follows:

$$\mathbf{n}_{t+1} = \Phi \cdot \mathbf{n}_t$$

with  $\Phi = \mathbf{DMS}$  and

$$\mathbf{n}_t = \begin{pmatrix} P \\ D \\ \text{NDH} \\ \text{NDP} \\ \text{NDO} \\ \dagger \end{pmatrix}$$

in which  $P$  is the state philopatric,  $D$  the state disperser, † the state dead since more than one time interval, NDH the state newly dead hunting (i.e., a hare whose mortality cause was hunting), NDP the state newly dead predation, and NDO the state newly dead other.

The initial survival process involving the transition from  $\mathbf{n}_t$  to the first unobservable intermediate state vector  $\mathbf{s}_{t+1}$  using the matrix  $\mathbf{S}$  is given by

$$\mathbf{s}_{t+1} = \begin{pmatrix} A_p \\ A_d \\ \text{ND}_p \\ \text{ND}_d \\ \dagger \end{pmatrix}_{t+1}$$

$$= \begin{pmatrix} s_p & 0 & 0 & 0 & 0 & 0 \\ 0 & s_d & 0 & 0 & 0 & 0 \\ 1-s_p & 0 & 0 & 0 & 0 & 0 \\ 0 & 1-s_d & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 1 & 1 & 1 \end{pmatrix} \begin{pmatrix} P \\ D \\ \text{NDH} \\ \text{NDP} \\ \text{NDO} \\ \dagger \end{pmatrix}$$

in which  $A_p$  is the state alive philopatric (i.e., a living philopatric hare that has not yet dispersed),  $A_d$  the state

alive disperser,  $ND_p$  the state newly dead philopatric (i.e., a philopatric hare that died during the considered time interval), and  $ND_d$  the state newly dead disperser;  $s$  is the probability of survival for philopatric ( $s_p$ ) or dispersing ( $s_d$ ) hares.

The mortality process involving the transition between the two unobservable intermediate state vector  $\mathbf{s}_{t+1}$  and  $\mathbf{m}_{t+1}$  using the matrix  $\mathbf{M}$  is given by

$$\begin{pmatrix} \mathbf{m}_{t+1} \\ A_p \\ A_d \\ NDH \\ NDP \\ NDO \\ \dagger \end{pmatrix}_{t+1} = \overbrace{\begin{pmatrix} 1 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & \alpha_p & \alpha_d & 0 \\ 0 & 0 & \beta_p & \beta_d & 0 \\ 0 & 0 & 1 - \alpha_p - \beta_p & 1 - \alpha_d - \beta_d & 0 \\ 0 & 0 & 0 & 0 & 1 \end{pmatrix}}^{\mathbf{M}} \times \begin{pmatrix} \mathbf{s}_{t+1} \\ A_p \\ A_d \\ ND_p \\ ND_d \\ \dagger \end{pmatrix}_{t+1}$$

in which  $\alpha_p$  and  $\alpha_d$ ,  $\beta_p$  and  $\beta_d$  are the proportions of philopatric (p) and dispersing (d) individuals that died respectively from hunting and predation. Lastly the dispersal process is modeled using the matrix  $\mathbf{D}$  as follows:

$$\begin{pmatrix} \mathbf{n}_{t+1} \\ P \\ D \\ NDH \\ NDP \\ NDO \\ \dagger \end{pmatrix}_{t+1} = \overbrace{\begin{pmatrix} 1-d & 0 & 0 & 0 & 0 \\ d & 1 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 0 & 1 \end{pmatrix}}^{\mathbf{D}} \begin{pmatrix} \mathbf{n}_{t+1} \\ A_p \\ A_d \\ NDH \\ NDP \\ NDO \\ \dagger \end{pmatrix}_{t+1}$$

in which  $d$  is the probability of dispersal from time  $t$  to  $t + 1$ . Note that in this parameterization, the survival probability differs between the states  $P$  and  $D$ , as well as the proportion of individuals dying from hunting ( $\alpha$ ) and predation ( $\beta$ ).

*The basic MS-CR model*

We aim to test for the effects of state (philopatric vs. disperser), sex, and birth zone (NHZ vs. HZ) on both survival probability  $s$ , dispersal rate  $d$ , and the proportions of individual dying from different mortality causes  $\alpha$ ,  $\beta$ , and  $1 - \alpha - \beta$ . We defined thus a general model using the following structures as a basis for the selection of alternative models. For the survival probability  $s$ , we started with a three-way interaction model named  $S_{dsp,z,s}$  (see Table 1 for notations and biological interpretation of the models). For the proportion of individuals dying from different mortality causes,  $\alpha$  (hunting) and  $\beta$  (predation), we started with a model in which  $\alpha$  differs between birth zones and between states

during the hunting period and is fixed to 0 during the rest of the year. As a consequence,  $\beta$  differs between states and between these two periods (hunting vs. nonhunting) in this model because only two mortality causes are possible during the nonhunting period (predation and other mortality causes). We have no a priori reason to suspect a zone effect on  $\beta$ . This model can thus be denoted (see Table 1) as

$$\alpha_{dsp,z}^{Hper} \alpha^{NHper}(0) \beta_{dsp,per}$$

For the dispersal probability  $d$ , we used previous results to define the starting model. Bray et al. (2007) have shown that dispersal occurs more often in the HZ and that males disperse more than females in both zones. We thus used the model  $d_{z+s}^{age1} d^{age2}(0)$  in which the dispersal probability for juveniles younger than 202 days depends on the sex and the zone in an additive way, and the dispersal probability is fixed to 0 for older juveniles since 202 days was the maximum age at dispersal observed in our population (Bray et al. 2007). We did not change this dispersal structure in any of the following analyses.

*Individual MS-CR history and MS-CR model computation*

We aim to estimate the unknown parameters using multinomial probability distributions, assuming that the fates of the hares are independent from each other and that all the hares have the same probability of survival, of being dead from a given cause, and of dispersal in a given time interval. Typical MS-CR history from the available data on hares can be numerically recorded as follows with the correspondence between the numerical and the nominal labeling of states given in Table 2: for example, an individual marked as philopatric (state 1) at capture occasion one and hunted during the fourth interval (state 3) after having dispersed during the second interval (state 2) can be marked as 1122300 (Table 2).

We used the program E-SURGE (Choquet 2007, Choquet et al. 2009; see Appendix B) for modeling and maximum likelihood parameter estimation. This program is specifically devoted to building multievent models (Pradel 2005) in capture–recapture studies but also facilitated implementation of multistate models with a subdivided transition matrix (Grosbois and Tavecchia 2003) in the framework of multievent models. Multievent models require two other matrices,  $\mathbf{\Pi}$ , which reports the probability of being in a given state when first encountered, and  $\mathbf{B}$ , which reports the relative probabilities of being in different states conditional on a given observation, in addition to the transition matrix  $\mathbf{\Phi}$  (Pradel 2005). Because all individuals were first trapped in their birth site before the minimum age at dispersal and the probabilities of detection  $p$  for a live and for a dead animal are all equal to one, these two matrices are very simple in our case (see Appendix B for more details). Accordingly, the probability of the previous

TABLE 1. Abbreviations used in model notations for the European hare (*Lepus europaeus*) and their biological interpretation.

Abbreviations	Biological interpretation
<b>Parameter</b>	
$s$	survival probability
$d$	dispersal probability, conditional on survival
$\alpha$	probability of dying from hunting, conditional on mortality $1 - s$
$\beta$	probability of dying from predation, conditional on mortality $1 - s$
<b>Subscript</b>	
$i$	no effect of any factors on transition probabilities
dsp	transition probability differs between philopatric and dispersing individuals
$z$	difference between the hunting and the nonhunting birth zone
per	difference between the periods (hunting vs. nonhunting)
$s$	difference between the sexes
<b>Model notation and linear modeling examples</b>	
$s_{z,s}$	$\text{logit}(s) = b_0 + b_1 \times z + b_2 \times s + b_3 \times z \times s$
$s_{z+s}$	$\text{logit}(s) = b_0 + b_1 \times z + b_2 \times s$
$s(0)$	parameter $s$ is fixed to 0
<b>Notation when some parameters are fixed</b>	
age1	transition probability concerning only individuals younger than 202 days during a given time interval
age2	transition probability concerning only individuals aged 202 days and older during a given time interval
Hper	transition probability concerning only the time intervals encompassed by the hunting period from 1 September to 30 November
NHper	transition probability concerning the nonhunting period for the rest of the year
<b>Model examples</b>	
$d_{z+s}^{\text{age1}} d^{\text{age2}}(0)$	the dispersal probability $d$ is fixed to 0 for individuals older than 202 days at a given time ( $d^{\text{age2}}(0)$ ); for younger individuals (age1), $d$ depends on the birth zone and the sex in an additive way
$\alpha_{\text{dsp},z}^{\text{Hper}} \alpha^{\text{NHper}}(0) \beta_{\text{dsp},\text{per}}$	the probability of dying from hunting $\alpha$ is fixed to 0 [ $\alpha^{\text{NHper}}(0)$ ] in the nonhunting period and differs between philopatric and dispersing individuals in an interactive way with the birth zone during the hunting period; the probability of dying from predation $\beta$ depends on the dispersal state (disperser vs. philopatric) and on the period of the year in an interactive way

example MS-CR history can be written as follows:  $P(1122300) = s_P(1 - d)s_P d s_D(1 - s_D)\alpha_D$ . Then, parameters can be additionally constrained depending on the gender, the birth zone of the individual, and the period of the year the individual died.

*Model selection procedure*

Starting from the general model just defined, we reduced the number of parameters in a three-step approach to select the most parsimonious alternative model. In the first step, we focused on survival probability and defined a set of 13 plausible models representing different combinations of state, birth zone, and sex dependence in the survival probability (Table 3). As we adjusted only the parameters in the transition matrix for survival  $S$  in this first analytical step, all 13

models have the same model structure for the transition matrices for mortality causes  $M$  and for dispersal  $D$ , defined in the general starting model. We used the Akaike Information Criterion adjusted for small sample size and we calculated the  $AIC_c$  weight of each model ( $AIC_c$ , calculated from the model deviance, the number of estimated parameters, and the effective sample size; Burnham and Anderson 2002) to identify the most plausible among these 13 models. When several models received equal support from the data, i.e., with  $AIC_c$  differing by fewer than two points, we applied the parsimony principle (Lebreton et al. 1992) by selecting the one with the fewest number of parameters.

In the second step, we started from the best model at the previous step and specifically tested using four candidate models if survival is lower in the hunting

TABLE 2. Correspondence between the numerical and the nominal labeling of states in multi-state capture–recapture (MS-CR) histories of individual hares.

Label	Philopatric	Disperser	Newly dead, by cause			Older dead
			Hunting	Predation	Other	
Nominal	P	D	NDH	NDP	NDO	†
Numerical	1	2	3	4	5	0

TABLE 3. Model selection based on AIC<sub>c</sub> for the first analytical step using a set of 13 candidate models displaying variability of the transition matrix **S**.

Model no.	Model notation	<i>k</i>	Deviance	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	AIC <sub>c</sub> weight
5†	S <sub>dsp</sub>	13	580.14	606.14	0.00	0.42
11‡	S <sub>dsp+z</sub>	14	579.68	607.68	1.53	0.20
12‡	S <sub>dsp+s</sub>	14	580.11	608.11	1.96	0.16
3	S <sub>dsp,z</sub>	15	579.56	609.56	3.42	0.08
4	S <sub>dsp,s</sub>	15	580.11	610.11	3.96	0.06
9	S <sub>z</sub>	13	585.64	611.64	5.49	0.03
10	S <sub>i</sub>	12	587.72	611.72	5.57	0.03
7	S <sub>z+s</sub>	14	585.52	613.52	7.37	<0.01
13	S <sub>dsp+z+s</sub>	17	579.66	613.66	7.52	<0.01
8	S <sub>s</sub>	13	587.69	613.69	7.55	<0.01
6	S <sub>z,s</sub>	15	584.06	614.06	7.91	<0.01
1	S <sub>dsp,z,s</sub>	19	578.67	616.67	10.53	0
2	S <sub>dsp,[z+s]</sub>	19	579.50	617.50	11.35	0

Notes: These 13 models do not display variability in the transition matrices for cause of mortality **M** and dispersal **D**, which were defined in the general starting model; *k* represents the number of parameters in the model.

† The best model.

‡ Models receiving equal support from the data.

period than in the nonhunting period, in combination or not with the previously selected factors (Table 4: Step 2). Again, these four candidate models have the same model structure for the transition matrices **M** and **D** defined in the general starting model.

Finally, in the third step, we modeled the proportion of individuals dying from hunting, predation, and other causes and formulated a second set of five candidate models representing different combinations of state and birth zone dependence on the proportion of individuals dying from hunting and predation (Table 4: Step 3). As a result of the general starting model for dispersal probability and the two previous steps, all the models tested in step 3 have the same parameters for dispersal and survival probabilities. AIC<sub>c</sub> weights were used to

rank the models according to their support by the data in both steps two and three.

Here, note that based on the results of Bray et al. (2007), and for simplicity due to the relative sparseness of the data, we neglected the effect of year on the proportions of individuals dying from different mortality causes, and on dispersal and survival probabilities. We thus pooled the data to perform the analysis. For the same reasons, we did not test for a continuous time effect and restricted the temporal variability of parameters to two periods within the year (hunting vs. nonhunting periods).

Finally, the goodness-of-fit (GOF) test for multistate models (Pradel et al. 2003) does not allow for non-observable states. To our knowledge, and due to the

TABLE 4. Model selection based on AIC<sub>c</sub> for the second and third analytical step.

Model no.	Model notation	<i>k</i>	Deviance	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	AIC <sub>c</sub> weight
a) Step 2						
15†	S <sub>dsp+per</sub>	14	571.55	599.55	0.00	0.64
14‡	S <sub>dsp,per</sub>	15	571.41	601.41	1.86	0.25
16	S <sub>per</sub>	13	577.78	603.78	4.22	0.08
5	S <sub>dsp</sub>	13	580.14	606.14	6.59	0.02
b) Step 3						
15†	α <sup>Hper</sup> <sub>dsp,z</sub> α <sup>NHper</sup> (0) β <sub>dsp,per</sub>	14	571.55	599.55	0.00	0.67
19	α <sup>Hper</sup> <sub>dsp,z</sub> α <sup>NHper</sup> (0) β <sub>per</sub>	12	578.18	602.18	2.63	0.18
20	α <sup>Hper</sup> <sub>dsp,z</sub> α <sup>NHper</sup> (0) β <sub>dsp,per,z</sub>	17	569.29	603.29	3.74	0.10
17	α <sup>Hper</sup> <sub>z</sub> α <sup>NHper</sup> (0) β <sub>per</sub>	10	586.17	606.17	6.62	0.02
18	α <sup>Hper</sup> <sub>z</sub> α <sup>NHper</sup> (0) β <sub>dsp,per</sub>	12	582.33	606.33	6.78	0.02

Notes: (a) Step 2 shows the effect of the hunting period on survival probability starting from the best model in the first analytical step (model number 5, Table 3). As for models used in Step 1 (Table 3), the four fitted models do not display variability in the transition matrices for mortality cause **M** and dispersal **D** (general starting model). (b) Step 3 shows the effect of the dispersal state (philopatric vs. disperser) on the probability of dying from hunting α and from predation β starting from the previous best model (model number 15 in Step 2). The five candidate models have the same transition matrices for survival **S** and dispersal **D** defined by model number 15; *k* represents the number of parameters in the model.

† The best model.

‡ Models receiving equal support from the data.

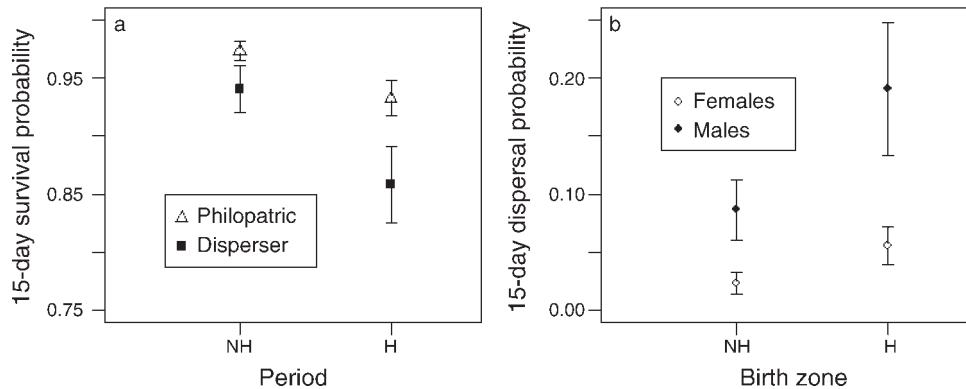


FIG. 1. (a) Estimates of 15-day survival probability  $s$  (mean  $\pm$  SD) for the European hare (*Lepus europaeus*), showing the additive effects of the dispersal state (disperser vs. philopatric) and the period of the year (hunting H vs. nonhunting NH), and (b) estimates of 15-day dispersal probability  $d$  (mean  $\pm$  SD), showing the additive effects of the sex and the birth zone (H vs. NH). Parameter estimates were obtained from model number 15:  $s_{\text{dsp+per}}, \alpha_{\text{dsp,z}}^{\text{Hper}}, \alpha_{\text{dsp,z}}^{\text{NHper}}(0)\beta_{\text{dsp}}, a_{z+s}^{\text{age1}}, a_{z+s}^{\text{age2}}(0)$ , where  $s$  and  $d$  denote survival and dispersal probability, respectively, and where  $\alpha$  and  $\beta$  are the probabilities of dying from hunting and predation, respectively, conditional on mortality.

particular data set combining live telemetry locations and dead recoveries, there is no test available to assess the GOF of our general model. Since there is no gap in capture histories, we assume that our general model fits well with the data.

## RESULTS

Of the set of the 13 candidate models used to assess the influence of sex, birth zone, and dispersal state (philopatric vs. disperser) on survival probability in our first analytical step (Table 3), model number 5 in which the 15-day survival probability differs between philopatric and dispersing individuals received considerably more support from the data than the other 12 models (AIC<sub>c</sub> weight = 0.42, at least twice that of any other model; Table 3). Starting from model number 5 to specifically assess the influence of period (hunting vs. nonhunting) on survival (step 2; Table 4: Step 2), we retained model number 15 (AIC<sub>c</sub> weight = 0.64) as the most plausible, in which the effect of the period is additive to the effect of the dispersal state, i.e., survival probabilities are higher during the nonhunting period (from 1 December to 31 August) than during the hunting period (from 1 September to 30 November), but dispersers showed a lower survival probability than philopatric individuals in both periods (Fig. 1a). Using the formula  $(S_{\text{Hper}})^6(S_{\text{NHper}})^{18}$  to roughly estimate a survival probability between 3 and 15 months old, the survival probability of juvenile hares that dispersed between these ages is three times lower than the survival probability of juvenile hares that remained philopatric (0.131 vs. 0.403).

In the third analytical step, testing for the influence of the dispersal state on  $\alpha$  and  $\beta$  using five candidate models, model number 15 remained the most supported one (AIC<sub>c</sub> weight = 0.67; Table 4: Step 3). In fact, this model was our starting model for  $\alpha$  and  $\beta$  (see *Material*

*and methods*) and considers that  $\alpha$  is fixed to 0 during the nonhunting (NH) period and differs between philopatric and dispersing individuals in an interactive way with the birth zone during the hunting (H) period. The probability of dying from predation  $\beta$  depends on the dispersal state (disperser vs. philopatric) and on the period of the year in an interactive way. Indeed, all the philopatric juvenile hares that died during the hunting period in the hunting zone (HZ) were hunted (i.e., no predation case) whereas only about half of the dispersers that died in both zones were killed by hunters (Fig. 2a). Similarly, philopatric juvenile hares appeared to die mainly from predation relative to other causes of mortality (except poaching) during the nonhunting period, whereas the proportions of juvenile hares that died from predation are similar in philopatric and dispersing individuals during the hunting period (Fig. 2b). Note that, as expected, the birth zone has no effect on  $\beta$  as illustrated by the relatively low support received by model number 20 (Table 4: Step 3).

Finally, for simplicity, we chose to model the dispersal probability  $d$  following the results of Bray et al. (2007), and the model structure for  $d$  was constant. This additive model allowed us to estimate a 15-day dispersal probability (Fig. 1b), illustrating the higher dispersal rate in juvenile males than in juvenile females, and the higher dispersal probability in the HZ than in the nonhunting zone (NHZ).

## DISCUSSION

### *Obtaining estimates of dispersal probability and costs*

We have proposed a new combined formulation of MS-CR models to estimate simultaneously natal dispersal probability, survival probability of dispersers vs. philopatric individuals, and the proportions of individuals dying from different causes. We have developed here a simplified version of this model for two main

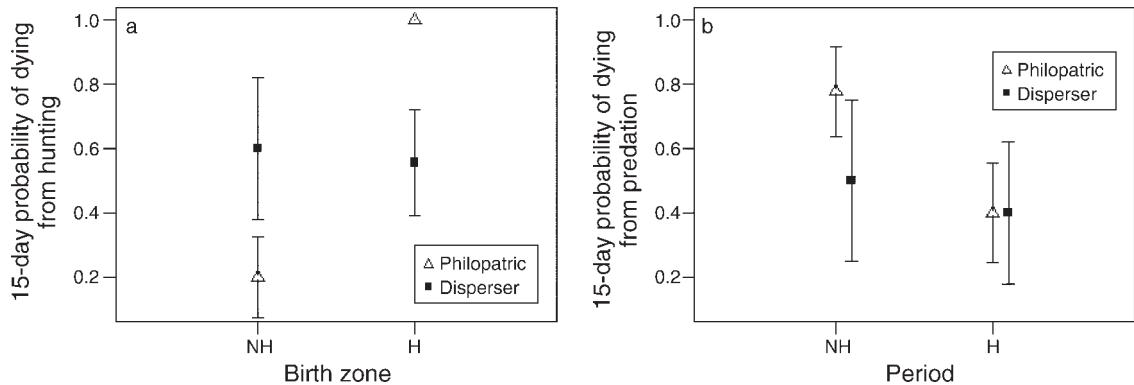


FIG. 2. Estimates of 15-days probability (mean  $\pm$  SD) of dying (a) from hunting ( $\alpha$ ) during the hunting period when born in both hunting (H) and nonhunting (NH) zones and (b) from predation ( $\beta$ ) during both the hunting (H) and nonhunting (NH) period, showing the effect of the dispersal state (disperser vs. philopatric) obtained from model 15,  $d_{z+s}^{age1} d_{age2}^{age2}(0)$ .

reasons. Firstly, our data set showed some particularities that allowed such a simplification. For example, the probability of remaining within the study area  $\delta$  was fixed at one because we did not lose any individual during their telemetry monitoring and the probability of detection was also equal to one. We no longer modeled a transient state, which could be named  $T$ , in the dispersal process because this dispersal stage never lasted longer than seven days for “one-way” dispersers (Bray et al. 2007), which is shorter than the time interval between successive trapping sessions (15 days). Secondly, the effect of time could not be assessed in our analysis due to the relative sparseness of the data which precluded the analysis in a continuous time context. We chose therefore to emphasize the possible effects of the birth zone and the period of hunting on the survival probability of the two dispersal states over the three years. In this simple version of the model, we had no problem with parameter identifiability, but we advocate searching for nonidentifiable parameters, possibly using computer algebra (Gimenez et al. 2003), when the model becomes more complex, especially if time dependence of the parameters is included. Indeed, the general combined formulation of the model allows us to easily include all these previous parameters, factors, or states, as well as state uncertainty (Pradel 2005). Incorporating a transient state in the dispersal process only requires adapting the transition matrices. We just have to add a departure and an arrival state  $T$  (transient) with its respective transitions to the other states, keeping in mind that a philopatric individual could now reach the dispersal state either directly or through state  $T$ . When the monitoring covers the life span, one can also easily integrate the breeding state of each individual at each trapping occasion (breeder vs. nonbreeder) to test for the influence of natal dispersal on future reproduction. Hence, it is also possible to add the breeding dispersal process in the transition matrices. In this way, in the same model, the two major components of individual

fitness (survival and reproduction) could be related to dispersal state (natal and breeding dispersal) and history of any individual. Moreover, we assumed that the mortality cause is known without error. But as we mentioned earlier, we consider predation as the most plausible mortality cause in several cases, which means that some uncertainty remained (e.g., the carnivore bites can be post mortem). Since our model is written in the multievent CR framework (Pradel 2005), such state uncertainty can be easily addressed by modifying the matrix  $\mathbf{B}$  that gives the event probabilities conditional on the “true” underlying state (see Pradel 2005 for more details).

One can also imagine integrating both the natal dispersal distance and the transience duration as individual covariates in the analysis. These two factors are often invoked to enhance the cost of dispersal (e.g., Steen 1994, Alberts and Altmann 1995). Finally, we did not take into account the litter rank of juvenile hares. One can expect that juveniles of the first litter of the year incur lower survival costs when dispersing than juveniles from the next litter (but see Gillis and Krebs 2000 for a counter example of snowshoe hare *Lepus americanus*) because they may be, for example, heavier at dispersing age or disperse in a habitat with a higher vegetal cover offering more food resources. Such a point should be investigated in future studies.

In addition to this quantitative measure of the dispersal cost, our model allowed us to assess the proportion of individuals dying from different mortality causes and hence, to discriminate between different possible costs of dispersal (predation, human-mediated mortality). In cases where the survival probabilities of dispersing and philopatric individuals are similar, we are able to test for a difference in the causes of mortality, which can be of great importance for wildlife biologists aiming at enhancing the persistence of a given population by promoting dispersal.



PLATE 1. Adult European hare in the study area. Photo credit: Frank Latraube, ONCFS.

#### *Hunters and predators make natal dispersal costly*

In our European hare population, we found that the survival probability of dispersers was lower than the survival probability of philopatric individuals of the same age whatever the period of the year (hunting and nonhunting). Additional information on the survival pattern in this population is provided by three models not retained by the model selection procedure (Tables 3 and 4a). Those models were nonetheless relatively well supported by the data (i.e.,  $\Delta\text{AIC} < 2$ ). Firstly, 15-day survival of both dispersing and philopatric hares is slightly higher in females (model number 12, Table 3) and in hares born in the nonhunting zone (NHZ; model number 11, Table 3) than in males and in hares born in the hunting zone (HZ), respectively. Secondly, the 15-day survival difference between dispersing and philopatric hares is higher during the hunting period as suggested by model number 14 (Table 4: Step 2). We ensured that the omission of the factors sex and zone (step 1) from the model selection procedure, and of the interaction between dispersal state and period (step 2, see the *Results* section) did not modify the main result of our analysis by performing model selection starting from these omitted models (results not shown).

Using estimates of the best model (number 15, Table 4), dispersers have a very low survival rate during the first 12 months after weaning (0.13), i.e., one-third of the survival rate of philopatric hares (0.40). All dead philopatric hares died within their home range and all dead dispersing hares died at least 15-days after their settlement on a new home range. Thus, we did not

observe mortality cases during the sudden, i.e., less than seven days, “one-way” dispersal movement, which means that mortality during transience and settlement is negligible in our study. We nonetheless acknowledge that stress and aggression during these two stages of the dispersal process, possibly depending on the dispersal distance, may have an impact on subsequent survival of individuals. Therefore, dispersers incurred survival costs to dispersal once they were settled in their new territory. This finding contrasts with the general idea that the costs of dispersal mainly arise during transience and settlement (see Van Vuren and Armitage 1994 on the yellow-bellied marmot *Marmota flaviventris*).

Both dispersers and philopatric individuals died mainly from predation and hunting. However the analysis of the causes of mortality in both states provides some interesting insights into why dispersers suffered from higher mortality rates. For different combinations of birth zones and periods, the probabilities for a disperser to die from hunting and predation, estimated by the product of the overall mortality rate and the proportion of dispersers that died from hunting and predation (respectively  $[1 - s_d]\alpha_d$  and  $[1 - s_d]\beta_d$ ), were always higher than for philopatric individuals ( $[1 - s_p]\alpha_p$  and  $[1 - s_p]\beta_p$ ; result not shown). This shows that dispersers are more prone to die from hunting and predation than philopatric individuals. Comparing the proportions of deaths attributed to different mortality causes between dispersers and philopatric individuals provides additional insight as to why dispersers had a lower survival. Two main points appeared from this analysis. Firstly, 60% of dispersing hares born in the

NHZ that died during the hunting period were hunted (vs., surprisingly, only 20% of philopatric individuals; Fig. 2a). Such a peculiar result underlines the fact that these hares were hunted in the periphery of the NHZ or in the HZ where they settled after dispersal (overall, 22/28 dispersers were in the hunting zone during the hunting period). Note also that the philopatric hares born in the NHZ that were surprisingly hunted during the hunting period were often those having their adult home range overlapping both the NHZ and the HZ. Secondly, philopatric individuals that died during the nonhunting period died mainly from predation (80%) whereas dispersers also died from other causes of mortality (disease, road, and unidentified; Fig. 2b). It appears from these two points that dispersers have to face up to two qualitative mortality risks that philopatric individuals seemed to incur less frequently: to be hunted when born in the NHZ and to die from other mortality causes other than hunting and predation.

#### *Implications in evolutionary and conservation biology*

Overall, dispersers suffered from a much higher mortality than philopatric hares from weaning to first breeding age. Two questions arise from both evolutionary and demographic viewpoints. (1) How can natal dispersal be considered as a product of natural selection if it incurs high fitness costs? (2) How could we integrate such a result into the conservation/management of the declining European hare populations?

1) In our analysis, we used only one measure of fitness (survival) during a short time period (weaning to first breeding). But life after dispersal does not stop at first breeding and benefits of natal dispersal including long-term survival and breeding success have been documented (see Larsen and Boutin 1994 in red squirrel *Tamiasciurus hudsonicus*). In addition, the reproductive costs of philopatry, e.g., inbreeding or local mate competition, might be cumulative over life. Hence, delayed costs of philopatry may counterbalance the early costs of natal dispersal. Such an idea underlines again the usefulness of monitoring individuals along their life span when studying the cost/benefit ratio of natal dispersal. Our model provides the opportunity to investigate such possible later costs of philopatry and benefits of dispersal.

2) The relevance of the high-density nonhunting reserve for the conservation of the European hare populations is demonstrated here. Indeed, higher density in the natal area is associated with lower dispersal rates. Basically, lowering the proportion of dispersers may increase the overall survival rate between weaning and first reproduction, and thus may increase the intrinsic growth rate of the populations. However, the juvenile dispersing hares born in the NHZ mainly dispersed in the surrounding HZ and suffered, as did dispersers born in the HZ, from a very high mortality (mainly hunting and predation) which drastically lowered their colonizing potential. Shortening the hunting period through an

earlier cessation (possibly 31 October) could allow the majority of juvenile hares to reach the mean age of dispersal (4.5 months) after the end of the hunting period. Such a management decision would enhance the survival probability and, hence, the reproductive output of dispersers in the low-density HZ.

To conclude, the new formulation of MS-CR models presented here gives us empirical estimates of the natal dispersal probability, the survival cost of natal dispersal, and the proportions of individuals dying from different causes. We provided an example of how such a modeling approach could be used in the management of declining European hare populations, which highlights the usefulness of the model in applied ecology (Macdonald and Johnson 2001). We also emphasized the reliability of our model in the broader context of the study of natal dispersal costs by including information on natal dispersal distance or reproductive success. Finally, we believe that the model presented here could be of great use when planning an empirical study of the costs/benefits ratio of natal dispersal, as it could provide a strong analytical framework for biologists.

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#### LITERATURE CITED

- Alberts, S. C., and J. Altmann. 1995. Balancing costs and opportunities: dispersal in male baboons. *American Naturalist* 145:280–306.
- Arnason, A. N. 1972. Parameter estimates from mark-recapture experiments on two populations subject to migration and death. *Researches on Population Ecology* 13:97–113.
- Bélichon, S., J. Clobert, and M. Massot. 1996. Are there differences in fitness components between philopatric and dispersing individuals? *Acta Oecologia* 17:503–517.
- Bray, Y., S. Devillard, E. Marboutin, B. Mauvy, and R. Peroux. 2007. Natal dispersal of European hare in France. *Journal of Zoology* 273:426–434.
- Bray, Y., and Y. Léonard. 2000. Efficacy and selectivity of hare (*Lepus europaeus*) “box traps.” *Game and Wildlife Science* 17:219–240.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodal inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.
- Choquet, R. 2007. E-SURGE 1.0 user’s manual. CEFE, Montpellier, France. (<http://www.cefe.cnrs.fr/biom/PDF/Choquet-E-SURGE-MANUAL-V1-0.pdf>)
- Choquet, R., L. Rouan, and R. Pradel. 2009. Program E-SURGE: a software application for fitting multievent models. Pages 845–865 in D. L. Thomson, E. G. Cooch, and M. J. Conroy, editors. Environmental and ecological statistics: modeling demographic processes in marked populations. Springer, New York, New York, USA.
- Clobert, J., E. Danchin, A. A. Dhondt, and J. D. Nichols. 2001. Dispersal: individual, population and community. Oxford University Press, Oxford, UK.

- Dobson, F. S. 1982. Competition for mates and predominant juvenile male dispersal in mammals. *Animal Behaviour* 30: 1183–1192.
- Gandon, S., and Y. Michalakis. 2001. Multiple causes for the evolution of dispersal. Pages 155–167 in J. Clobert, E. Danchin, A. A. Dhondt, and J. D. Nichols, editors. *Dispersal: individual, population and community*. Oxford Press University, Oxford, UK.
- Gillis, E. A., and C. J. Krebs. 2000. Survival of dispersing versus philopatric juvenile snowshoe hares: do dispersers die? *Oikos* 90:343–346.
- Gimenez, O., R. Choquet, and J. D. Lebreton. 2003. Parameter redundancy in multistate capture–recapture models. *Biometrical Journal* 45:704–722.
- Grosbois, V., and G. Tavecchia. 2003. Modeling dispersal with capture–recapture data: disentangling decisions of leaving and settlement. *Ecology* 84:1225–1236.
- Isbell, L. A., and D. VanVuren. 1996. Differential costs of locational and social dispersal and their consequences for female group-living primates. *Behaviour* 133:1–36.
- Johnson, M. L., and M. S. Gaines. 1990. Evolution of dispersal: theoretical models and empirical tests using birds and mammals. *Annual Review of Ecology and Systematics* 21: 449–480.
- Lambin, X. 1994. Natal philopatry, competition for resources, and inbreeding avoidance in Townsend's voles (*Microtus townsendii*). *Ecology* 75:224–235.
- Larsen, K. W., and S. Boutin. 1994. Movements, survival, and settlement of red squirrel (*Tamiasciurus hudsonicus*) offspring. *Ecology* 75:214–223.
- Lebreton, J. D. L., T. Almeras, and R. Pradel. 1999. Competing events, mixtures of information and multistratum recaptures models. *Bird Study* 46(Supplement):S39–S46.
- Lebreton, J. D., K. P. Burham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62:67–118.
- Lebreton, J. D., and R. Pradel. 2002. Multistate recapture models: modelling incomplete individual histories. *Journal of Applied Statistics* 29:353–369.
- Macdonald, D. W., and D. D. P. Johnson. 2001. Dispersal in theory and practice: consequences for conservation biology. Pages 361–374 in J. Clobert, E. Danchin, A. A. Dhondt, and J. D. Nichols, editors. *Dispersal: individual, population and community*. Oxford University Press, Oxford, UK.
- McShea, W. J., and D. M. Madisson. 1992. Alternative approaches to study of small mammal dispersal: insights from radiotelemetry. Pages 319–332 in N. C. Stenseth and W. Z. Lidicker, editors. *Animal dispersal: small mammals as a model*. Chapman and Hall, London, UK.
- Péroux, R., B. Mauvy, A. Lartiges, Y. Bray, and E. Marboutin. 1997. Point transect sampling: a new approach to estimate densities or abundances of European hare (*Lepus europaeus*) from spotlight counts. Pages 525–529 in XIIth Lagomorph Workshop. Gibier Faune Sauvage, Game and Wildlife, Clermont-Ferrand, France.
- Pollock, K. H., M. J. Conroy, and W. S. Hearn. 1995. Separation of hunting and natural mortality using ring-return models: an overview. *Journal of Applied Statistics* 22: 557–566.
- Pradel, R. 2005. Multievent: an extension of multistate capture–recapture models to uncertain states. *Biometrics* 61:442–447.
- Pradel, R., C. Wintrebert, and O. Gimenez. 2003. A proposal for a goodness-of-fit test to the Arnason-Schwarz multisite capture–recapture model. *Biometrics* 59:43–53.
- Schaub, M., and R. Pradel. 2004. Assessing the relative importance of different sources of mortality from recoveries of marked animals. *Ecology* 85:930–938.
- Small, R. J., J. C. Holzworth, and D. H. Rusch. 1993. Are ruffed grouse more vulnerable to mortality during dispersal? *Ecology* 74:2020–2026.
- Spinks, A. C., J. U. M. Jarvis, and N. C. Bennett. 2000. Comparative patterns of philopatry and dispersal in two common mole-rat populations: implications for the evolution of mole-rat sociality. *Journal of Animal Ecology* 69: 224–234.
- Steen, H. 1994. Low survival of long distance dispersers of the root vole (*Microtus oeconomus*). *Annales Zoologici Fennici* 31:271–274.
- VanVuren, D., and K. B. Armitage. 1994. Survival of dispersing and philopatric yellow-bellied marmots: what is the cost of dispersal? *Oikos* 69:179–181.

#### APPENDIX A

Determination of the dispersal vs. philopatric state of juvenile European hare at each capture occasion (Bray et al. 2007) (*Ecological Archives* E090-206-A1).

#### APPENDIX B

Instructions for implementing the multistate capture–recapture model with subdivided transition probability matrix between states using the software E-SURGE (*Ecological Archives* E090-206-A2).