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Efficient spatial multi-state capture-recapture model to study natal dispersal.

An application to the Alpine marmot.

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ABSTRACT

1. Studying natal dispersal in natural populations using capture-recapture data is challenging as an unknown proportion of individuals leaves the study area when dispersing and are never recaptured. Most dispersal (and survival) estimates from capture-recapture studies are thus biased and only reflect what happens within the study area, not the population.
2. Here, we elaborate on recent methodological advances to build a spatially-explicit multi-state capture-recapture model to study natal dispersal in a territorial mammal while accounting for imperfect detection and movement in and out of the study area.
3. We validate our model using a simulation study where we compare it to a non-spatial multi-state capture-recapture model. We then apply it to a long-term individual-based dataset on Alpine marmot (*Marmota marmota*).
4. Our model was able to accurately estimate natal dispersal and survival probabilities, as well as mean dispersal distance for a large range of dispersal patterns. By contrast, the non-spatial multi-state estimates underestimated both survival and natal dispersal even for short dispersal distances relative to the study area size.
5. We estimated higher inheritance probabilities of female Alpine marmots, which suggests higher levels of philopatry, although the probability to become dominant after dispersal did not differ between sexes. Nonetheless, the lower survival of young adult males suggests higher costs of dispersal for males. We further discuss the implications of our findings in light of the life-history of the species.
6. The flexibility of our spatially-explicit multi-state capture-recapture model makes it adjustable enough to be widely applicable in other species.

Keywords: Bayesian modelling · Dispersal kernel · Multi-state capture-recapture

49 models · Spatially explicit capture-recapture · Sex-specific dispersal ·

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INTRODUCTION

Dispersal, and especially natal dispersal, is a fundamental process in biology (Dobson, 2013). In practice, all organisms are faced with the decision to move and spread, or to stay and try to access reproduction on their natal site. This decision entails strong fitness consequences and understanding the causes and consequences of natal dispersal is thus of prime importance in evolutionary and population dynamics studies (Bowler & Benton, 2005).

Capture Recapture (CR) models are now widely recognized as essential tools in many fields of biological sciences, including population dynamics studies (Thomson *et al.* 2009). The main strength of the CR methodology resides in the ability to disentangle biological processes, *e.g.* survival (Tavecchia *et al.* 2001), dispersal (Bennetts *et al.* 2001) or reproduction (Rivalan *et al.* 2005), from observation processes. However, one limitation of most CR models is the “apparent survival” problem. When moving around, some individuals may leave the study area and settle permanently outside its boundaries. These emigrated individuals are then never recaptured and are undistinguishable from dead individuals. In this situation, the most common in CR studies, survival estimates returned by CR models correspond in fact to the probability for an individual to survive and not leave the study area, *i.e.* the apparent survival (Lebreton *et al.* 1992). This limitation is even more salient if the target of the study is to estimate animal movement itself. Since only a fraction of dispersing individuals can be recaptured inside the study area, any measure of dispersal obtained under these conditions will correspond to an “apparent dispersal”, thereby underestimating true dispersal. Some solutions exist when individuals can move into and out of the study area (*e.g.* temporary emigration, Kendall & Nichols, 2002; Bird *et al.*, 2014; breeding dispersal, Oro & Doak, 2020). However, when the goal is to study natal dispersal, a single event by definition, these methods do not apply. Even in the case of capture-recapture studies where multiple sites are monitored (Lebreton & Pradel, 2002), dispersal estimates only refer to transitions between sites and all

individuals dispersing elsewhere will be confounded with dead individuals if no additional information is considered (*e.g.* dead recoveries or count surveys from other sites; Péron *et al.* 2010). It is then crucial to deal with the issues of “apparent survival” and “apparent dispersal” if one wants to study natal dispersal using CR data.

In most CR studies, ancillary information about individual movements is readily available, as the locations of captures/detections are generally recorded in addition to the identity of the individual. This source of information was usually neglected but the emergence of spatial capture-recapture (SCR: Borchers & Efford, 2008, Royle & Young, 2008) together with the democratization of highly flexible softwares for Bayesian analyses using Markov Chain Monte Carlo (MCMC) methods (BUGS: Lunn *et al.*, 2000, JAGS: Plummer, 2003, NIMBLE: DeValpine *et al.*, 2017) recently motivated several attempts to use this additional information to solve the “apparent survival” problem (Schaub & Royle 2014. Ergon & Gardner 2014). Whilst originally thought as a way to account for the lower detection probabilities of animals living at the fringe of a given study area, SCR models also present a great potential for studying animal movements (Bischof, Milleret, *et al.*, 2020; Chandler & Clark, 2014).

Here, we introduce the Natal Dispersal model (ND), a multi-state capture-recapture model designed to simultaneously estimate natal dispersal probabilities, natal dispersal distance distributions and state-specific survival probabilities. Our model was motivated by the long-term study of a territorial and social mammal, the Alpine marmot (*Marmota marmota*). We start by presenting the Alpine marmots life cycle -on which the model structure was based- and the Alpine marmot dataset. We then present the Natal Dispersal model and how it differs from a classical multi-state model. We continue with a simulation study to evaluate how both models (ND *vs* classical multi-state) perform under different natal dispersal scenarios. Finally, we apply the model to an individual-based long-term dataset on Alpine marmots to study sex- and age-specific natal dispersal patterns in this species before discussing our results.

MATERIAL AND METHODS

1. Alpine marmot life cycle

Family groups The Alpine marmot is a hibernating, highly territorial and cooperatively breeding mammal living in family groups of 2 to 20 individuals. A family is typically composed of a dominant couple, adult (age ≥ 3 years old) and sub-adult (age=2 years old) subordinates, yearlings and juveniles born that year (Allainé, 2000). Alpine marmots of the same family group share and defend a common territory (ranging between 0.9 ha and 2.8 ha) comprising main and secondary burrows (Perrin *et al.*, 1993). The main burrows are usually centrally located and used for communal hibernation, sleeping during the active season, and to give birth (Perrin *et al.*, 1993). Secondary burrows are spread over the entire territory and mainly used to escape potential predators. Family territories are consistently used over the years by the same family (although the family composition may change; see below) and are found adjacent to one another.

Reproduction In each family, reproduction is monopolized by the dominant couple (apart from a few subordinate males reproducing through extra-pair copulation: Cohas *et al.*, 2006; Ferrandiz-Rovira *et al.*, 2016; Hackländer *et al.*, 2003). Reproductive status is therefore generally confounded with dominance status in this species. Mating occurs shortly after the end of hibernation (mid-April to early May) and gestation lasts for 30 days. Dominant females give birth to a litter of 1 to 7 pups (median = 4) once a year and pups stay in the main burrow for 40 days, where mothers lactate them until weaning. Pups emerge between mid-June and mid-July and start eating on their own. Marmot juveniles remain in their natal territory at least until sexual maturity, at two years of age.

Dispersal Once they reached sexual maturity at two years of age, subordinate marmots can either stay on their natal territory and help raise subsequent pups or disperse. Dispersal usually

takes place shortly after coming out of hibernation (Stephens *et al.* 2002). Subordinates that stay in the family group may become dominant by inheriting the position in their natal territory following the death of the same-sex dominant while dispersers have to evict the same-sex dominant from another territory (Dupont *et al.*, 2015). A third possibility to access a dominant status is the creation of a new territory by a couple of dispersing individuals, but this is highly unusual in the saturated population under study (only 3 occurrences in 25 years of the study). Once a subordinate disperses, it can either succeed or fail in securing a dominant position, but it never joins a new family group as subordinate. In case of failure in reaching a dominant status during the active season, the disperser becomes a floater, *i.e.* a wandering individual forced to hibernate alone and consequently exposed to very high risks of mortality (Magnolon 1999). Once the dominant position is secured, a marmot can remain dominant for several years until death or eviction by a new incomer (Lardy *et al.*, 2011). When evicted, dominant individuals also become floaters subject to a very high risk of mortality (Grimm *et al.*, 2003) and they usually never become dominant elsewhere. Dispersal in the Alpine marmot is therefore exclusively natal dispersal. Hence, we did not consider the possibility for evicted dominants to become dominant elsewhere in this study (fig.1).

Because Alpine marmots are highly territorial, any intrusion in the territory is met with strong aggressiveness from the same-sex dominant and affiliated subordinates. The cost of dispersal is thus expected to strongly increase with each new territory crossed. Because territories are variable in size, two marmots travelling the same distance may be subjected to very different cost levels. In addition, Alpine marmots have the physical ability to travel long distances and through unsuitable terrain but are rarely observed further than a few hundred meters from their natal territory. For these different reasons, it is thought that the main factor driving dispersal distance of Alpine marmots is the number of agonistic encounters, *i.e.* the number of territories crossed, rather than landscape characteristics or physiological capacities. Hence, we measured

natal dispersal distances as the minimum number of territories crossed between the natal territory and the territory where the marmot became dominant.

2. Alpine marmot dataset

The Alpine marmot population from the Grande Sassi re Nature Reserve (French Alps, 45 29'N, 65 90'E) has been studied since 1990. Between 10 and 35 family groups have been monitored each year using capture-mark-recapture and daily observations. Marmot territories are situated at the bottom of a small valley on either side of a touristic trail crossing the lower part of the reserve. The study area covers an average of 75 ha (1.5 km long and 0.5 km wide), and is situated at approx. 2,340 m.a.s.l. The valley is surrounded by high altitude mountain peaks (> 3,500 m.a.s.l.) and steep slopes on both sides. Whilst the flat part of the valley is suitable for the establishment of Alpine marmot territories, steeper parts are unsuitable given the thickness and instability of snow-packs, rocks and the quasi-absence of vegetation (Allain  et al. 1994, L pez et al. 2010; fig.2).

Marmots were captured each year continuously from mid-May to mid-July, i.e., after most of the dispersal events took place, using two-door live traps baited with dandelions (*Taraxacum densleonis*) placed near the entrances of the main burrows in the middle of each territory. Since Alpine marmots are highly territorial and only leave their natal territory to disperse, placing traps near the entrances of the main burrows allowed us to assign captured individuals to their family group with great confidence. In addition, field observations during the whole monitoring season allowed us to confirm that marmots were correctly assigned to a family territory. During the juvenile emergence period, territories are carefully observed to identify their emergence date. Juveniles are then counted and captured either using small two-door live traps or by hand. With this procedure, virtually all juveniles in the study area were captured within three days of their emergence from the burrows.

Once captured, individuals were placed in an opaque bag before being anesthetized with Zolétil 100 (0.1 mL kg⁻¹). They were then sexed, aged from their size (up to 3 years) if the exact age was unknown, and their social status was determined based on scrotal development for males and teats development for females. All individuals were individually marked using both a transponder chip injected under the skin of the neck and a numbered metal ear-tag (right ear for females and left for males to facilitate later observation). An additional colored plastic ear tag was placed on the opposite ear for dominant individuals. Captured marmots were also marked on the back with temporary hair dye to help identify them during subsequent observations in the following 7 to 15 days and verify their dominance status as well as their assignment to a family territory. When tranquillized marmots recovered, they were returned to their territory (see Cohas *et al.*, 2006 for more details on protocol).

We restricted the analysis to the data collected between 1990 and 2015 leading to a dataset composed of 1,270 individuals (577 females / 693 males). During this period, 170 dispersal events (69 females / 101 males) were recorded within the study area with a maximum dispersal distance of five territories crossed.

3. Multi-State Capture-Recapture models

Based on the life cycle described in section 1, we built two different multi-state models. First, a classical multi-state capture-recapture model which estimates only apparent survival and dispersal (the Apparent Dispersal model; AD). And second, a custom multi-state model that integrates the information available about individual dispersal movements to estimate true survival and dispersal (the Natal Dispersal model; ND). Both models are constructed around three different observable states; a subordinate state *S* (encompassing juveniles, yearlings and subordinate adults, *i.e.* pre-dispersal states), a local breeder state *LB* (individuals that became dominant on their natal territory by inheritance, *i.e.* a philopatric state), and a disperser breeder

state *DB* (individuals that became dominant after dispersal), and one non-observable state, dead or outside the study area \dagger (fig.1).

Multi state capture-recapture models can be described as hierarchical models composed of two sub-models; an ecological process model describing how individuals change states between consecutive capture occasions, and an observation process model describing how individual observations collected each year are related to their underlying state. As our focus was on estimating demographic parameters and not population size, we used models that were conditional on first capture.

a. Apparent dispersal model

At first capture, individuals can be in any of the three live states (*S*, *LB* and *DB*) so that z_{if_i} the state of individual *i* at the time of its first capture f_i follows a categorical distribution:

$$z_{if_i} \sim \text{dcat}(\alpha) \quad \text{eqn.1}$$

where α is a probability vector of length 3 with a Dirichlet distribution. The Dirichlet distribution enforces the constraint $\sum \alpha = 1$. From this initial state, each individual has the possibility to transition to the other states or remain in its current one each year. Each year a subordinate individual may survive (probability Φ'^S), stay on its natal territory (probability $1 - \Delta'$), and remain a subordinate (probability $1 - h$) with overall probability $\Phi'^S \cdot (1 - \Delta') \cdot (1 - h)$. It can also survive and inherit a dominant position on its natal territory (transition to state *LB*) with probability $\Phi'^S \cdot (1 - \Delta') \cdot h$, disperse and reach a dominant position elsewhere *within the study area* (transition to state *DB*) with probability $\Phi'^S \cdot \Delta'$, or die or disperse outside the study area with probability $1 - \Phi'^S$ (transition to state \dagger). Note that here, Φ'^S is the probability that a subordinate individual survives *and does not leave the study area* between two consecutive occasions, Δ' is the probability that a subordinate individual disperses and becomes dominant *within the study area*, and *h* is the probability that a not-dispersing subordinate

222 inherits a dominant position on its natal territory between two consecutive capture occasions.
 223 Note also that we assume the different events (survival, dispersal, and inheritance) to be
 224 independent. As we did not consider the possibility for an evicted dominant to survive and
 225 become dominant elsewhere, a locally recruited breeder can only survive and remain in state
 226 LB with probability Φ^{LB} or die with probability $1 - \Phi^{LB}$. Similarly, a disperser breeder can
 227 either survive and remain in state DB with probability Φ^{DB} or die with probability $1 - \Phi^{DB}$.
 228 Finally, a dead individual remains in its current state \dagger with probability 1. These different state
 229 transition probabilities can be represented in a so-called transition matrix where each row
 230 corresponds to the departure state and each column to the arrival state of an individual:

$$231 \quad \Omega = \begin{bmatrix} \Phi'^S(1 - \Delta')(1 - h) & \Phi'^S(1 - \Delta')h & \Phi'^S\Delta' & 1 - \Phi'^S \\ 0 & \Phi^{LB} & 0 & 1 - \Phi^{LB} \\ 0 & 0 & \Phi^{DB} & 1 - \Phi^{DB} \\ 0 & 0 & 0 & 1 \end{bmatrix}$$

232 The state of an individual a given year can then be modelled as a random draw from a
 233 categorical distribution with probability vector corresponding to the individual's state the
 234 previous year:

$$235 \quad z_{it} \sim \text{dcat}(\Omega[z_{it-1}, 1:4]) \quad \text{eqn.2}$$

236 Like the transition matrix, we can represent the different detection probabilities linking the
 237 state of an individual (in rows) to the different possible observations (in columns) at each
 238 capture occasion in an observation matrix (Θ). In our situation, we assumed that we were able
 239 to determine the state of an individual with certainty when captured so that the different
 240 possible observations were: an individual was captured and identified as a subordinate (1), an
 241 individual was captured and identified as a local breeder (2), an individual was captured and
 242 identified as a disperser breeder (3) or the individual was not captured (4):

$$\theta = \begin{bmatrix} p^S & 0 & 0 & 1 - p^S \\ 0 & p^{LB} & 0 & 1 - p^{LB} \\ 0 & 0 & p^{DB} & 1 - p^{DB} \\ 0 & 0 & 0 & 1 \end{bmatrix}$$

where p^x is the recapture probability of an individual in state x . The observation recorded for a given individual in a given year, conditional on the underlying individual state, can then be modelled as a realization from a categorical process with probability vector corresponding to the individual's underlying state:

$$y_{it} \sim \text{dcat}(\theta[z_{it}, 1:4]) \quad \text{eqn.3}$$

b. Natal dispersal model

In the AD model presented above, both the survival and dispersal parameters correspond to apparent probabilities since all individuals dispersing outside the study area cannot be observed and are therefore un-distinguishable from dead individuals. We can however reformulate this model by expressing the apparent dispersal probability (Δ') as $\Delta * r$, the product of the dispersal probability (Δ) and the probability to remain in the study when dispersing (r). We can then construct a new model with a modified state-transition matrix (Ω):

$$\Omega = \begin{bmatrix} \Phi^S \cdot (1 - \Delta) \cdot (1 - h) & \Phi^S \cdot (1 - \Delta) \cdot h & \Phi^S \cdot \Delta \cdot r & (1 - \Phi^S) + \Phi^S \cdot \Delta \cdot (1 - r) \\ 0 & \Phi^{LB} & 0 & 1 - \Phi^{LB} \\ 0 & 0 & \Phi^{DB} & 1 - \Phi^{DB} \\ 0 & 0 & 0 & 1 \end{bmatrix}$$

Under this formulation, Δ is the true dispersal probability *i.e.* the probability to become dominant after dispersal (in or out of the study area) and Φ^S is the true survival probability. However, based on classical CR data, only the product as $\Delta * r$ is identifiable and we need additional information to estimate the probabilities to remain in the study area when dispersing r , and consequently Δ and Φ^S .

The probability to settle within the study area when dispersing is necessarily individual-specific as it depends on *i*) the location of the natal territory an individual is dispersing from,

ii) the dispersal direction, and *iii*) the distance travelled during dispersal (Gilroy *et al.* 2012).
 If we consider dispersal as homogeneous in direction, *i.e.* individuals have the same probability
 to choose any direction when dispersing, the probability to remain in the study area when
 dispersing can be calculated for each territory s and each potential dispersal distance d as:

$$r_{sd} = \frac{n_{sd}}{N_{sd}} \quad \text{eqn.4}$$

where n_{sd} and N_{sd} are the number of territories inside the study area and the total number of
 territories situated at a distance d from the natal territory s respectively. In other words, the
 probability to remain in the study area for an individual dispersing a distance d is equal to the
 proportion of territories situated at a distance d from its natal territory s where recapture is
 possible. Note that d refers to the minimum number of territories crossed between the natal and
 settlement territories, but the same method can be applied to more classical distance
 measurements such as the Euclidean distance between the centroids of territories.

In our situation, the location of the natal territory s was known for all individuals born
 within the study area and the dispersal distance d was known for individuals that dispersed and
 were recaptured within the study area but had to be inferred for *i*) individuals that dispersed
 and settled outside the study area and *ii*) individuals that dispersed and settled inside the study
 area but were never recaptured. Since we measured dispersal distances as the number of
 territories crossed between the natal and settlement territories, we modelled them as following
 a Poisson distribution to which we added 1:

$$d'_i \sim \text{Poisson}(\tau) \quad \text{eqn.5}$$

$$d_i = d'_i + 1 \quad \text{eqn.6}$$

The addition of 1 was used to enforce that all dispersers moved at least one territory away from
 their natal one. Note that if dispersal distances are measured in a different spatial unit, and/or
 depending on the species' characteristics, a different distribution can be used to model dispersal

distances, with the only constraint that it is strictly positive. Note also that the parameters of the chosen distribution may be functions of individual characteristics to investigate potential drivers of natal dispersal distances (see Alpine marmot example below).

4. Simulation study

To compare the two models presented above, we simulated different CR datasets with increasing mean dispersal distances τ from 0 to 12 territories with steps 0.5. We picked values of the other parameters in the model based on our knowledge of the Alpine marmot (Berger *et al.*, 2016; Dupont *et al.*, 2015; Ferrandiz-Rovira, 2015). We set the true survival probabilities to be equal and high for both breeder states ($\Phi^{DB} = \Phi^{LB} = 0.95$), and slightly lower for subordinates ($\Phi^S = 0.85$). We also considered that recapture probabilities differed between dominants and subordinates ($p^{DB} = p^{LB} = 0.65$ and $p^S = 0.95$). Dispersal probability Δ was set to 0.4 and inheritance probability h to 0.12. To avoid potential confounding effects due to the shape of the study area, it was randomly generated by sampling 35 cells from a 10×6 grid for each simulated data set, *i.e.* 35 territories where recaptures are possible were randomly selected. We simulated the dataset for 20 years of captures. Each year, with the exception of the last one, 40 individuals were newly captured leading to a total of 760 individuals in each simulated dataset. We randomly assigned the 760 individuals to one of the 35 territories and individual dispersal distances were sampled following eqn. 5 and 6 with the chosen value for τ . We assumed that the landscape was homogeneous, *i.e.* the habitat was suitable for settlement anywhere inside or outside the study area. Based on this map, a matrix of the probabilities to remain in the study area when dispersing for all territories and dispersal distances was constructed following eqn.4 (see also Supplementary Material 2). State-transition and observation matrices similar to those in the ND model were then filled with these different probabilities. Individual capture histories were generated using eqn.3 after sampling individual states using eqn.2. Dispersal distances were kept for individuals that dispersed and settled

inside the study area only to mimic true capture-recapture data. We repeated the simulation process 100 times for each value of τ , leading to a total of 2,500 simulated data sets. We then fitted both the AD and ND models to all simulated datasets and compared their parameter estimates.

5. Alpine marmot analysis

To account for the specifics of the Grande Sassi re reserve monitoring, the analysis of the Alpine marmot dataset incorporated additional features.

First, the number of family territories monitored each year varied over the course of the study between 10 and 35. Consequently, the probability for an individual to emigrate outside the study area and the probability to observe a dispersal event inside the study area also varied between years. To account for this change in the study area size and shape, we used annual maps representative of the territories' relative positions for each year.

Second, Alpine marmot territories are variable in size and disposition, meaning that the number of territories situated at a distance d can vary depending on the territory taken as reference. The matrix of territory-specific probabilities to remain in the study area when dispersing a distance d (r_{sd}) was thus calculated by hand based on the same annual maps of the territories.

Third, the Grande Sassi re study area is surrounded by high altitude mountain tops, where habitat is unsuitable for Alpine marmots. The homogeneous landscape and dispersal assumptions were therefore unrealistic. We have shown in a supplementary analysis that the proportion of suitable habitat outside the study area strongly influences both survival and dispersal estimates (see Supplementary Material 3), and we therefore discarded unsuitable areas surrounding the study area from the potential settlement territories (fig.2).

Fourth, following results from previous studies on the same population (Dupont *et al.*

2015; Berger *et al.* 2016; Rézouki *et al.* 2016), we considered recapture probabilities to vary with time, age and sex. In addition to the sex-effect in which we were interested, we accounted for age-specific subordinate survival and transitions probabilities by considering four age classes: juvenile (from zero to one-year-old), yearling (from one to two), subadult (from two to three) and adult (three years old and older). We also accounted for an effect of the logarithm of the number of male helpers on the juvenile survival, as it was shown to be an important driver of the juvenile survival during hibernation in this species (Allainé & Theuriau 2004; Dupont *et al.* 2015). Because no individual attained a dominant status before two years old, only the two last age classes were used for dominant individuals.

Finally, we considered sex-specific dispersal patterns, *i.e.* two independent Poisson distributions with sex-specific mean. The full set of model parameters was then $p_{t,age,sex}$ the time, age and sex-specific recapture probabilities, $\Phi^{IB}_{age,sex}$ and $\Phi^{LB}_{age,sex}$ the age and sex-specific survival probabilities of dominant individuals, $\Phi^S_{age,sex}$ the age and sex-specific survival probabilities of subordinate individuals, $\Delta_{age,sex}$ the age and sex-specific dispersal probabilities, $h_{age,sex}$ the age and sex-specific inheritance probabilities, r_i the individual-specific probability to remain in the study area when dispersing, and τ_{sex} the sex-specific mean dispersal distance. The R and JAGS script for the Alpine marmot analysis is provided in Supplementary Material 3.

6. Model fitting

All models were fitted using Markov Chain Monte Carlo (MCMC) simulations with the computer program JAGS (Plummer 2003) called through R3.2.5 (R core team 2016) via the R package jagsUI (Kellner 2014). All parameter priors were chosen to be weak or un-informative. All survival, dispersal, inheritance and recapture probabilities were given uniform priors between 0 and 1. The prior for the mean of the Poisson distribution in the ND model was given a vague gamma distribution $\Gamma(0.0001, 0.0001)$. All models in the simulation study were fitted

by running three independent MCMC chains of 10,000 iterations each with a burning period of 6,000 iterations, leading to 12,000 posterior MCMC samples per simulation. For the Alpine marmot analysis, we ran three chains of 15,000 iterations each with a burning period of 10,000 iterations, leading to a total of 15,000 posterior MCMC samples. We assessed convergence for all models by looking at parameter traceplots and calculating the potential scale reduction factor \hat{R} (Gelman & Rubin, 1992).

RESULTS

1. Simulation study

Based on the visual inspection and \hat{R} values (all parameters with $\hat{R} < 1.1$), we considered all simulation runs to have reached convergence. Both the AD and ND models returned unbiased estimates of the recapture probabilities (AD: posterior mean \pm se; $p^S = 0.95 \pm 0.01$ and $p^{DB} = p^{LB} = 0.65 \pm 0.02$; ND: $p^S = 0.95 \pm 0.01$ and $p^{DB} = p^{LB} = 0.65 \pm 0.02$), inheritance probability (AD: $h = 0.12 \pm 0.10$; ND: $h = 0.12 \pm 0.12$) and dominant survival probabilities (AD: $\Phi^{IB} = \Phi^{LB} = 0.95 \pm 0.01$; ND: $\Phi^{IB} = \Phi^{LB} = 0.95 \pm 0.01$) under all scenarios.

Subordinate survival and dispersal estimates, on the other hand, differed considerably between models. The AD model consistently under-estimated both parameters and this negative bias increased with mean dispersal distance to reach a lower plateau when the mean dispersal distance was larger than the maximum length of the study area d_{max} (fig.3). The estimated apparent dispersal probability Δ was between 26% and 99% lower than the simulated dispersal probability when the mean dispersal distance increased from 0 to 10 territories. In the same time, the apparent subordinate survival Φ^{IS} was estimated from 15% to 40% lower than the simulated value. Additionally, when the mean simulated dispersal distance was over d_{max} , the mean apparent dispersal estimates tended towards zero.

The pattern was different with the ND model. Although the difference between the

simulated and estimated values of both parameters also increased with increasing dispersal distances, it was consistently lower than for the AD model. The mean parameter estimates were at most 84% and 30% lower than the simulated values for the dispersal probability and subordinate survival probability respectively. Most importantly, the dispersal and subordinate survival estimates returned by the ND model were virtually unbiased ($< 1\%$) for simulated dispersal distances up to $0.5 d_{max} = 5$ territories and relatively small ($< 10\%$) up to $0.75 d_{max}$. By contrast, the negative bias in both dispersal and subordinate survival was at least 10% with the AD model.

The ND model was also able to accurately estimate the mean dispersal distance τ for a large range of simulated values (fig.4). However, we found that τ estimates decreased drastically when the simulated value reached d_{max} .

2. Sex-specific dispersal in the Alpine marmot

The 95% confidence intervals of the ND posterior estimates indicated that recapture probabilities varied with time and decreased with age. Differences in recapture probabilities (on the logit scale) between yearlings and two-years and between yearlings and adults were $\Delta p_{two} = -1.40 [-1.91; -0.94]$ and $\Delta p_{ad} = -1.90 [-2.37; -1.50]$ respectively. Recapture probabilities were also higher for females than for males (difference in recapture probabilities between females and males $\Delta p_{sex} = -0.28 [-0.55; -0.02]$). Mean dispersal distance was very similar between males and females ($\tau_{females} = 1.69 [1.55; 1.85]$ and $\tau_{males} = 1.71 [1.56; 1.86]$). As expected, juvenile subordinate survival increased with the logarithm of the number of male subordinates (helpers) present during hibernation for both sexes ($\beta_{help_m} = 0.41 [0.33; 0.49]$ for females and $0.53 [0.44; 0.61]$ for males on the logit scale). Subordinate survival increased with age but did not vary significantly between sexes although two-year-old subordinate males seemed to have a lower survival probability than females (fig.5a and table 1). Dispersal probabilities increased with age similarly for both sexes (fig.5b and table1). Inheritance

probabilities also varied with age and a sex difference was evidenced for the two-year age class (fig.5c and table1). Because inheritance is conditional on survival and dispersal, this indicates that females in their third year of life had more chances to inherit a dominant position than males. To help understand these results, figure 6 presents the fate of a cohort of subordinate individuals as the proportions of individuals in each state at each age as predicted by the model (fig.6).

Survival probabilities of young dominants, *i.e.* two-year age class, were higher than those of adults but no sex difference was evidenced for both locally recruited and immigrant breeders (table 1). Additionally, no difference between locally recruited and immigrant breeders was evidenced both for two-year-old ($\Delta\Phi_{sub}^{LB} = 10.43 [-34.32; 64.69]$ on a logit scale) and older dominants ($\Delta\Phi_{ad}^{LB} = 0.14 [-0.36; 0.63]$ on a logit scale).

DISCUSSION

1. Simulation study

With this study, we showed how using the spatial information associated with individual detections in a multi-state capture-recapture model can allow the estimation of unbiased natal dispersal and survival probabilities even when a significant proportion of the population settles outside the study area after dispersal. We also showed how the magnitude of the underestimation of these demographic parameters by classical multi-state models depends on the mean dispersal distance (relative to the study area size). The Natal Dispersal model presented here uses the information available on dispersal movements observed within the study area and the location of individual birth territories relative to the boundaries of the study area to estimate individual-specific probabilities to leave the study area when dispersing and discriminate between mortality and emigration. Using a single model to simultaneously estimate survival and natal dispersal patterns presents the double benefit of *i*) being able to estimate true instead of apparent survival and dispersal probabilities, and *ii*) account for the

imperfect detectability inherent in most field studies while rigorously propagating the resulting uncertainty to all parameter estimates.

The modularity of our approach also makes it flexible enough to be widely applicable. First, the matrix of probabilities to remain in the study area can be easily derived for any shape and discretization of the study area, whether it is based on territories, as in this study, or regular grid cells of the desired resolution. Second, the model for individual dispersal distances is easily modified to accommodate species-specific dispersal patterns through the use of other distributions (e.g. exponential or log-normal; Ergon & Gardner, 2014). It can also easily account for variation in dispersal patterns amongst individuals (e.g. sex-specific dispersal distributions in the Alpine marmot example). These reasons make our approach especially suitable to study natal dispersal in various biological systems including other rodent (e.g. Eurasian beaver (*Castor fiber*), Mayer *et al.*, 2017), carnivore (e.g. African wild dogs (*Lycaon pictus*), Behr *et al.*, 2020) or bird species (e.g. Egyptian vultures (*Neophron percnopterus*), Serrano *et al.*, 2021).

However, this approach still has some limitations. Notably, and as mentioned above, the performance of the model depends on the ratio of the mean dispersal distance relative to the size of the study area, *i.e.* on the proportion of dispersal events observable within the study area. When the mean dispersal distance becomes too large, most dispersers leave the study area and the model fails to estimate the correct dispersal distance distribution. In the extreme case, the dispersal distance is much larger than the study area and all dispersers settle outside. In such situation, the model has no information to rely on to estimate dispersal distances and considers that all dispersers are dead instead. In such situation, the choice of prior becomes crucial as in our simulation study, where the choice of a gamma distribution with mass close to 0 led to underestimating the mean dispersal distance. Checking the sensitivity of the estimates to the choice of prior for the dispersal distance parameter is thus highly recommended. As noted

by Schaub & Royle (2014): “if censoring becomes too strong (dispersal distances very large relative to the size of the study area), [the] model is not successful anymore in correctly estimating dispersal and consequently survival. But it is hard to imagine that any model would succeed in obtaining meaningful estimates in this case.”. It is thus crucial when studying dispersal to ensure that the dataset at hands contains enough observed dispersal events to accurately estimate dispersal distances. According to our simulation results, the study area should be twice as long as the mean dispersal distance to ensure good estimation of the dispersal pattern.

Another aspect worth-considering is that the efficiency of the model to produce unbiased natal dispersal and survival estimates likely depends on the assumed dispersal distance distribution being correct, which raises the problem of selecting a good dispersal model. In our example, we used a Poisson distribution, which seems like an adequate choice for the Alpine marmots, based on the vast majority of short-distanced and low variance in dispersal events we observed (at least much shorter than the size of the study area). However, it is not possible to rule out the possibility that some individuals display a different dispersal strategy and move much longer distances. In that case, a bimodal distribution or a distribution with a longer tail would probably be a better fit although it could not be detected from the data (Dupont *et al.*, 2021). Alternative dispersal distance distributions, associated with specialized goodness of fit tests (such as Bayesian p-values, *e.g.* Ergon & Gardner, 2014) have the potential to help identify a good dispersal distribution, although the power of such analysis to identify the correct dispersal distance distribution based on such data is still an open question.

Finally, our second simulation study stresses out the importance to correctly specify the available habitat both within and outside the study area. If no information is available about the suitability of the surrounding habitat and one assumes dispersers may settle anywhere outside the study area, inferences about the dispersal pattern, and therefore about survival, may

be inaccurate (see Supplementary Material). It is therefore crucial to correctly characterize the habitat suitability outside the study area, either by using prior knowledge (as in our study case) or through a more formal analysis (*e.g.* habitat selection studies).

Other studies tackled the question of apparent survival in a capture-recapture context (Ergon & Gardner, 2014; Gilroy *et al.*, 2012; Schaub & Royle, 2014). Gilroy *et al.* (2012) proposed a modelling approach in which they first estimate a dispersal kernel for the study species from which they derive emigration probability for each marked individual to adjust apparent survival estimates obtained from a separate capture-recapture model. Estimating the dispersal distance distribution within the capture-recapture model as we did here presents the advantage to allow for a better propagation of uncertainty in the different parameters of the model. Ergon & Gardner (2014) and Schaub & Royle (2014) also used a framework that does not require to separately estimate individual emigration probabilities outside the capture-recapture model. Instead, they used open-population spatial capture-recapture models, which explicitly model the location of each individual at each time step, even if outside the study area, thus only implicitly modelling individual emigration probabilities. Whilst relatively similar to our approach, spatial capture-recapture models present the benefit of being able to infer the movement of individuals between any two consecutive occasions thereby making it theoretically possible to also study breeding dispersal. The downside of this approach is that modelling individual locations at each time step comes at a big computational cost for already computationally intensive models (but see Bischof *et al.*, 2020; Milleret *et al.*, 2019; Turek *et al.*, 2021).

2. Sex-specific dispersal in the Alpine marmot

The application of the Natal Dispersal model to the Alpine marmot dataset shed new light on the dispersal process in this species. Notably, we obtained estimates of adult subordinate survival much higher than in previous CR studies of the same population (0.99 against 0.53 in

Dupont *et al.* 2015). We also estimated the probability to become dominant through dispersal to be higher than previous estimates even though no difference was made between inheritance and dispersal (0.58 against 0.45 in Rézouki *et al.* 2016). In addition, we estimated the probability to become dominant through dispersal to not differ between sexes contrary to the inheritance probability where we estimated that females had three times as much chances of inheriting the dominant position than males. Based on the estimated mean dispersal distance for both sexes ($\tau_{females} = 1.69 [1.55; 1.85]$ and $\tau_{males} = 1.71 [1.56; 1.86]$) relative to the size of the study area, and the results from the simulation study, we are confident that these estimates are not underestimating the true survival and dispersal probabilities of subordinate Alpine marmots. While we observed a decrease in estimated dispersal distance for simulated dispersal distances larger than the size of the study area in our simulation study, this was accompanied by a decrease in both survival and dispersal probabilities; a pattern we did not observe in the Alpine marmot. Finally, and as expected from the results of the simulation study, the other parameter estimates (*i.e.* recapture probabilities, juvenile survival and dominant survival) were consistent with previous capture-recapture studies on the same population (Cohas *et al.* 2009; Dupont *et al.* 2015; Berger *et al.* 2016; Rézouki *et al.* 2016). These results suggest that the vast majority of subordinate individuals are in fact able to become dominant if they survive their two first winters and that the high mortality reported for subordinate sub-adults and adults in previous studies was almost entirely due to dispersal outside the study area (fig.6).

Contrary to what is generally reported in the literature for mammals, neither the proportion of dispersers (*i.e.* the age-specific dispersal probability) nor the dispersal pattern (*i.e.* the mean dispersal distance) differed between sexes (Dobson 2013). This absence of sex-specific dispersal pattern is not so surprising for a monogamous and monomorphic mammal such as the Alpine marmot (Lukas & Clutton-Brock 2012). However, this absence of sex difference in dispersal probability should be considered with caution, given the formulation of

our model. Because dispersal probability only reflects successful dispersal, *i.e.* individuals that dispersed *and* became dominant in another territory, it does not reflect the dispersal “decision”, *i.e.* the probability that an individual leaves its natal territory, independently of the success of this dispersal. This probability cannot be estimated using our model because no information was available about dispersing individuals that failed to become dominant (*i.e.* floaters). These unsuccessful dispersers disappeared from the dataset and most likely died in the process (Lardy *et al.* 2011). The slight difference in survival of two-year-old subordinates males and females (and the difference in the proportion of dead males and females; fig.6) is in accordance and tends to indicate that a greater number of males disperse after their second winter compared to females. This would also indicate a lower probability of success and therefore a higher cost of dispersal for males. This alleged male-biased natal dispersal, although unexpected from theory for a monogamous mammal, might be explained in Alpine marmots by the possibility of extra-pair paternities. Although reproduction is largely suppressed in subordinate Alpine marmots (Arnold & Dittami, 1997; Hackländer *et al.*, 2003), dominant females have the possibility to mate with multiple males, including subordinates from other families and Cohas *et al.* (2008) found that most extra-pair paternities in the Grande Sassi re population were the result of male dispersers (80% of litters containing extra-pair young). This possibility for subordinate males to access reproduction through extra-pair copulation, even when failing to secure a dominant position, suggests that the expected fitness of a dispersing male is likely to be higher than that of a female. This could explain why more male subordinates disperse despite higher levels of competition among males to disperse and access reproduction, as suggested by the lower survival of two-year-old subordinate males. The higher proportion of females inheriting the dominant position from their mother (fig.6) also suggests female-biased philopatry (or equivalently male-biased dispersal). However, further research on factors triggering dispersal and dispersal costs in this species is needed to confirm these interpretations.

To determine whether males truly dispersed more than females would require taking into account the success of the dispersal event for each individual, *i.e.* disentangle “natural mortality” from “dispersal related mortality”. Such model requires additional information about individuals during dispersal or about their fate. Potential data types useable for this purpose are GPS-collar data and dead recoveries. Incorporating information about when and where individuals go after leaving their territories or where and when they were found dead would potentially allow to estimate what proportion of the dispersing individuals dies in the process. Unfortunately, these solutions are unlikely to work for Alpine marmots as marmots are almost always never recovered (they are either eaten by predators or die inside their burrows) and GPS methods are generally unfit for ground-dwelling species.

To conclude, the ND model we presented here is a new step towards a more complete and realistic assessment of natal dispersal and its drivers for which biologists of many fields have a great interest. As all models, it presents some limitations, but, with a clear understanding of its underlying assumptions, it can contribute to increasing the knowledge about this central phenomenon in population biology that is natal dispersal.

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585 **Conflict of interest:** The authors declare that they have no conflict of interest.

586 **Data availability statement:** data, R, JAGS and NIMBLE scripts to reproduce the simulation
587 study and marmot analysis are available from the GitHub repository:
588 <https://github.com/PierreDupont/marmotDispersal>

589 **Supplementary material 1:** Additional simulation study results.pdf

590 **Supplementary material 2:** Landscape heterogeneity effect on estimates from the Natal
591 Dispersal capture-recapture model.pdf

592 **Supplementary material 3:** Simulation study JAGS model scripts.pdf

593 **Supplementary material 4:** Alpine marmot Natal Dispersal JAGS model.pdf

594

595 1- Landscape heterogeneity effect on estimates from the Natal Dispersal capture-recapture
596 model.pdf

597 2- Simulation study R and Jags script.pdf

598 3- Alpine marmot analysis R and Jags script.pdf

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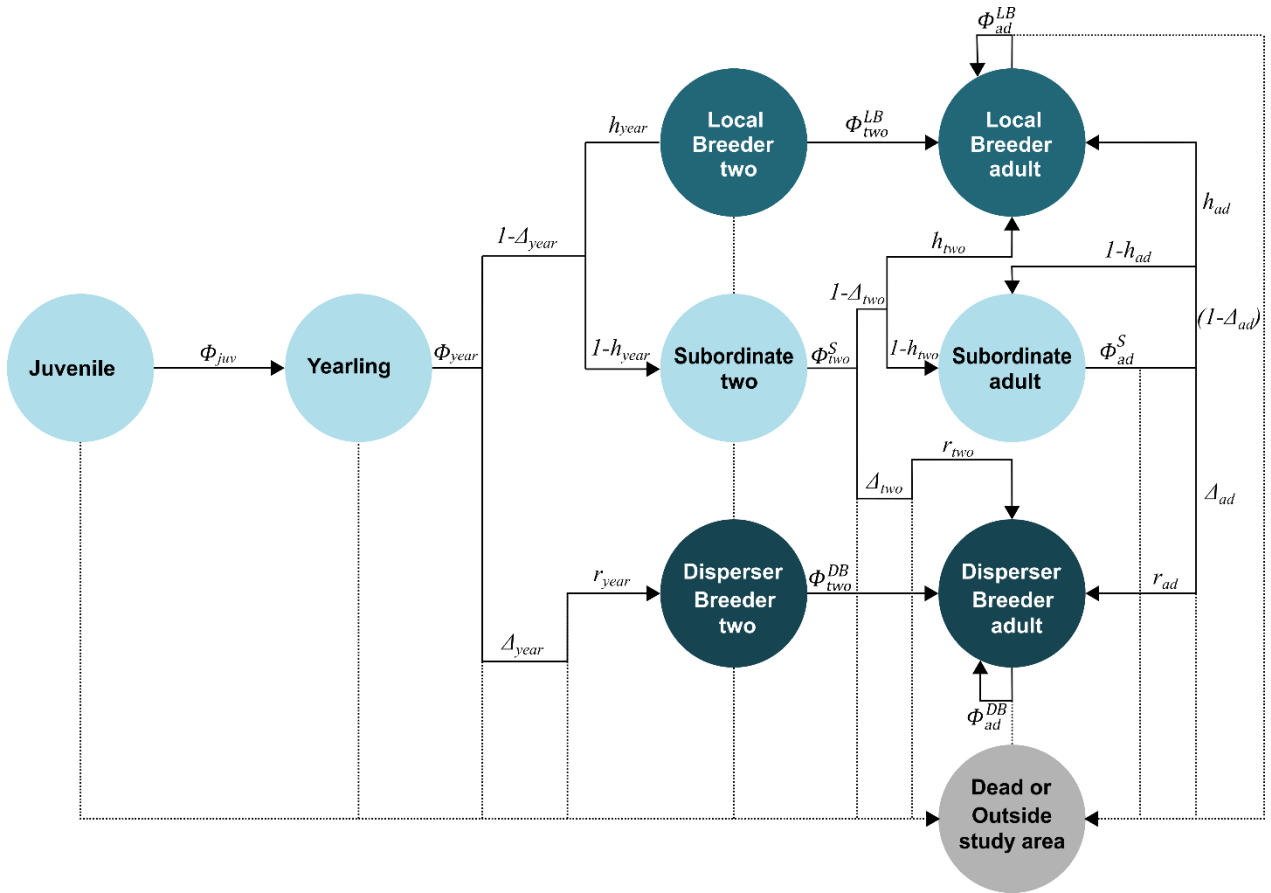


Figure 1. Schematic representation of the Alpine marmot's life cycle as used in the natal dispersal capture-recapture model. Solid lines indicate transitions between observable states while dotted lines indicate transitions to un-observable states. Parameters are survival (Φ), dispersal (Δ) and inheritance probabilities (h), as well as r , the probability to remain in the study area when dispersing. Subscripts correspond to the age classes: juveniles, yearlings, two-year-olds and adults.

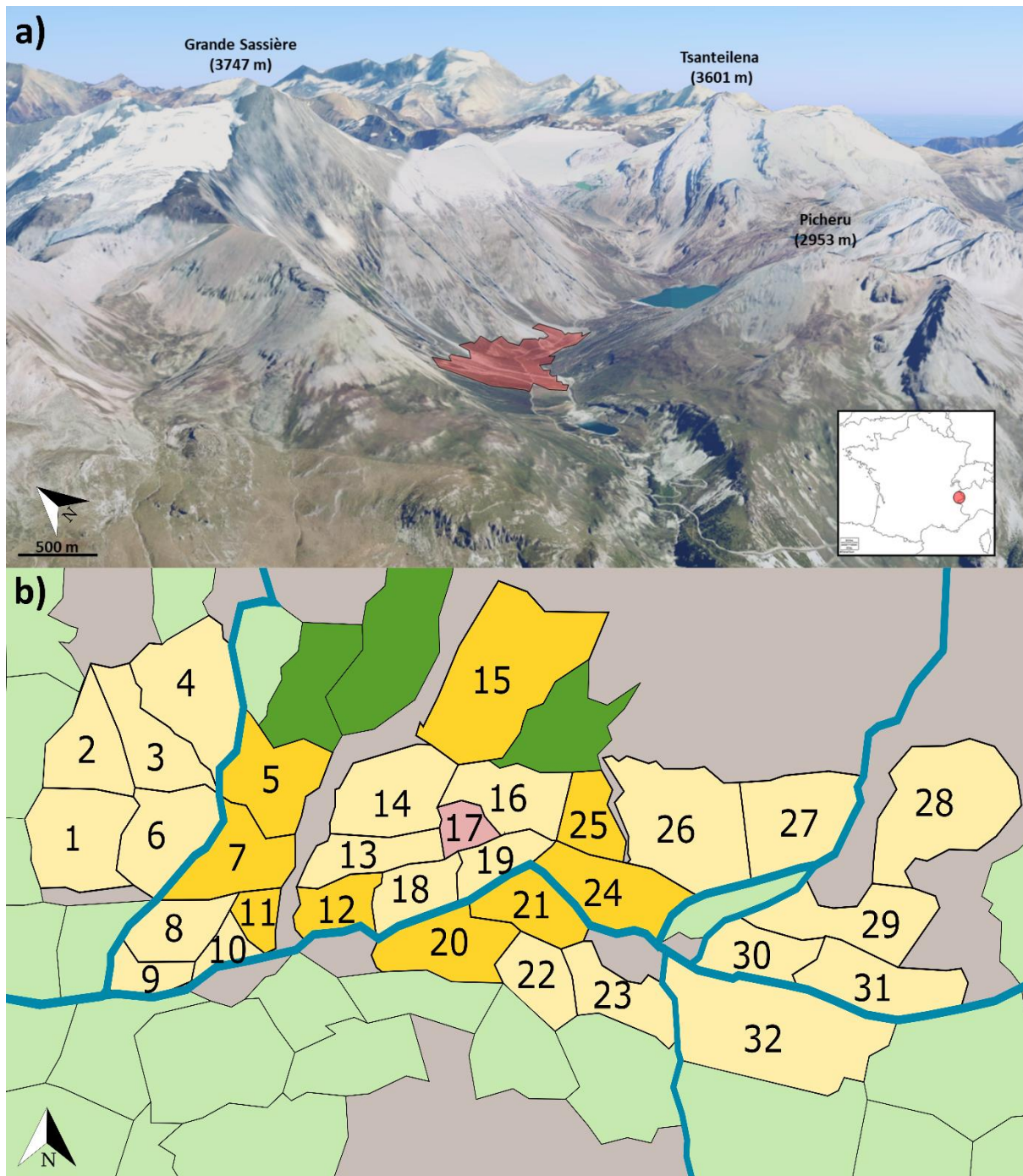
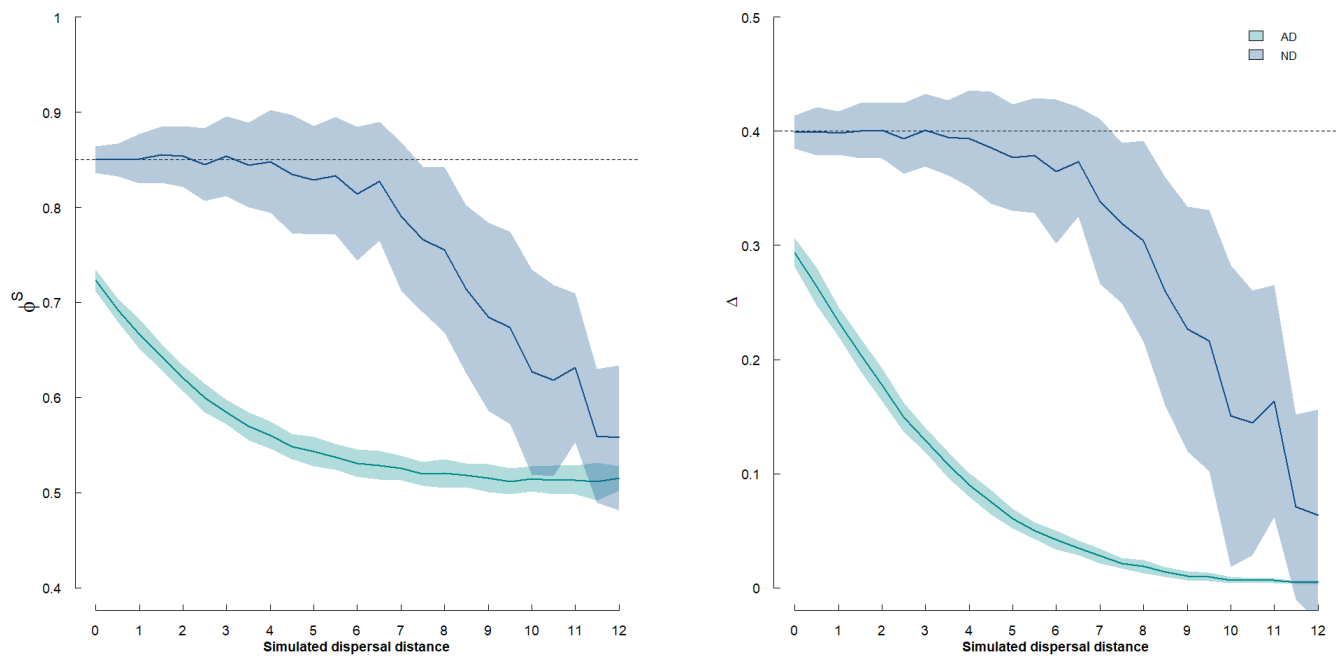


Figure 2. 3D (a) and schematic map (b) of the Grande Sassi re nature reserve and marmot territories monitored in 2015. Numbered polygons represent monitored territories. Green polygons represent territories outside the study area suitable for Alpine marmots. Grey areas represent unsuitable habitat (rocky and snowy areas). The probability to stay in the study area when dispersing a given distance d is calculated as the number of territories monitored divided by the total number of territories situated at a distance d from the territory of origin. For

766 example, an individual that leaves from territory 17 (in light red) and travels a distance $d = 2$,
767 will have a probability to settle in a monitored territory of $r_{13,2} = 9$ (territories in bright
768 yellow)/12 (territories in bright yellow + bright green) = 0.75.

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772 **Figure 3.** Mean subordinate survival (Φ^S) and dispersal probabilities (Δ) estimates returned by
 773 the Apparent Dispersal (AD) and Natal Dispersal (ND) models for increasing mean dispersal
 774 distances. Solid lines represent the mean over 100 replicates and shaded areas represent the
 775 associated 95% confidence intervals. Horizontal dashed lines indicate simulated values of the
 776 parameter.

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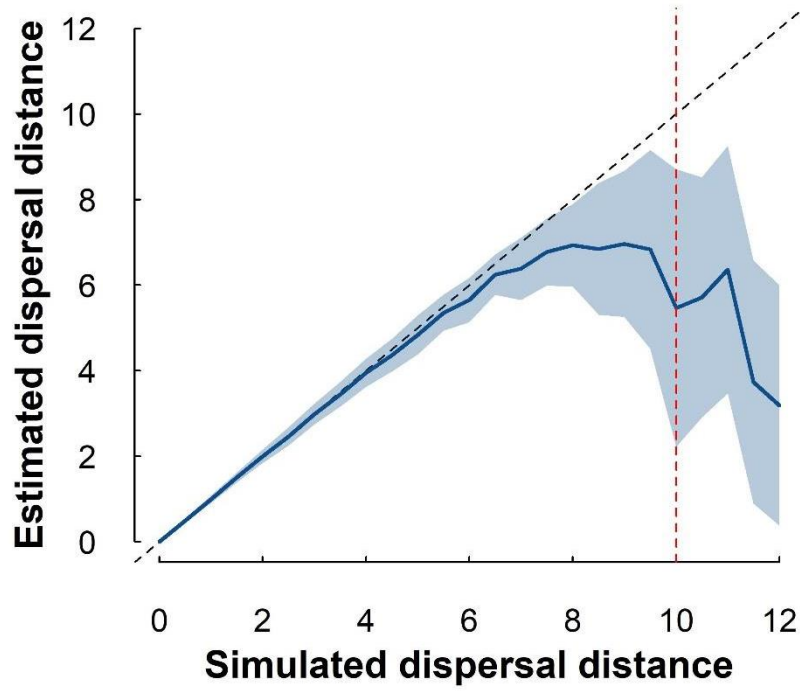


Figure 4. Simulated and estimated dispersal distance for the Natal Dispersal model. Solid line represents the mean over 100 replicates and the shaded area the associated 95% confidence interval. Vertical dashed line indicates the maximal distance between two territories inside the study area (d_{max}).

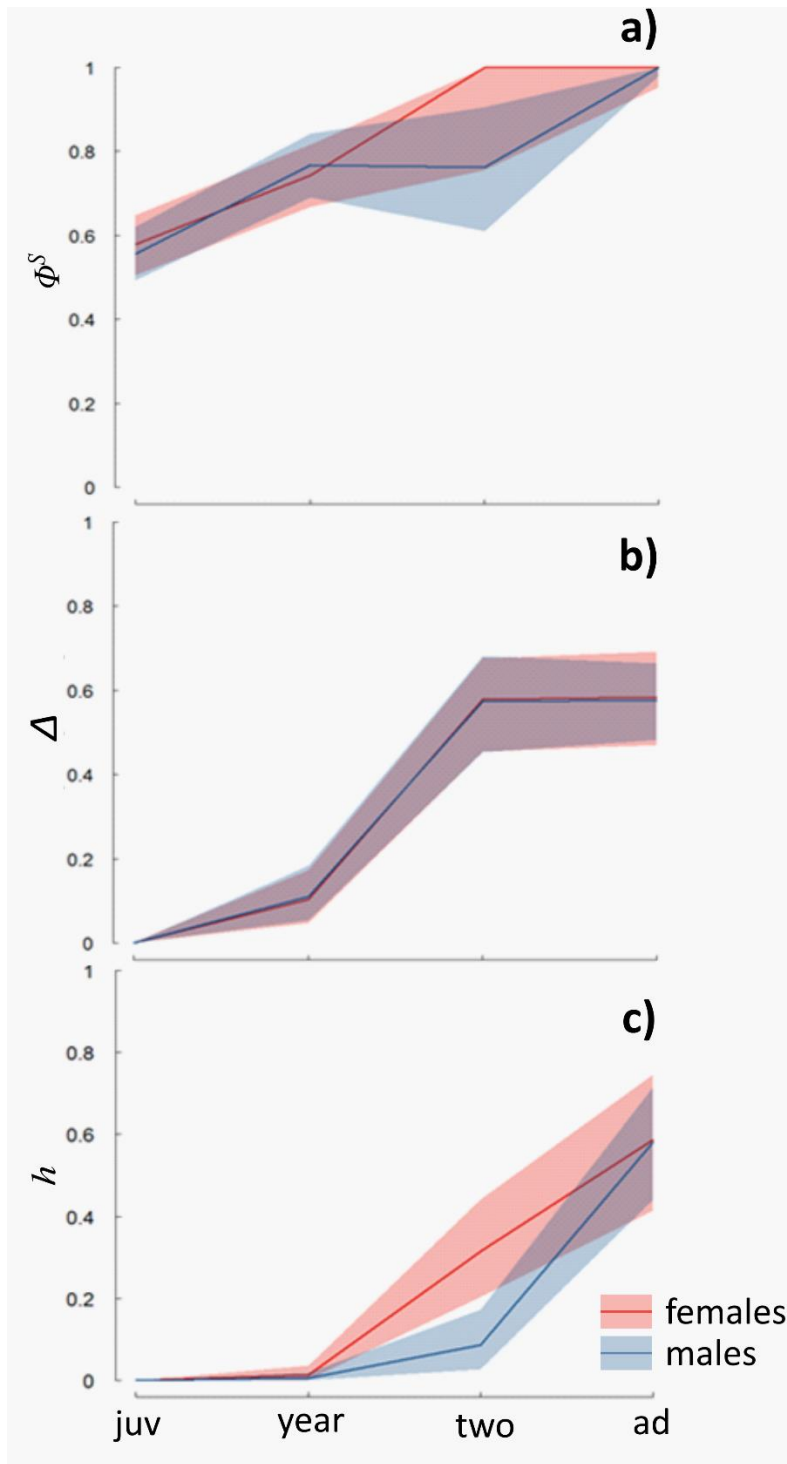
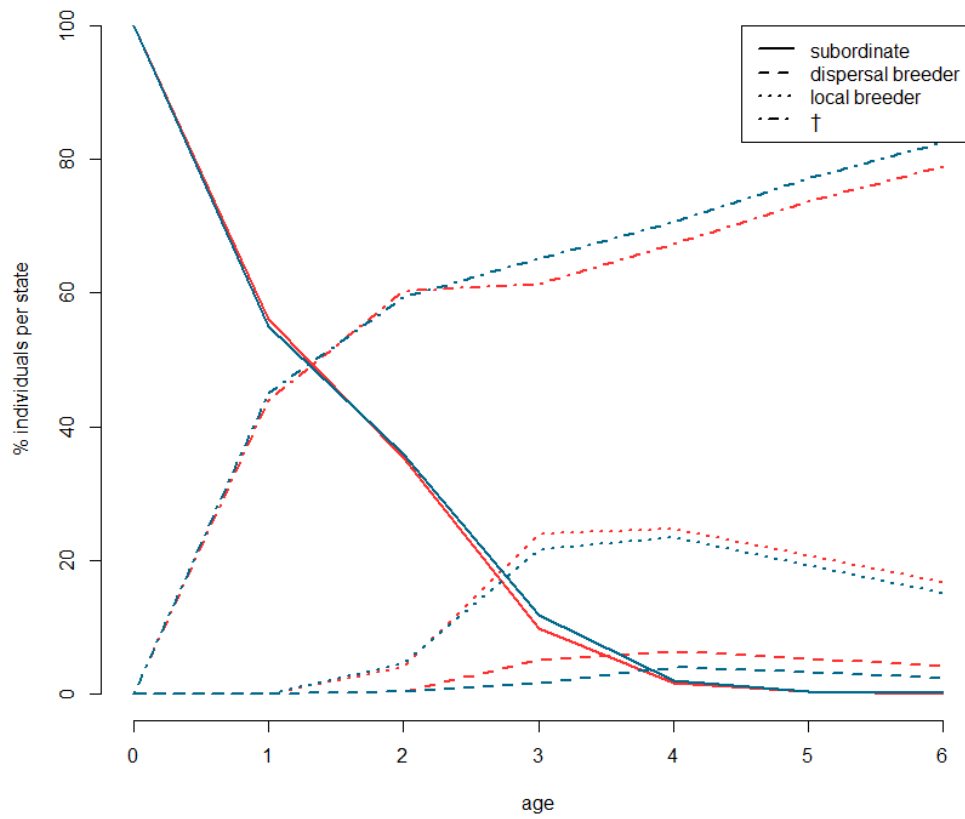


Figure 5. Age- and sex-specific survival Φ (a), dispersal Δ (b), and inheritance h (c) probabilities of Alpine marmots according to the ND model. Solid lines represent the mean posterior estimates and shaded areas represent the standard error of the mean associated to each parameter.



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789 **Figure 6.** Fate of a cohort of Alpine marmots with age for females (red lines) and males (blue

790 lines) as predicted by the Natal Dispersal model fitted to the Grande Sassi re dataset.

Table.1 Age- and sex-specific posterior mean estimates (standard deviation) of the survival, dispersal and inheritance probabilities of Alpine marmots. Sex difference indicates if the 95% credible interval of the sex difference parameter does not overlap the value 0.

parameter	females	males	sex difference
Φ_{juv}^S	0.56 (0.03)	0.55 (0.02)	NO
Φ_{year}^S	0.71 (0.04)	0.74 (0.04)	NO
Φ_{two}^S	0.97 (0.05)	0.84 (0.11)	NO
Φ_{ad}^S	0.99 (0.01)	0.99 (0.01)	NO
Φ_{two}^{LB}	0.99 (0.04)	0.99 (0.07)	NO
Φ_{ad}^{LB}	0.78 (0.03)	0.70 (0.04)	NO
Φ_{two}^{IB}	0.99 (0.06)	0.99 (0.10)	NO
Φ_{ad}^{IB}	0.80 (0.03)	0.77 (0.03)	NO
Δ_{juv}	0.00 (0.00)	0.00 (0.00)	NO
Δ_{year}	0.10 (0.03)	0.11 (0.03)	NO
Δ_{two}	0.58 (0.06)	0.57 (0.06)	NO
Δ_{ad}	0.58 (0.06)	0.58 (0.05)	NO
h_{juv}	0.00 (0.00)	0.00 (0.00)	NO
h_{year}	0.01 (0.01)	0.01 (0.01)	NO
h_{two}	0.32 (0.06)	0.09 (0.04)	YES
h_{ad}	0.59 (0.09)	0.58 (0.07)	NO