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

3 **An application to the Alpine marmot.**

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25 **ABSTRACT**

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

47

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

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

50

51 INTRODUCTION

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

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

76 individuals dispersing elsewhere will be confounded with dead individuals if no additional
77 information is considered (*e.g.* dead recoveries or count surveys from other sites; Péron *et al.*
78 2010). It is then crucial to deal with the issues of “apparent survival” and “apparent dispersal”
79 if one wants to study natal dispersal using CR data.

80 In most CR studies, ancillary information about individual movements is readily
81 available, as the locations of captures/detections are generally recorded in addition to the
82 identity of the individual. This source of information was usually neglected but the emergence
83 of spatial capture-recapture (SCR: Borchers & Efford, 2008, Royle & Young, 2008) together
84 with the democratization of highly flexible softwares for Bayesian analyses using Markov
85 Chain Monte Carlo (MCMC) methods (BUGS: Lunn *et al.*, 2000, JAGS: Plummer, 2003,
86 NIMBLE: DeValpine *et al.*, 2017) recently motivated several attempts to use this additional
87 information to solve the “apparent survival” problem (Schaub & Royle 2014. Ergon & Gardner
88 2014). Whilst originally thought as a way to account for the lower detection probabilities of
89 animals living at the fringe of a given study area, SCR models also present a great potential for
90 studying animal movements (Bischof, Milleret, *et al.*, 2020; Chandler & Clark, 2014).

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

101 MATERIAL AND METHODS

102 1. Alpine marmot life cycle

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

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

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

125 takes place shortly after coming out of hibernation (Stephens *et al.* 2002). Subordinates that
126 stay in the family group may become dominant by inheriting the position in their natal territory
127 following the death of the same-sex dominant while dispersers have to evict the same-sex
128 dominant from another territory (Dupont *et al.*, 2015). A third possibility to access a dominant
129 status is the creation of a new territory by a couple of dispersing individuals, but this is highly
130 unusual in the saturated population under study (only 3 occurrences in 25 years of the study).
131 Once a subordinate disperses, it can either succeed or fail in securing a dominant position, but
132 it never joins a new family group as subordinate. In case of failure in reaching a dominant
133 status during the active season, the disperser becomes a floater, *i.e.* a wandering individual
134 forced to hibernate alone and consequently exposed to very high risks of mortality (Magnolon
135 1999). Once the dominant position is secured, a marmot can remain dominant for several years
136 until death or eviction by a new incomer (Lardy *et al.*, 2011). When evicted, dominant
137 individuals also become floaters subject to a very high risk of mortality (Grimm *et al.*, 2003)
138 and they usually never become dominant elsewhere. Dispersal in the Alpine marmot is
139 therefore exclusively natal dispersal. Hence, we did not consider the possibility for evicted
140 dominants to become dominant elsewhere in this study (fig.1).

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

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

152 **2. Alpine marmot dataset**

153 The Alpine marmot population from the Grande Sassière Nature Reserve (French Alps,
154 45°29'N, 65°90'E) has been studied since 1990. Between 10 and 35 family groups have been
155 monitored each year using capture-mark-recapture and daily observations. Marmot territories
156 are situated at the bottom of a small valley on either side of a touristic trail crossing the lower
157 part of the reserve. The study area covers an average of 75 ha (1.5 km long and 0.5 km wide),
158 and is situated at approx. 2,340 m.a.s.l. The valley is surrounded by high altitude mountain
159 peaks (> 3,500 m.a.s.l.) and steep slopes on both sides. Whilst the flat part of the valley is
160 suitable for the establishment of Alpine marmot territories, steeper parts are unsuitable given
161 the thickness and instability of snow-packs, rocks and the quasi-absence of vegetation (Allainé
162 *et al.* 1994, López *et al.* 2010; fig.2).

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

174 Once captured, individuals were placed in an opaque bag before being anesthetized with Zolétil
175 100 (0.1 mL kg⁻¹). They were then sexed, aged from their size (up to 3 years) if the exact age
176 was unknown, and their social status was determined based on scrotal development for males
177 and teats development for females. All individuals were individually marked using both a
178 transponder chip injected under the skin of the neck and a numbered metal ear-tag (right ear
179 for females and left for males to facilitate later observation). An additional colored plastic ear
180 tag was placed on the opposite ear for dominant individuals. Captured marmots were also
181 marked on the back with temporary hair dye to help identify them during subsequent
182 observations in the following 7 to 15 days and verify their dominance status as well as their
183 assignment to a family territory. When tranquilized marmots recovered, they were returned to
184 their territory (see Cohas *et al.*, 2006 for more details on protocol).

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

189 **3. Multi-State Capture-Recapture models**

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

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

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

206 **a. Apparent dispersal model**

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

$$209 \quad z_{if_i} \sim \text{dcat}(\alpha) \quad \text{eqn.1}$$

210 where α is a probability vector of length 3 with a Dirichlet distribution. The Dirichlet
211 distribution enforces the constraint $\sum \alpha = 1$. From this initial state, each individual has the
212 possibility to transition to the other states or remain in its current one each year. Each year a
213 subordinate individual may survive (probability Φ'^S), stay on its natal territory (probability $1 -$
214 Δ'), and remain a subordinate (probability $1 - h$) with overall probability $\Phi'^S \cdot (1 - \Delta') \cdot (1 -$
215 $h)$. It can also survive and inherit a dominant position on its natal territory (transition to state
216 *LB*) with probability $\Phi'^S \cdot (1 - \Delta') \cdot h$, disperse and reach a dominant position elsewhere *within*
217 *the study area* (transition to state *DB*) with probability $\Phi'^S \cdot \Delta'$, or die or disperse outside the
218 study area with probability $1 - \Phi'^S$ (transition to state †). Note that here, Φ'^S is the probability
219 that a subordinate individual survives *and does not leave the study area* between two
220 consecutive occasions, Δ' is the probability that a subordinate individual disperses and becomes
221 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 † 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):

243
$$\theta = \begin{bmatrix} p^S & 0 & 0 & 1 - p^S \\ 0 & p^{LB} & 0 & 1 - p^{LB} \\ 0 & 0 & p^{DB} & 1 - p^{DB} \\ 0 & 0 & 0 & 1 \end{bmatrix}$$

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

248
$$y_{it} \sim \text{dcat}(\theta[z_{it}, 1:4]) \quad \text{eqn.3}$$

249 **b. Natal dispersal model**

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

256
$$\Omega = \begin{bmatrix} \Phi^S \cdot (1 - \Delta) \cdot (1 - h) & \Phi^S \cdot (1 - \Delta) \cdot h & \Phi^S \cdot \Delta \cdot r & (1 - \Phi^S) + \Phi^S \cdot \Delta \cdot (1 - r) \\ 0 & \Phi^{LB} & 0 & 1 - \Phi^{LB} \\ 0 & 0 & \Phi^{DB} & 1 - \Phi^{DB} \\ 0 & 0 & 0 & 1 \end{bmatrix}$$

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

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

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

$$268 \quad r_{sd} = \frac{n_{sd}}{N_{sd}} \quad \text{eqn.4}$$

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

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

$$283 \quad d'_i \sim \text{Poisson}(\tau) \quad \text{eqn.5}$$

$$284 \quad d_i = d'_i + 1 \quad \text{eqn.6}$$

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

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

291 **4. Simulation study**

292 To compare the two models presented above, we simulated different CR datasets with
293 increasing mean dispersal distances τ from 0 to 12 territories with steps 0.5. We picked values
294 of the other parameters in the model based on our knowledge of the Alpine marmot (Berger *et*
295 *al.*, 2016; Dupont *et al.*, 2015; Ferrandiz-Rovira, 2015). We set the true survival probabilities
296 to be equal and high for both breeder states ($\Phi^{DB} = \Phi^{LB} = 0.95$), and slightly lower for
297 subordinates ($\Phi^S=0.85$). We also considered that recapture probabilities differed between
298 dominants and subordinates ($p^{DB} = p^{LB} = 0.65$ and $p^S = 0.95$). Dispersal probability Δ was set
299 to 0.4 and inheritance probability h to 0.12. To avoid potential confounding effects due to the
300 shape of the study area, it was randomly generated by sampling 35 cells from a 10×6 grid for
301 each simulated data set, *i.e.* 35 territories where recaptures are possible were randomly selected.
302 We simulated the dataset for 20 years of captures. Each year, with the exception of the last one,
303 40 individuals were newly captured leading to a total of 760 individuals in each simulated
304 dataset. We randomly assigned the 760 individuals to one of the 35 territories and individual
305 dispersal distances were sampled following eqn. 5 and 6 with the chosen value for τ . We
306 assumed that the landscape was homogeneous, *i.e.* the habitat was suitable for settlement
307 anywhere inside or outside the study area. Based on this map, a matrix of the probabilities to
308 remain in the study area when dispersing for all territories and dispersal distances was
309 constructed following eqn.4 (see also Supplementary Material 2). State-transition and
310 observation matrices similar to those in the ND model were then filled with these different
311 probabilities. Individual capture histories were generated using eqn.3 after sampling individual
312 states using eqn.2. Dispersal distances were kept for individuals that dispersed and settled

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

317 **5. Alpine marmot analysis**

318 To account for the specifics of the Grande Sassièrè reserve monitoring, the analysis of the
319 Alpine marmot dataset incorporated additional features.

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

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

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

336 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

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

368 **RESULTS**

369 **1. Simulation study**

370 Based on the visual inspection and \widehat{R} values (all parameters with $\widehat{R} < 1.1$), we considered all
371 simulation runs to have reached convergence. Both the AD and ND models returned unbiased
372 estimates of the recapture probabilities (AD: posterior mean \pm se; $p^S = 0.95 \pm 0.01$ and $p^{DB} =$
373 $p^{LB} = 0.65 \pm 0.02$; ND: $p^S = 0.95 \pm 0.01$ and $p^{DB} = p^{LB} = 0.65 \pm 0.02$), inheritance probability
374 (AD: $h = 0.12 \pm 0.10$; ND: $h = 0.12 \pm 0.12$) and dominant survival probabilities (AD: $\Phi^{IB} =$
375 $\Phi^{LB} = 0.95 \pm 0.01$; ND: $\Phi^{IB} = \Phi^{LB} = 0.95 \pm 0.01$) under all scenarios.

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

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

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

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

397 **2. Sex-specific dispersal in the Alpine marmot**

398 The 95% confidence intervals of the ND posterior estimates indicated that recapture
399 probabilities varied with time and decreased with age. Differences in recapture probabilities
400 (on the logit scale) between yearlings and two-years and between yearlings and adults were
401 $\Delta p_{two} = -1.40 [-1.91; -0.94]$ and $\Delta p_{ad} = -1.90 [-2.37; -1.50]$ respectively. Recapture probabilities
402 were also higher for females than for males (difference in recapture probabilities between
403 females and males $\Delta p_{sex} = -0.28 [-0.55; -0.02]$). Mean dispersal distance was very similar
404 between males and females ($\tau_{females} = 1.69 [1.55; 1.85]$ and $\tau_{males} = 1.71 [1.56; 1.86]$). As
405 expected, juvenile subordinate survival increased with the logarithm of the number of male
406 subordinates (helpers) present during hibernation for both sexes ($\beta_{help_m} = 0.41 [0.33; 0.49]$ for
407 females and $0.53 [0.44; 0.61]$ for males on the logit scale). Subordinate survival increased with
408 age but did not vary significantly between sexes although two-year-old subordinate males
409 seemed to have a lower survival probability than females (fig.5a and table 1). Dispersal
410 probabilities increased with age similarly for both sexes (fig.5b and table1). Inheritance

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

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

422 DISCUSSION

423 1. Simulation study

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

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

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

450 However, this approach still has some limitations. Notably, and as mentioned above,
451 the performance of the model depends on the ratio of the mean dispersal distance relative to
452 the size of the study area, *i.e.* on the proportion of dispersal events observable within the study
453 area. When the mean dispersal distance becomes too large, most dispersers leave the study area
454 and the model fails to estimate the correct dispersal distance distribution. In the extreme case,
455 the dispersal distance is much larger than the study area and all dispersers settle outside. In
456 such situation, the model has no information to rely on to estimate dispersal distances and
457 considers that all dispersers are dead instead. In such situation, the choice of prior becomes
458 crucial as in our simulation study, where the choice of a gamma distribution with mass close to
459 0 led to underestimating the mean dispersal distance. Checking the sensitivity of the estimates
460 to the choice of prior for the dispersal distance parameter is thus highly recommended. As noted

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

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

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

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

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

507 **2. Sex-specific dispersal in the Alpine marmot**

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

511 Dupont *et al.* 2015). We also estimated the probability to become dominant through dispersal
512 to be higher than previous estimates even though no difference was made between inheritance
513 and dispersal (0.58 against 0.45 in Rézouki *et al.* 2016). In addition, we estimated the
514 probability to become dominant through dispersal to not differ between sexes contrary to the
515 inheritance probability where we estimated that females had three times as much chances of
516 inheriting the dominant position than males. Based on the estimated mean dispersal distance
517 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
518 the study area, and the results from the simulation study, we are confident that these estimates
519 are not underestimating the true survival and dispersal probabilities of subordinate Alpine
520 marmots. While we observed a decrease in estimated dispersal distance for simulated dispersal
521 distances larger than the size of the study area in our simulation study, this was accompanied
522 by a decrease in both survival and dispersal probabilities; a pattern we did not observe in the
523 Alpine marmot. Finally, and as expected from the results of the simulation study, the other
524 parameter estimates (*i.e.* recapture probabilities, juvenile survival and dominant survival) were
525 consistent with previous capture-recapture studies on the same population (Cohas *et al.* 2009;
526 Dupont *et al.* 2015; Berger *et al.* 2016; Rézouki *et al.* 2016). These results suggest that the vast
527 majority of subordinate individuals are in fact able to become dominant if they survive their
528 two first winters and that the high mortality reported for subordinate sub-adults and adults in
529 previous studies was almost entirely due to dispersal outside the study area (fig.6).

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

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

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

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

576

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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

599

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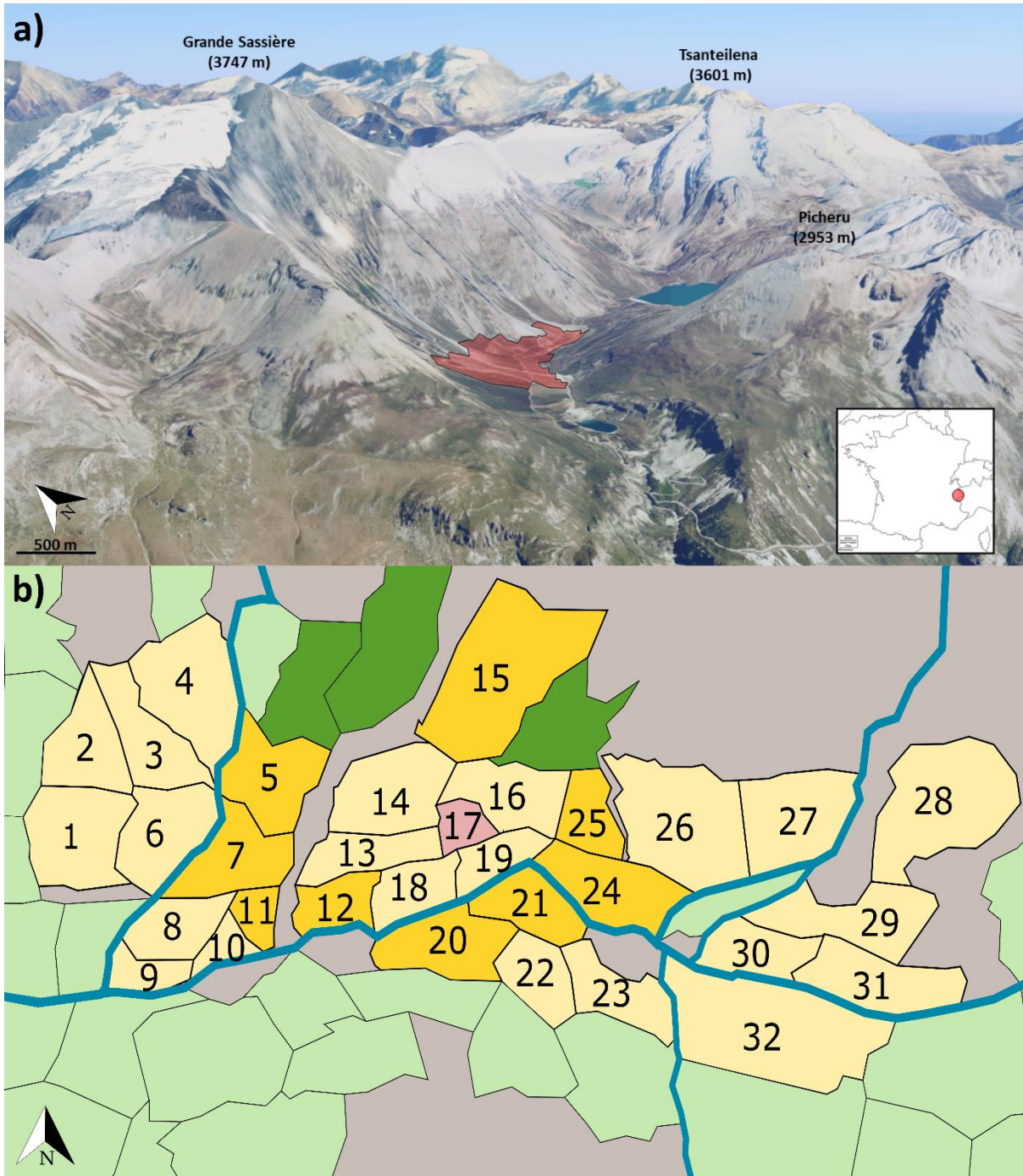
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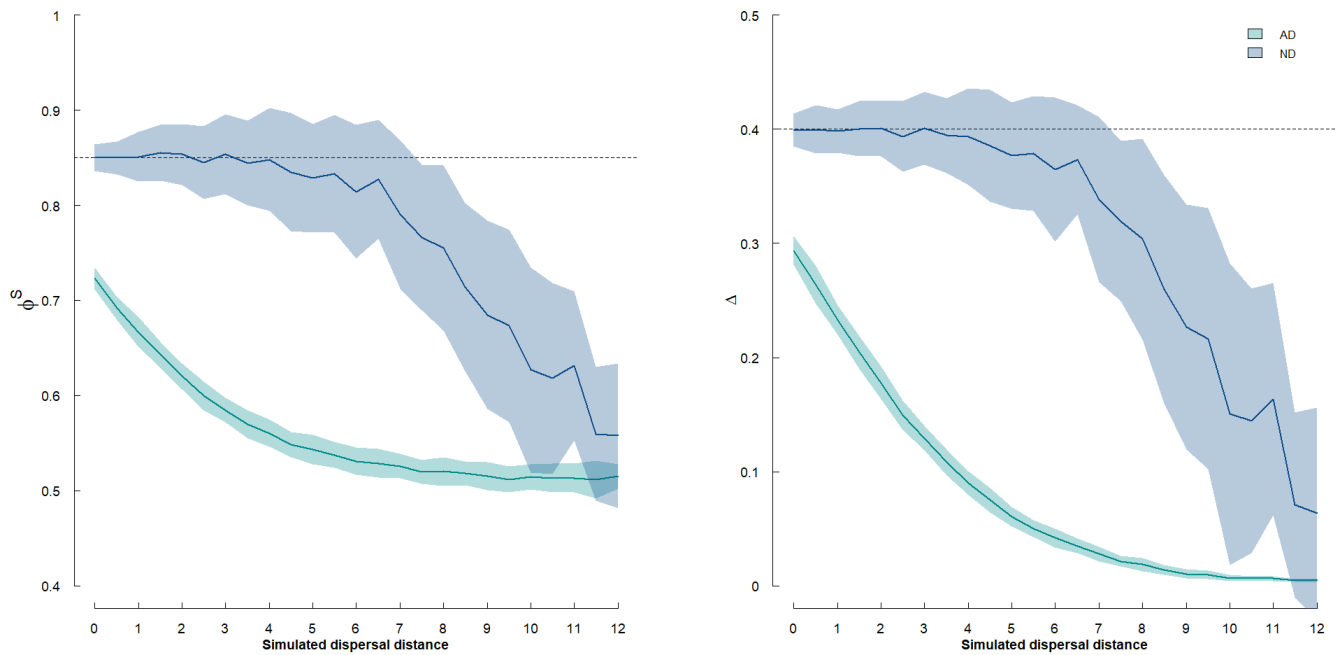
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760 **Figure 2.** 3D (a) and schematic map (b) of the Grande Sassière nature reserve and marmot
 761 territories monitored in 2015. Numbered polygons represent monitored territories. Green
 762 polygons represent territories outside the study area suitable for Alpine marmots. Grey areas
 763 represent unsuitable habitat (rocky and snowy areas). The probability to stay in the study area
 764 when dispersing a given distance d is calculated as the number of territories monitored divided
 765 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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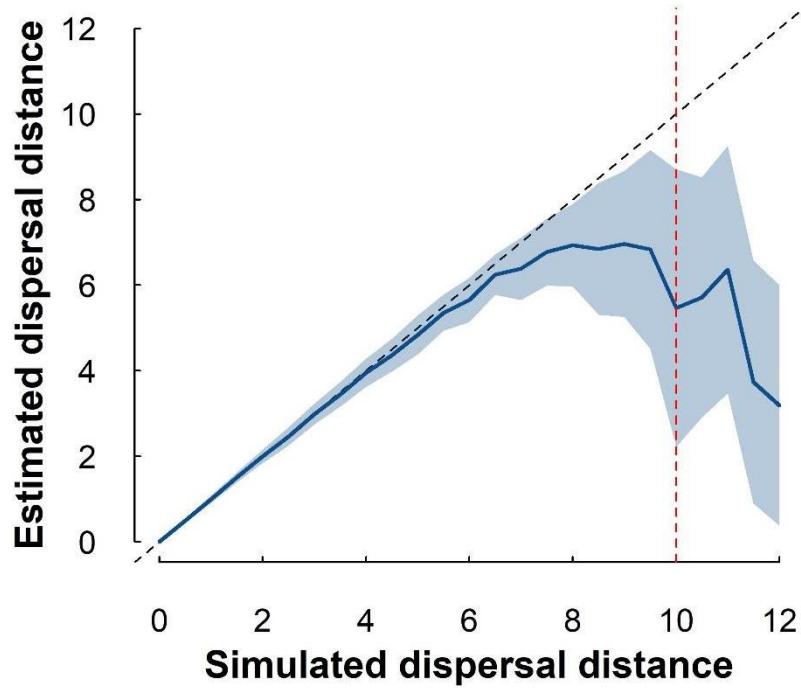
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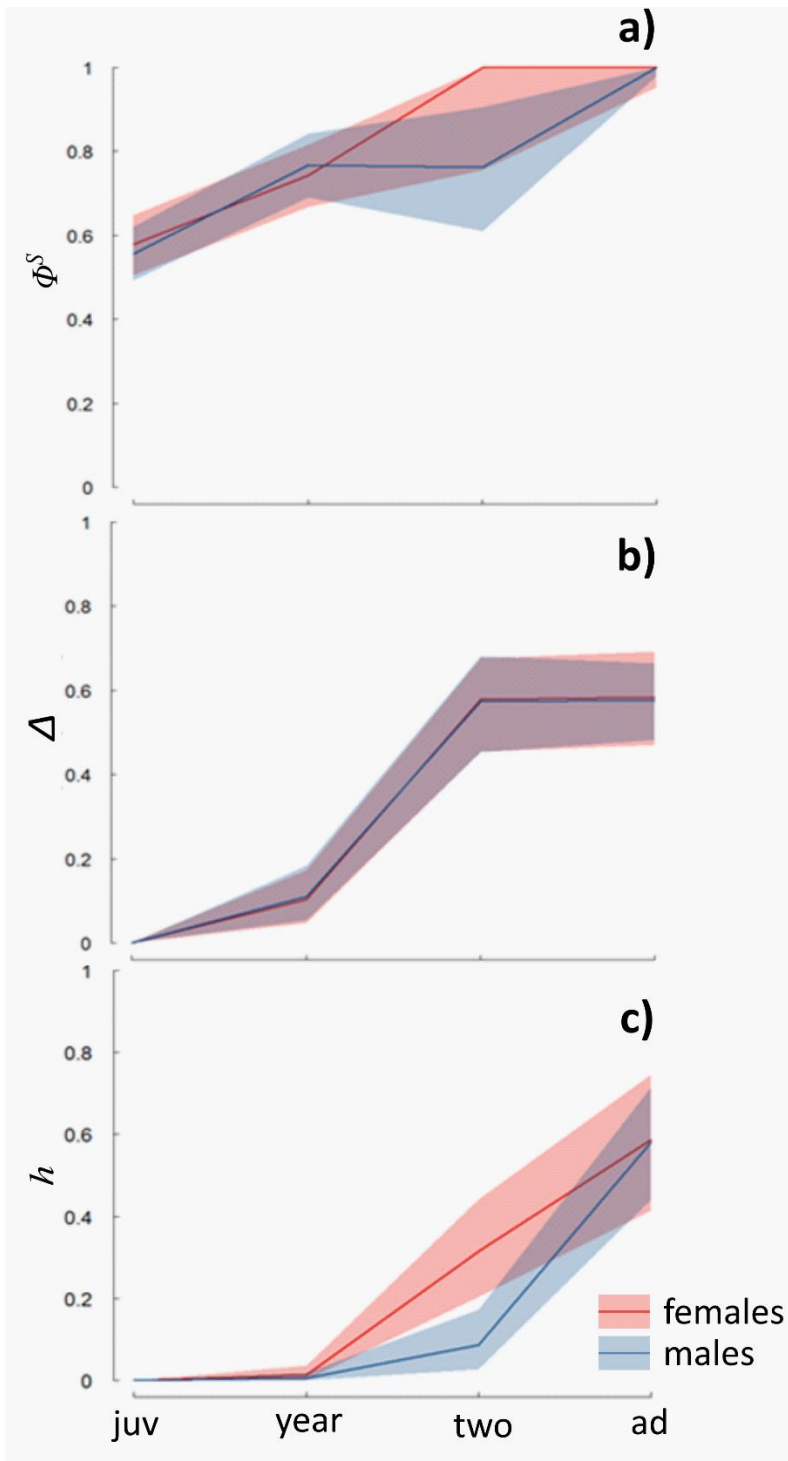
772 **Figure 3.** Mean subordinate survival (Φ^S) and dispersal probabilities (Δ) estimates returned by
773 the Apparent Dispersal (AD) and Natal Dispersal (ND) models for increasing mean dispersal
774 distances. Solid lines represent the mean over 100 replicates and shaded areas represent the
775 associated 95% confidence intervals. Horizontal dashed lines indicate simulated values of the
776 parameter.

777



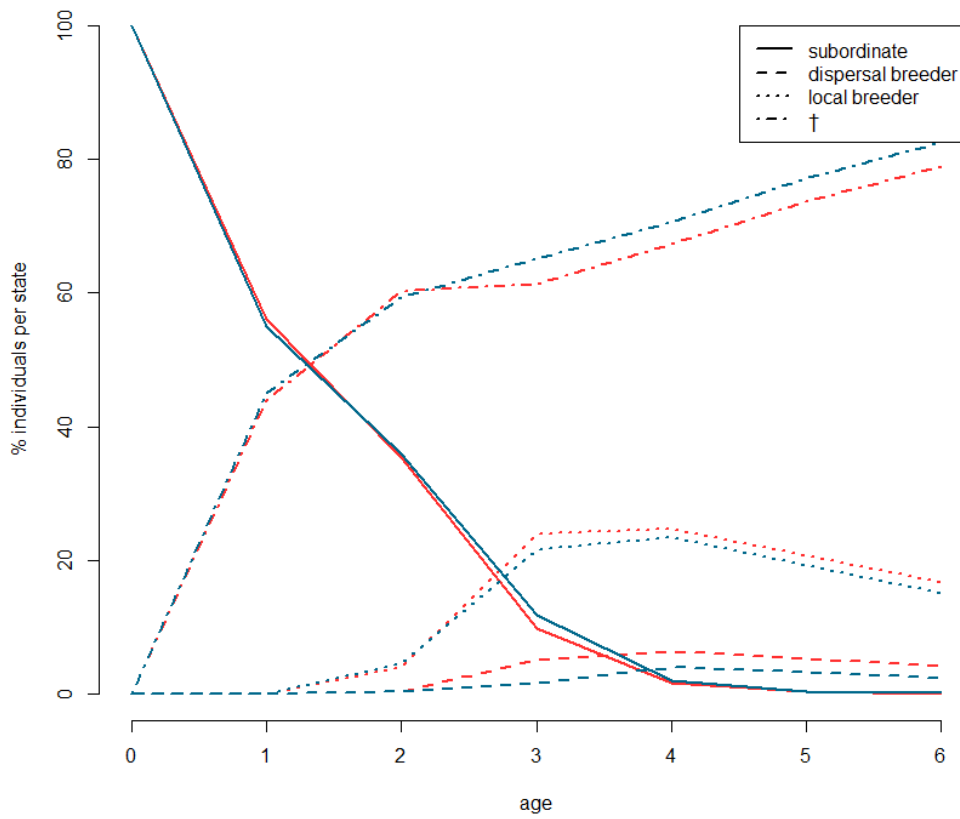
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779 **Figure 4.** Simulated and estimated dispersal distance for the Natal Dispersal model. Solid line
 780 represents the mean over 100 replicates and the shaded area the associated 95% confidence
 781 interval. Vertical dashed line indicates the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



783

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



788

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 Sassièrè dataset.

791 **Table.1** Age- and sex-specific posterior mean estimates (standard deviation) of the survival,
792 dispersal and inheritance probabilities of Alpine marmots. Sex difference indicates if the 95%
793 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

794