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Age and sex-specific natal dispersal pattern of Alpine marmots from capture-recapture data

Pierre Dupont ^{1,2*}, Dominique Allainé ¹, Mariona Ferrandiz-Rovira ^{3,4} & Roger
Pradel ⁵

¹. *Université de Lyon, Université Lyon 1, CNRS, UMR 5558, Laboratoire de Biométrie et Biologie Évolutive, 43 boulevard du 11 novembre 1918, Villeurbanne F-69622, France*

². *Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, PB 5003, NO-1432 Ås, Norway*

³. *CREAF, Cerdanyola del Vallès 08193, Catalonia*

⁴. *BABVE, Universitat Autònoma de Barcelona, Cerdanyola del Vallès 08193, Catalonia*

⁵. *CEFE, CNRS, Univ. Montpellier, Univ. Paul Valéry Montpellier 3, EPHE, IRD,, 34293 Montpellier, France*

*corresponding author: pierre.dup@live.fr;

https://www.researchgate.net/profile/Pierre_Dupont8;

<https://orcid.org/0000-0002-7438-7995>

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26 **ABSTRACT**

27 1. Studying natal dispersal in natural populations using capture-recapture data is challenging
28 as an unknown proportion of individuals leaves the study area when dispersing and are
29 never recaptured. Most dispersal (and survival) estimates from capture-recapture studies
30 are thus biased and only reflect what happens within the study area, not the population.

31 2. Here, we elaborate on recent methodological advances to build a spatially-explicit multi-
32 state capture-recapture model to study natal dispersal in a territorial mammal while
33 accounting for imperfect detection and movement in and out of the study area.

34 3. We validate our model using a simulation study where we compare it to a non-spatial multi-
35 state capture-recapture model. We then apply it to a long-term individual-based dataset on
36 Alpine marmot (*Marmota marmota*).

37 4. Our model was able to accurately estimate natal dispersal and survival probabilities, as well
38 as mean dispersal distance for a large range of dispersal patterns. By contrast, the non-
39 spatial multi-state estimates underestimated both survival and natal dispersal even for short
40 dispersal distances relative to the study area size.

41 5. We evidenced higher inheritance probabilities of females, which suggests higher levels of
42 philopatry, although the probability to become dominant after dispersal did not differ
43 between sexes. However, the lower survival of young adult males suggests higher costs of
44 dispersal for males. We further discuss the implications of our findings in light of the life-
45 history of the species.

46

47 **Keywords:** Bayesian modelling · Dispersal kernel · Multi-state capture-recapture
48 models · Spatially explicit capture-recapture · Sex-specific dispersal ·

49 INTRODUCTION

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

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

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

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

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

99 MATERIAL AND METHODS

100 1. Alpine marmot life cycle

101 The Alpine marmot is a hibernating, territorial and cooperatively breeding mammal living in
102 family groups of 2 to 20 individuals. A family is typically composed of a dominant couple,
103 adult (age ≥ 3 years old) and sub-adult (age=2 years old) subordinates, yearlings and juveniles
104 born that year (Allainé, 2000). Alpine marmots of the same family group share a common
105 multi-purpose territory (range between 0.9 ha and 2.8 ha) comprising main and secondary
106 burrows (Perrin et al., 1993). The main burrows are usually centrally located and used for
107 hibernation, communal sleeping during the active season and to give birth (Perrin et al., 1993).
108 Secondary burrows are spread over the entire territory and mainly used to escape potential
109 predators. In each family, reproduction is monopolized by the dominant couple (apart from a
110 few subordinate males reproducing through extra-pair copulation: Cohas et al., 2006;
111 Ferrandiz-Rovira et al., 2016; Hackländer et al., 2003). Reproductive status is therefore
112 generally confounded with dominance status in this species. Mating occurs shortly after the
113 end of hibernation (mid-April to early May) and gestation lasts for 30 days. Dominant females
114 give birth to a litter of 1 to 7 pups (median = 4) once a year and pups stay in the main burrow
115 for 40 days, where mothers lactate them until weaning. Pups then emerge between mid-June
116 and mid-July and start eating on their own and discovering the territory. Marmot juveniles
117 remain in their natal territory at least until sexual maturity, at two years of age. From this age,
118 they can either stay as subordinate and help raise subsequent pups or disperse (Stephens *et al.*
119 2002). Subordinates that stay in the family group may become dominant by inheriting the
120 position in their natal territory following the death of the same-sex dominant while dispersers
121 usually have to evict the same-sex dominant from another territory (Dupont et al., 2015). A
122 third possibility to access a dominant status is the creation of a new territory by a couple of
123 dispersing individuals, but this is highly unusual in the saturated population under study (only

124 3 occurrences in 25 years of the study). Once a subordinate disperses, it either secures a
125 dominant position or dies during the following winter but never joins a new family group as
126 subordinate. Instead, in case of failure in reaching a dominant status, it becomes a floater, *i.e.*
127 a wandering individual forced to hibernate alone and consequently exposed to very high risks
128 of mortality (Magnolon 1999). Once the dominant position secured, a marmot can remain
129 dominant for several years until death or eviction by a new incomer (Lardy et al., 2011). When
130 evicted, dominant individuals also become floaters subject to a very high risk of mortality
131 (Grimm et al., 2003) and they usually never become dominant elsewhere. Dispersal in the
132 Alpine marmot is therefore almost exclusively natal dispersal (fig.1).

133 **2. Alpine marmot dataset**

134 The Alpine marmot population from the Grande Sassièrre Nature Reserve (2,340 m.a.s.l.,
135 French Alps, 45°29'N, 65°90'E) has been studied since 1990. Between 10 and 35 family groups
136 have been monitored each year from mid-April to mid-July using capture-mark-recapture and
137 daily observations. Marmot territories are situated at the bottom of a small valley on either side
138 of a touristic trail crossing the lower part of the reserve. Monitored territories are roughly at
139 the same altitude and cover an area of 0.75 km² (1.5 km long and 0.5 km wide). The valley is
140 surrounded by high altitude mountain tops (> 3,500 m.a.s.l.) and steep slopes on both sides.
141 Whilst the flat part of the valley is suitable for the establishment of Alpine marmot territories,
142 the steeper parts are unsuitable given the thickness and instability of snow-packs, rocks and the
143 quasi-absence of vegetation (López et al. 2010; fig.2).

144 Marmots were captured each year using two-door live traps baited with dandelions
145 (*Taraxacum densleonis*) placed near the entrances of the main burrows of each territory to
146 facilitate assignment of captured individuals to their family group. Traps were checked
147 regularly to limit the time a marmot would spend inside the trap. In addition, during the juvenile
148 emergence period, territories are carefully observed to identify their emergence date. Juveniles

149 are then counted and captured either using small two-door live traps or by hand. With this
150 procedure, virtually all juveniles are captured within the three days following their first
151 emergence from the burrows. Once captured, individuals were placed in an opaque bag before
152 being anesthetized with Zolétil 100 (0.1 mL kg⁻¹). They were then sexed, aged (from their size
153 (up to 3 years) if the exact age is unknown), and their social status was determined based on
154 scrotal development for males and teats development for females. All individuals were
155 individually marked using both a transponder chip injected under the skin of the neck and a
156 numbered metal ear-tag (right ear for females and left for males to facilitate later observation).
157 An additional colored plastic ear tag was placed on the opposite ear for dominant individuals.
158 When tranquilized marmots recovered, they were returned in their territory (see Cohas et al.,
159 2006 for more details on protocol).

160 We restricted the analysis to the data collected between 1990 and 2015 leading to a
161 dataset composed of 1270 individuals (577 females / 693 males). During this period, 170
162 dispersal events (69 females / 101 males) were recorded in the study area with a maximum
163 dispersal distance of five territories crossed. Because the cost of dispersal in the Alpine marmot
164 is thought to be directly linked to the number of agonistic encounters, and therefore the number
165 of territories travelled, we measured natal dispersal distances in numbers of territories crossed.

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

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

174 dominant on their natal territory by inheritance, *i.e.* a philopatric state), a disperser breeder state
 175 *DB* (individuals that became dominant after dispersal), and a dead state † (fig.1). Multi state
 176 capture-recapture models can be described as hierarchical models composed of two sub-models;
 177 an ecological process model describing how individuals change states between consecutive
 178 capture occasions, and an observation process model describing how individual observations
 179 collected each year are related to their underlying state. As our focus was on estimating
 180 demographic parameters and not population size, we used models that were conditional on first
 181 capture.

182 **a. Apparent dispersal model**

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

$$185 \quad z_{if_i} \sim \text{dcat}(\alpha) \quad \text{eqn.1}$$

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

198 dominant position on its natal territory between two consecutive capture occasions. As we did
 199 not consider the possibility for an evicted dominant to survive and become dominant elsewhere,
 200 a locally recruited breeder can only survive and remain in state LB with probability Φ^{LB} or die
 201 with probability $1 - \Phi^{LB}$. Similarly, a disperser breeder can either survive and remain in state
 202 DB with probability Φ^{DB} or die with probability $1 - \Phi^{DB}$. Finally, a dead individual remains
 203 in its current state \dagger with probability 1. These different state transition probabilities can be
 204 represented in a so-called transition matrix where each row corresponds to the departure state
 205 and each column to the arrival state of an individual:

$$206 \quad \Omega = \begin{bmatrix} \Phi^S \cdot (1 - \Delta') \cdot (1 - h) & \Phi^S \cdot (1 - \Delta') \cdot h & \Phi^S \cdot \Delta' & 1 - \Phi^S \\ 0 & \Phi^{LB} & 0 & 1 - \Phi^{LB} \\ 0 & 0 & \Phi^{DB} & 1 - \Phi^{DB} \\ 0 & 0 & 0 & 1 \end{bmatrix}$$

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

$$210 \quad z_{it} \sim \text{dcat}(\Omega[z_{it-1}, 1:4]) \quad \text{eqn.2}$$

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

$$218 \quad \Theta = \begin{bmatrix} p^S & 0 & 0 & 1 - p^S \\ 0 & p^{LB} & 0 & 1 - p^{LB} \\ 0 & 0 & p^{DB} & 1 - p^{DB} \\ 0 & 0 & 0 & 1 \end{bmatrix}$$

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

$$223 \quad y_{it} \sim \text{dcat}(\theta[z_{it}, 1:4]) \quad \text{eqn.3}$$

224 **b. Natal dispersal model**

225 In the AD model presented above, both the survival and dispersal parameters correspond to
 226 apparent probabilities since all individuals dispersing outside the study area cannot be observed
 227 and are therefore un-distinguishable from dead individuals. We can however reformulate this
 228 model by expressing the apparent dispersal probability (Δ) as $\Delta * r$, the product of the dispersal
 229 (Δ) and residency probabilities (r), where r is the probability that an individual remains within
 230 the boundaries of the study area when dispersing. We can then construct a new model with a
 231 modified state-transition matrix (Ω):

$$232 \quad \Omega = \begin{bmatrix} \Phi^S \cdot (1 - \Delta) \cdot (1 - h) & \Phi^S \cdot (1 - \Delta) \cdot h & \Phi^S \cdot \Delta \cdot r & (1 - \Phi^S) + \Phi^S \cdot \Delta \cdot (1 - r) \\ 0 & \Phi^{LB} & 0 & 1 - \Phi^{LB} \\ 0 & 0 & \Phi^{DB} & 1 - \Phi^{DB} \\ 0 & 0 & 0 & 1 \end{bmatrix}$$

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

237 The probability to settle within the study area when dispersing is necessarily individual-
 238 specific as it depends on *i)* the location of the natal territory an individual is dispersing from,
 239 *ii)* the dispersal direction, and *iii)* the distance travelled during dispersal (Gilroy *et al.* 2012).
 240 If we consider dispersal as homogeneous in direction, *i.e.* individuals have the same probability
 241 to choose any direction when dispersing, the residency probability can be calculated for each

242 territory s and each potential dispersal distance d as:

$$243 \quad r_{sd} = \frac{n_{sd}}{N_{sd}} \quad \text{eqn.4}$$

244 where n_{sd} and N_{sd} are the number of territories inside the study area and the total number of
 245 territories situated at a distance d from the natal territory s respectively. In other words, the
 246 residency probability for an individual dispersing a distance d is equal to the proportion of
 247 territories situated at a distance d from its natal territory s where recapture is possible. For
 248 example, an individual that leaves from territory 13 on Fig. 2 and travels a distance $d = 2$, will
 249 have a probability to settle in a territory that is also monitored of $r_{13,2} = 11/15 = 0.73$.

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

$$257 \quad d'_i \sim \text{Poisson}(\tau) \quad \text{eqn.5}$$

$$258 \quad d_i = d'_i + 1 \quad \text{eqn.6}$$

259 The addition of 1 was used to enforce that all dispersers moved at least one territory away from
 260 their natal one.

261 **4. Simulation study**

262 To compare the two models presented above, we simulated different CR datasets with
 263 increasing mean dispersal distances τ from 0 to 12 territories with steps 0.5. We picked values
 264 of the other parameters in the model based on our knowledge of the Alpine marmot (Berger et

265 al., 2016; Dupont et al., 2015; Ferrandiz-Rovira, 2015). We set the true survival probabilities
266 to be equal and high for both breeder states ($\Phi^{DB} = \Phi^{LB} = 0.95$), and slightly lower for
267 subordinates ($\Phi^S=0.85$). We also considered that recapture probabilities differed between
268 dominants and subordinates ($p^{DB} = p^{LB} = 0.65$ and $p^S = 0.95$). Dispersal probability Δ was set
269 to 0.4 and inheritance probability h to 0.12. To avoid potential confounding effects due to the
270 shape of the study area, it was randomly generated by sampling 35 cells from a 10×6 grid for
271 each simulated data set, *i.e.* 35 territories where recaptures are possible were randomly selected.
272 We simulated the dataset for 20 years of captures. Each year, with the exception of the last one,
273 40 individuals were newly captured leading to a total of 760 individuals in each simulated
274 dataset. We randomly assigned the 760 individuals to one of the 35 territories and individual
275 dispersal distances were sampled following eqn. 5 and 6 with the chosen value for τ . We
276 assumed that the landscape was homogeneous, *i.e.* the habitat was suitable for settlement
277 anywhere inside or outside the study area. Based on this map, a matrix of the residency
278 probabilities for all territories and dispersal distances was constructed following eqn.4. State-
279 transition and observation matrices similar to those in the ND model were then filled with these
280 different probabilities. Individual capture histories were generated using eqn.3 after sampling
281 individual states using eqn.2. Dispersal distances were kept for individuals that dispersed and
282 settled inside the study area only to mimic true capture-recapture data. We repeated the
283 simulation process 100 times for each value of τ , leading to a total of 2,500 simulated data sets.
284 We then fitted both the AD and ND models to all simulated datasets and compared their
285 parameter estimates.

286 **5. Alpine marmot analysis**

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

289 First, the number of family territories monitored each year varied over the course of the

290 study between 13 and 35. Consequently, the probability for an individual to emigrate outside
291 the study area and the probability to observe a dispersal event inside the study area also varied
292 between years. To account for this change in the study area size and shape, we used annual
293 maps representative of the territories' relative positions for each year.

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

300 Third, following results from previous studies on the same population (Dupont *et al.*
301 2015; Berger *et al.* 2016; Rézouki *et al.* 2016), we considered recapture probabilities to vary
302 with time, age and sex. In addition to the sex-effect in which we were interested, we accounted
303 for age-specific subordinate survival and transitions probabilities by considering four age
304 classes: juvenile (from zero to one-year-old), yearling (from one to two), subadult (from two
305 to three) and adult (three years old and older). We also accounted for an effect of the logarithm
306 of the number of male helpers on the juvenile survival, as it was shown to be an important
307 driver of the juvenile survival during hibernation in this species (Allainé & Theuriau 2004;
308 Dupont *et al.* 2015). Because no individual attained a dominant status before two years old,
309 only the two last age classes were used for dominant individuals.

310 Finally, we considered sex-specific dispersal patterns, *i.e.* two independent Poisson
311 distributions with sex-specific mean. The full set of model parameters was then $p_{t,age,sex}$ the
312 time, age and sex-specific recapture probabilities, $\Phi^{IB}_{age,sex}$ and $\Phi^{LB}_{age,sex}$ the age and sex-
313 specific survival probabilities of dominant individuals, $\Phi^S_{age,sex}$ the age and sex-specific
314 survival probabilities of subordinate individuals, $\Delta_{age,sex}$ the age and sex-specific dispersal

315 probabilities, $h_{age,sex}$ the age and sex-specific inheritance probabilities, r_i the individual-specific
 316 residency probability and τ_{sex} the sex-specific mean dispersal distance.

317 **6. Model fitting**

318 All models were fitted using Markov Chain Monte Carlo (MCMC) simulations with the
 319 computer program JAGS (Plummer 2003) called through R3.2.5 (R core team 2016) via the R
 320 package jagsUI (Kellner 2014). All parameter priors were chosen to be weak or un-informative.
 321 All survival, dispersal, inheritance and recapture probabilities were given uniform priors
 322 between 0 and 1. The prior for the mean of the Poisson distribution in the ND model was given
 323 a vague gamma distribution $\Gamma(0.0001,0.0001)$. All models in the simulation study were fitted
 324 by running three independent MCMC chains of 10,000 iterations each with a burning period
 325 of 6,000 iterations, leading to 12,000 posterior MCMC samples per simulation. For the Alpine
 326 marmot analysis, we ran three chains of 15,000 iterations each with a burning period of 10,000
 327 iterations, leading to a total of 15,000 posterior MCMC samples. We assessed convergence for
 328 all models by looking at parameter traceplots and calculating the potential scale reduction
 329 factor \hat{R} (Gelman & Rubin, 1992).

330 **RESULTS**

331 **1. Simulation study**

332 Based on the visual inspection and \hat{R} values (all parameters with $\hat{R} < 1.1$), we considered all
 333 simulation runs to have reached convergence. Both the AD and ND models returned unbiased
 334 estimates of the recapture probabilities (AD: posterior mean \pm se; $p^S = 0.95 \pm 0.01$ and $p^{DB} =$
 335 $p^{LB} = 0.65 \pm 0.02$; ND: $p^S = 0.95 \pm 0.01$ and $p^{DB} = p^{LB} = 0.65 \pm 0.02$), inheritance probability
 336 (AD: $h = 0.12 \pm 0.10$; ND: $h = 0.12 \pm 0.12$) and dominant survival probabilities (AD: $\Phi^{IB} =$
 337 $\Phi^{LB} = 0.95 \pm 0.01$; ND: $\Phi^{IB} = \Phi^{LB} = 0.95 \pm 0.01$) under all scenarios.

338 Subordinate survival and dispersal estimates, on the other hand, differed considerably

339 between models. The AD model consistently under-estimated both parameters and this
340 negative bias increased with mean dispersal distance to reach a lower plateau when the mean
341 dispersal distance was larger than the maximum length of the study area d_{max} (fig.3). The
342 estimated apparent dispersal probability Δ' was between 26% and 99% lower than the
343 simulated dispersal probability when the mean dispersal distance increased from 0 to 10
344 territories. In the same time, the apparent subordinate survival Φ^S was estimated from 15% to
345 40% lower than the simulated value. Additionally, when the mean simulated dispersal distance
346 was over d_{max} , the mean apparent dispersal estimates tended towards zero.

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

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

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

360 The 95% confidence intervals of the ND posterior estimates indicated that recapture
361 probabilities varied with time and decreased with age (difference in recapture probabilities
362 between yearlings and two-years $\Delta p_{two} = -1.40 [-1.91; -0.94]$ (posterior mean; [95% confidence

363 interval]) and difference between yearlings and adults $\Delta p_{ad} = -1.90 [-2.37; -1.50]$ on the logit
364 scale). Recapture probabilities were also higher for females than for males (difference in
365 recapture probabilities between females and males $\Delta p_{sex} = -0.28 [-0.55; -0.02]$ on the logit
366 scale). Mean dispersal distance did not differ between males and females ($\tau_{females} = 1.69 [1.55;$
367 $1.85]$ and $\tau_{males} = 1.71 [1.56; 1.86]$). As expected, juvenile subordinate survival increased with
368 the logarithm of the number of male subordinates (helpers) present during hibernation for both
369 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).
370 Subordinate survival increased with age but did not vary significantly between sexes although
371 two-year-old subordinate males seemed to have a lower survival probability than females
372 (fig.5a and table 1). Dispersal probabilities increased with age similarly for both sexes (fig.5b
373 and table1). Inheritance probabilities also varied with age and a sex difference was evidenced
374 for the two-year age class (fig.5c and table1). Because inheritance is conditional on survival
375 and dispersal, this indicates that females in their third year of life had more chances to inherit
376 a dominant position than males. To help understanding these results, figure 6 presents the fate
377 of a cohort of subordinate individuals as the proportions of individuals in each state at each age
378 as predicted by the model (fig.6).

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

384

385 **DISCUSSION**

386 **1. Simulation study**

387 With this study, we showed how using the spatial information associated with individual
388 detections in a multi-state capture-recapture model can allow the estimation of unbiased natal
389 dispersal and survival probabilities even when a significant proportion of the individuals settle
390 outside the study area after dispersal. We also showed how the magnitude of the
391 underestimation of these demographic parameters by classical multi-state models depends on
392 the mean dispersal distance (relative to the study area size). The Natal Dispersal model
393 presented here uses the information available on dispersal movements observed within the
394 study area and the location of individual birth territories relative to the boundaries of the study
395 area to estimate individual-specific probabilities to leave the study area when dispersing and
396 discriminate between mortality and emigration. Using a single model to simultaneously
397 estimate survival and natal dispersal patterns presents the double benefit of *i*) being able to
398 estimate true instead of apparent survival and dispersal probabilities, and *ii*) account for the
399 imperfect detectability inherent in most field studies while rigorously propagating the resulting
400 uncertainty to all parameter estimates.

401 However, this approach still has some limitations. Notably, and as mentioned above,
402 the performance of the model depends on the ratio of the mean dispersal distance relative to
403 the size of the study area, *i.e.* on the proportion of dispersal events observable within the study
404 area. When the mean dispersal distance becomes too large, most dispersers leave the study area
405 and the model fails to estimate the correct dispersal distance distribution. In the extreme case,
406 the dispersal distance is much larger than the study area and all dispersers settle outside. In
407 such situation, the model has no information to rely on to estimate dispersal distances and
408 considers that all dispersers are dead instead. As noted by Schaub & Royle (2014): “if censoring
409 becomes too strong (dispersal distances very large relative to the size of the study area), [the]

410 model is not successful anymore in correctly estimating dispersal and consequently survival.
411 But it is hard to imagine that any model would succeed in obtaining meaningful estimates in
412 this case.” It is thus crucial when studying dispersal to ensure that the dataset at hands contains
413 enough observed dispersal events to accurately estimate dispersal distances. According to our
414 simulation results, the study area should be twice as long as the mean dispersal distance to
415 ensure good estimation of the dispersal pattern.

416 Another aspect worth-considering is that the efficiency of the model to produce
417 unbiased natal dispersal and survival estimates likely depends on the assumed dispersal
418 distance distribution being correct, which raises the problem of selecting a good dispersal
419 model. In our example, we used a Poisson distribution, which seems like an adequate choice
420 for the Alpine marmots, based on the vast majority of short-distanced dispersal events we
421 observed (at least much shorter than the size of the study area). However, it is not possible to
422 rule out the possibility that some individuals display a different dispersal strategy and move
423 much longer distances. In that case, a bimodal distribution or a distribution with a longer tail
424 would probably be a better fit although it could not be detected from the data (Dupont et al., *in*
425 *press*). Finally, our second simulation study stresses out the importance to correctly specify the
426 available habitat both within and outside the study area. If no information is available about
427 the suitability of the surrounding habitat and one assumes dispersers may settle anywhere
428 outside the study area, inferences about the dispersal pattern, and therefore about survival, may
429 be inaccurate (see Supplementary Material). It is therefore crucial to correctly characterize the
430 habitat suitability outside the study area, either by using prior knowledge (as in our study case)
431 or through a more formal analysis (e.g. habitat selection studies).

432 Other studies tackled the question of apparent survival in a capture-recapture context
433 (Ergon & Gardner, 2014; Gilroy et al., 2012; Schaub & Royle, 2014). Gilroy et al. (2012)
434 proposed a modelling approach in which they first estimate a dispersal kernel for the study

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

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

451 The application of the Natal Dispersal model to the Alpine marmot dataset shed new light on
452 the dispersal process in this species. Notably, we obtained estimates of adult subordinate
453 survival much higher than in previous CR studies of the same population (0.99 against 0.53 in
454 Dupont *et al.* 2015). We also estimated the probability to become dominant through dispersal
455 to be higher than previous estimates even though no difference was made between inheritance
456 and dispersal (0.58 against 0.45 in Rézouki *et al.* 2016). In addition, we estimated the
457 probability to become dominant through dispersal to not differ between sexes contrary to the
458 inheritance probability where we estimated that females had three times as much chances of
459 inheriting the dominant position than males. Based on the estimated mean dispersal distance

460 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
461 the study area, and the results from the simulation study, we are confident that these estimates
462 are not underestimating the true survival and dispersal probabilities of subordinate Alpine
463 marmots. Finally, and as expected from the results of the simulation study, the other parameter
464 estimates (*i.e.* recapture probabilities, juvenile survival and dominant survival) were consistent
465 with previous capture-recapture studies on the same population (Cohas *et al.* 2009; Dupont *et*
466 *al.* 2015; Berger *et al.* 2016; Rézouki *et al.* 2016). These results suggest that the vast majority
467 of subordinate individuals are in fact able to become dominant if they survive their two first
468 winters and that the high mortality reported for subordinate sub-adults and adults in previous
469 studies was almost entirely due to dispersal outside the study area (fig.6).

470 Contrary to what is generally reported in the literature for mammals, neither the
471 proportion of dispersers (*i.e.* the age-specific dispersal probability) nor the dispersal pattern (*i.e.*
472 the mean dispersal distance) differed between sexes (Dobson 2013). This absence of sex-
473 specific dispersal pattern is not so surprising for a monogamous and monomorphic mammal
474 such as the Alpine marmot (Lukas & Clutton-Brock 2012). However, this absence of sex
475 difference in dispersal probability should be considered with caution, given the formulation of
476 our model. Because dispersal probability only reflects successful dispersal, *i.e.* individuals that
477 dispersed *and* became dominant in another territory, it does not reflect the dispersal “decision”,
478 *i.e.* the probability that an individual leaves its natal territory, independently of the success of
479 this dispersal. This probability cannot be estimated using our model because no information
480 was available about dispersing individuals that failed to become dominant. These unsuccessful
481 dispersers disappeared from the dataset and most likely died in the process (Lardy *et al.* 2011).
482 The slight difference in survival of two-year-old subordinates males and females (and the
483 difference in the proportion of dead males and females; fig.6) is in accordance and tends to
484 indicate that a greater number of males disperse after their second winter compared to females.

485 This would also indicate a lower probability of success and therefore a higher cost of dispersal
486 for males. This alleged male-biased natal dispersal, although unexpected from theory for a
487 monogamous mammal, might be explained in Alpine marmots by the possibility of extra-pair
488 paternities. Although reproduction is largely suppressed in subordinate Alpine marmots
489 (Arnold & Dittami, 1997; Hackländer et al., 2003), dominant females have the possibility to
490 mate with multiple males, including subordinates from other families and Cohan *et al.* (2008)
491 found that most extra-pair paternities in the Grande Sassièrè population were the result of male
492 dispersers (80% of litters containing extra-pair young). This possibility for subordinate males
493 to access reproduction through extra-pair copulation, even when failing to secure a dominant
494 position, suggests that the expected fitness of a dispersing male is likely to be higher than that
495 of a female. This could explain why more male subordinates disperse despite higher levels of
496 competition among males to disperse and access reproduction, as suggested by the lower
497 survival of two-year-old subordinate males. The higher proportion of females inheriting the
498 dominant position from their mother (fig.6) also suggests female-biased philopatry (or
499 equivalently male-biased dispersal). However, further research on factors triggering dispersal
500 and dispersal costs in this species is needed to confirm these interpretations.

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

510 and GPS methods are generally unfit for ground-dwelling species.

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

516

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

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

528 **Supplementary material:** Landscape heterogeneity effect on estimates from the Natal
529 Dispersal capture-recapture model.pdf

530

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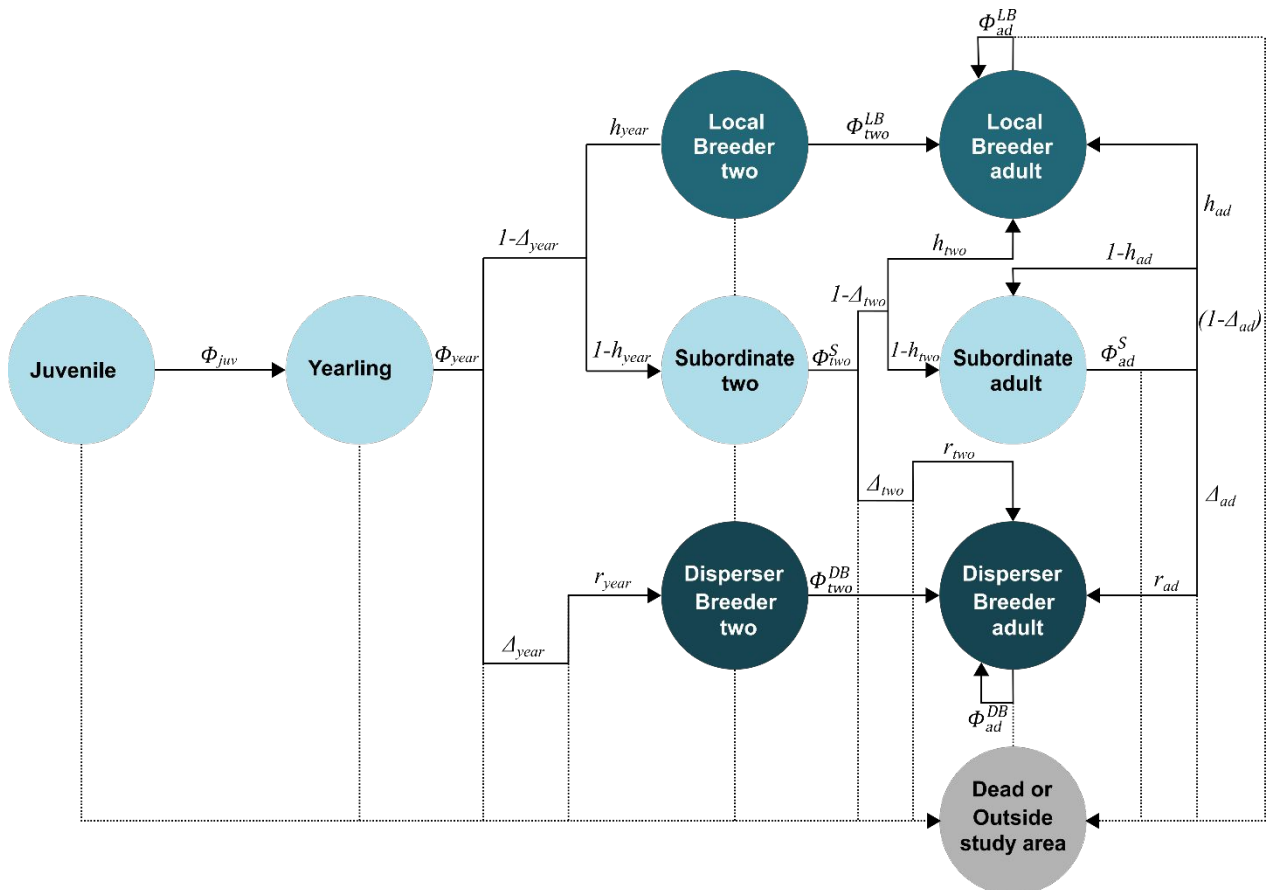
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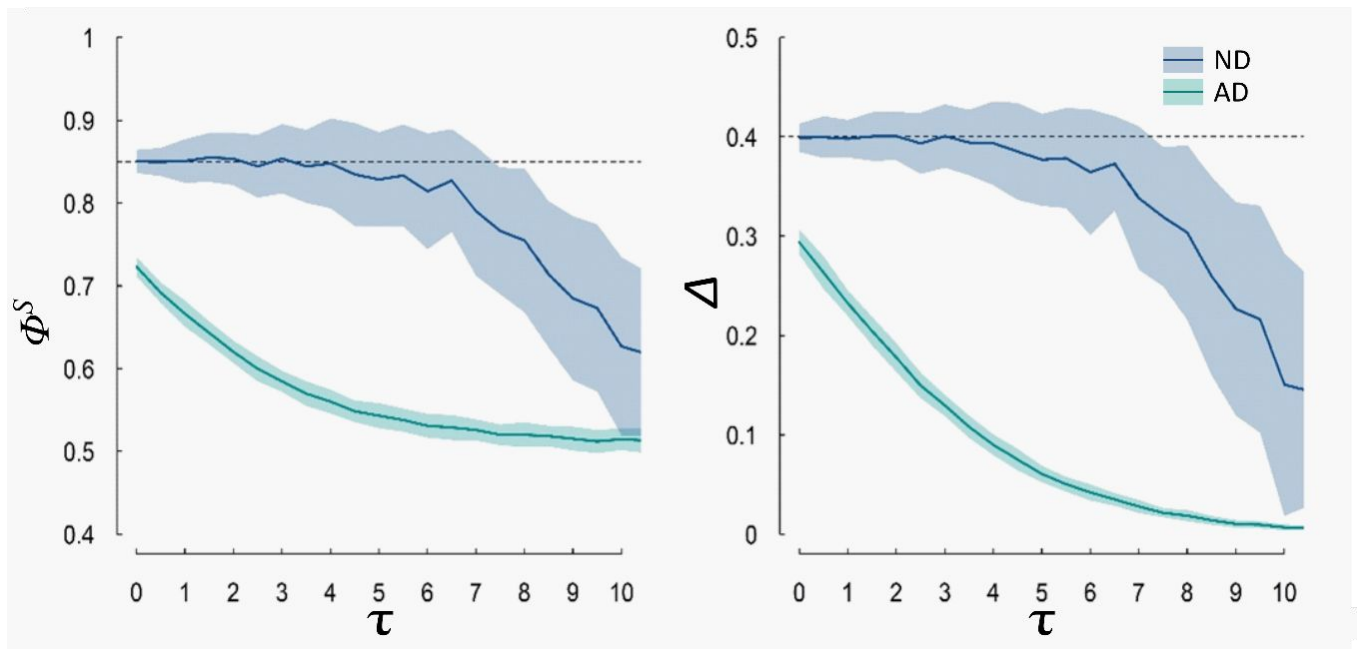
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669 e03385. <https://doi.org/10.1002/ecs2.3385>



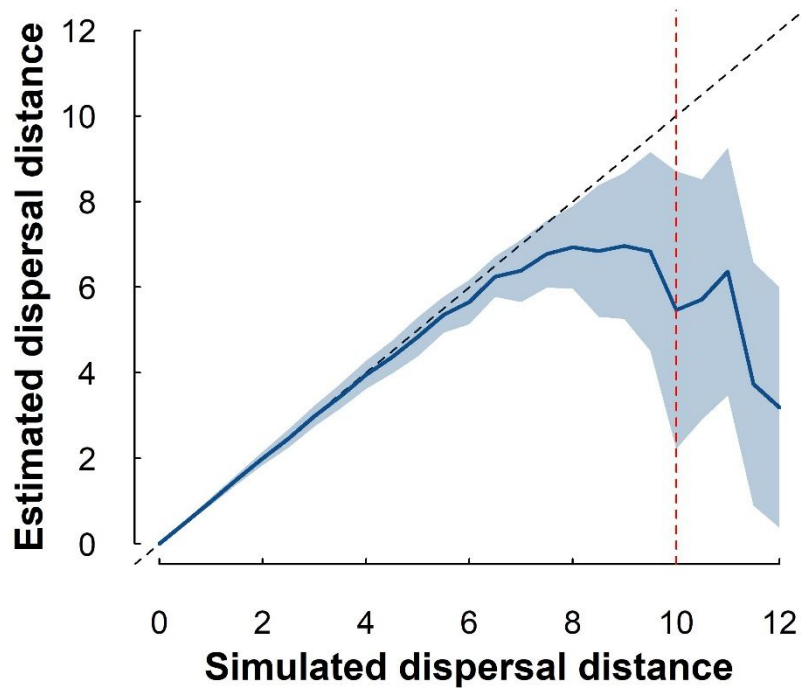
670 **Figure 1.** Schematic representation of the Alpine marmot's life cycle as used in the natal
 671 dispersal capture-recapture model. Solid lines indicate transitions between observable states
 672 while dotted lines indicate transitions to un-observable states. Parameters are survival (Φ),
 673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



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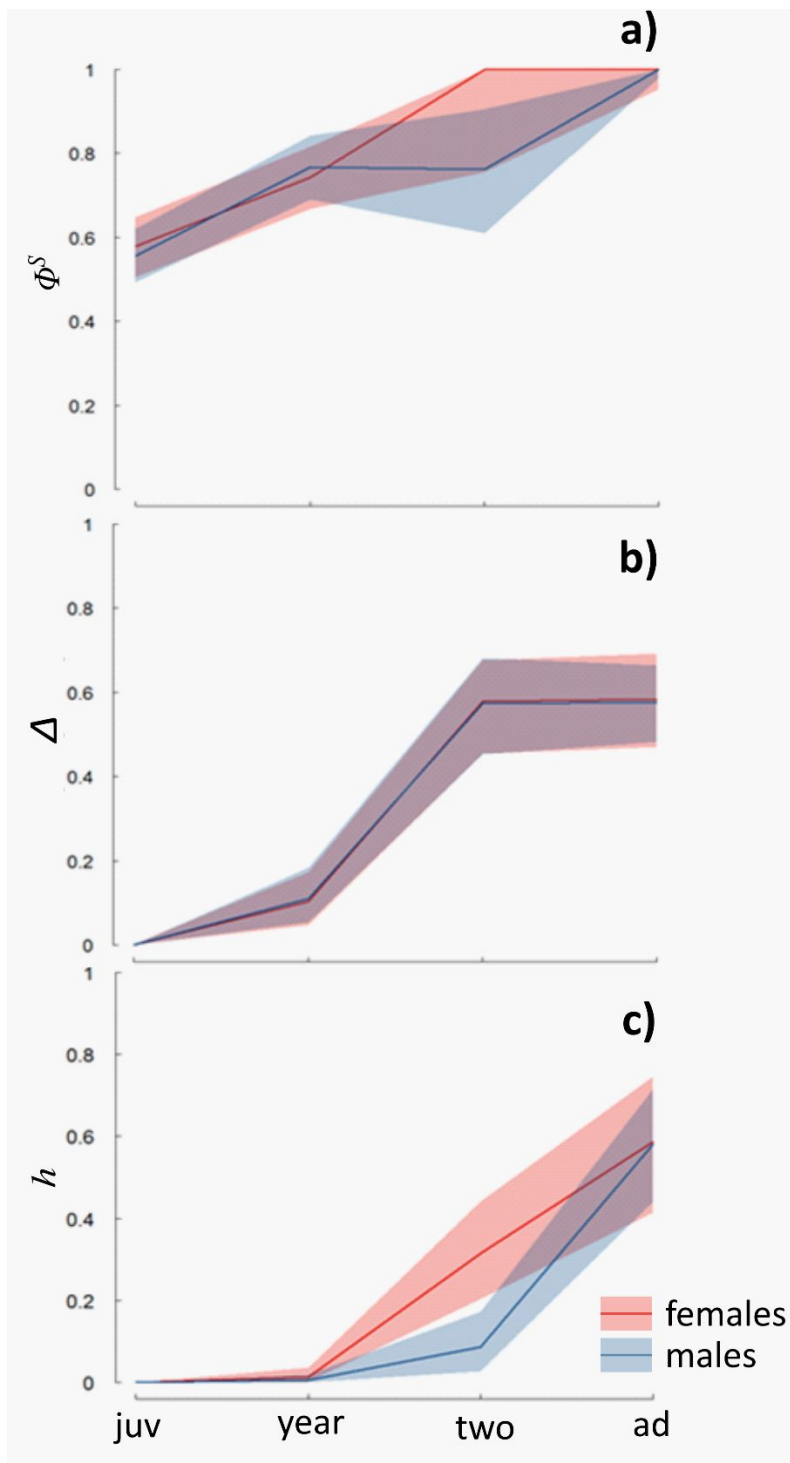
684 **Figure 3.** Mean subordinate survival (Φ^S) and dispersal probabilities (Δ) estimates returned by
 685 the Apparent Dispersal (AD) and Natal Dispersal (ND) models for increasing mean dispersal
 686 distances (τ). Solid lines represent the mean over 100 replicates and shaded areas represent the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

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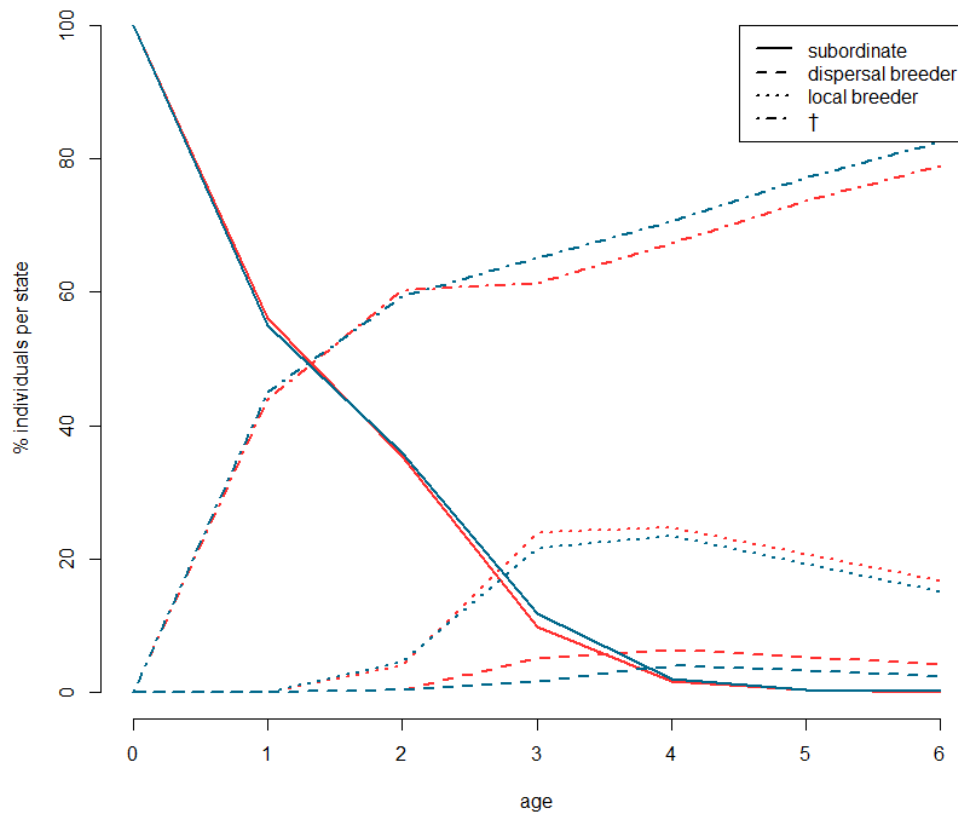
690

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



695

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



700

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

702 lines) as predicted by the Natal Dispersal model fitted to the Grande Sassièrè dataset.

703 **Table.1** Age- and sex-specific posterior mean estimates (standard deviation) of the survival,
 704 dispersal and inheritance probabilities of Alpine marmots. Sex difference indicates if the 95%
 705 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

706

Landscape heterogeneity effect on estimates from the Natal Dispersal capture-recapture model

Supplementary Material for

Age and sex-specific natal dispersal pattern of Alpine marmots from capture-recapture data

Pierre Dupont ^{1,2*}, Dominique Allainé ¹, Mariona Ferrandiz-Rovira ^{3,4} & Roger
Pradel⁵

¹. *Université de Lyon, Université Lyon 1, CNRS, UMR 5558, Laboratoire de Biométrie et Biologie Évolutive, 43
boulevard du 11 novembre 1918, Villeurbanne F-69622, France*

². *Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences,
PB 5003, NO-1432 Ås, Norway*

³. *CREAF, Cerdanyola del Vallès 08193, Catalonia*

⁴. *BABVE, Universitat Autònoma de Barcelona, Cerdanyola del Vallès 08193, Catalonia*

⁵. *CEFE, CNRS, Univ. Montpellier, Univ. Paul Valéry Montpellier 3, EPHE, IRD., 34293 Montpellier, France*

**corresponding author: pierre.dup@live.fr:*

https://www.researchgate.net/profile/Pierre_Dupont8 :

<https://orcid.org/0000-0002-7438-7995>

We performed this additional analysis to determine the consequences of ignoring the landscape structure when using the Natal Dispersal model (ND). If the landscape is heterogeneous, certain patches of habitat will be unsuitable for the organism under study, which will impact the residency probabilities of dispersers and consequently the estimation of the other demographic parameters. However, to what degree demographic parameters will be impacted is not clear. Here, we simulated and analysed multiple capture-recapture datasets with the ND model using different landscape structures to answer this question.

The landscape for each simulation was constructed in two steps. First, we generated a study area by randomly sampling 35 cells in a 10×6 grid. Because any individual dispersing further than the largest distance inside the study area (d_{max}) will never be recaptured, residency probabilities need not be calculated for distances larger than d_{max} . Thus, calculating the different residency probabilities only requires knowledge of the landscape in a radius of d_{max} around the study area. The second step of the landscape simulation therefore consisted in creating an enlarged grid map with d_{max} territories added on each side of the study area, leading to a grid map of 30×26 cells centered on the study area (fig. S1). Territories outside the study area were then randomly assigned as suitable or unsuitable following with increasing proportion of unsuitable habitat. The residency probability matrix was constructed based on the simulated landscape, and filled with r_{sd} :

$$r_{sd} = \frac{n_{sd}}{N_{sd}}$$

where n_{sd} is the number of territories inside the study area situated at a distance d from territory s and N_{sd} is the total number of suitable habitat territories situated at a distance d from territory s . Each individual was then randomly assigned to one of the territories inside the study area. Individual dispersal distances were then sampled from a Poisson distribution with mean 1.0, as we know from previous simulations (see main text) that the ND model performs well for such mean dispersal distance. Finally, given its natal territory and individual dispersal distance, each individual was assigned a residency probability r_{sd} .

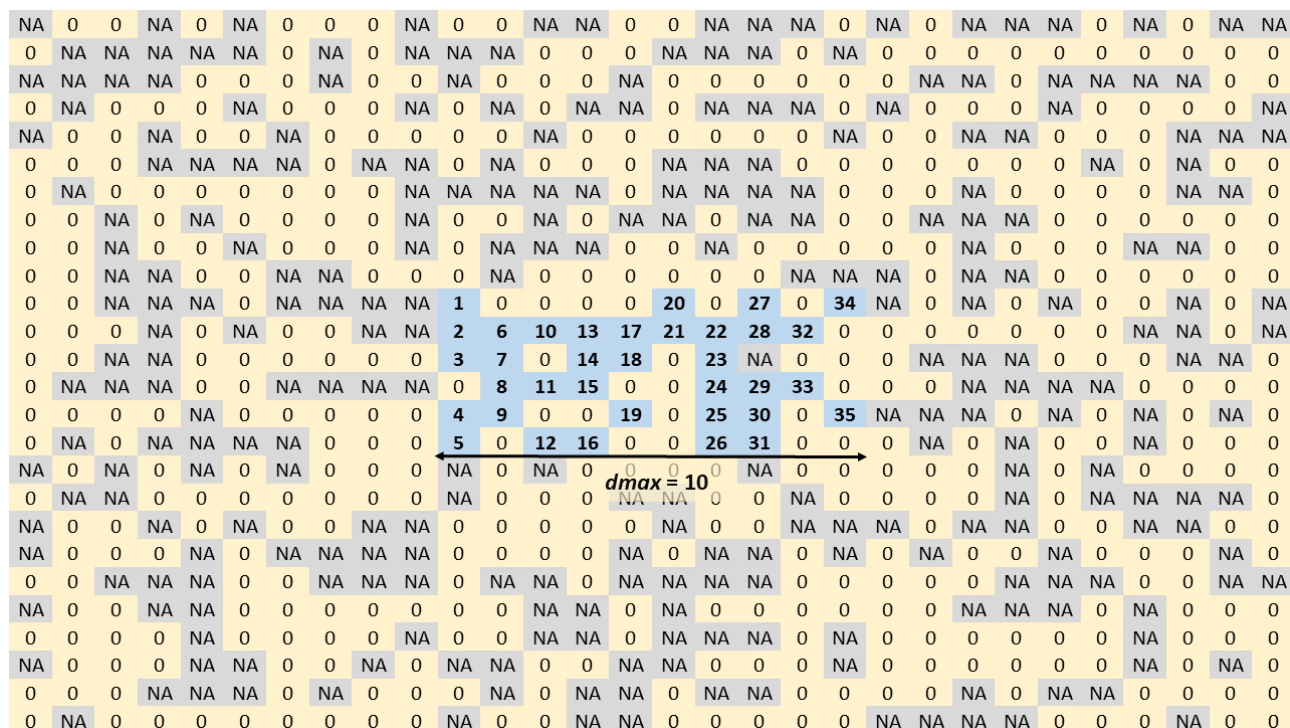


Figure S1. Example of a randomly generated study area map as used in the simulation study. The study area is represented by the light blue area. Each number represents a territory where trapping occurs. Yellow cells (0) represent suitable habitat patches outside the study area and grey cells (NA) represent unsuitable habitat.

All other parameters of the simulation were based on estimates from previous studies on Alpine marmots (Dupont *et al.* 2015; Berger *et al.* 2016; Rézouki *et al.* 2016). Breeders survival was set to $\Phi^{IB} = \Phi^{LB} = 0.95$ and subordinate survival to $\Phi^S = 0.85$. Recapture probabilities differed between dominants and subordinates ($p^{DB} = p^{LB} = 0.65$ and $p^S = 0.95$). Dispersal probability was set to $\Delta = 0.4$ and inheritance probability to $h = 0.12$.

Individual capture histories were constructed by sampling individual states and observed events for capture occasion in the corresponding state-transition and observation process matrices of the ND model. The location of the natal territory was kept for all individuals but dispersal distances were kept only for individuals that did not disperse outside the study area to mimic true capture-recapture data. Each simulated data set consisted of 20 capture occasions with 40 individuals marked at each occasion (except for the last one), leading to a total of 760 capture histories per data set.

We simulated data sets with a proportion of unsuitable area $P = 0, 10, 20, 30, 40, 50, 60, 70, 80,$ and 90% of the territories outside the study area assigned as unsuitable habitat. We repeated the

simulation process 100 times for each P , leading to a total of 1,000 simulated data sets. We then fitted two different models to each data set, one with the true residency probability matrix as generated in the simulation process (the heterogeneity model) and one with the residency probability matrix calculated with all territories outside the study area considered as suitable: the homogeneity model. All models were fitted using Markov Chain Monte Carlo (MCMC) simulations with the computer program JAGS (Plummer 2003) through R3.2.5 (R core team 2016) with the R package jagsUI (Kellner 2014). Three chains were run independently for 10,000 iterations with a burning period of 6,000 iterations and a thinning rate of 1.

RESULTS

Posterior means \pm se of the recapture, dominant survival and inheritance probabilities were identical between models and equal to their simulated values for both models and for all values of P (heterogeneous model: $p^S = 0.95 \pm 0.01$; $p^{IB} = p^{LB} = 0.65 \pm 0.02$; $\Phi^{IB} = \Phi^{LB} = 0.95 \pm 0.02$; $h = 0.12 \pm 0.01$ and homogeneous model: $p^S = 0.95 \pm 0.01$; $p^{IB} = p^{LB} = 0.65 \pm 0.02$; $\Phi^{IB} = \Phi^{LB} = 0.95 \pm 0.01$; $h = 0.12 \pm 0.02$).

As expected, the proportion of unsuitable habitat outside the study area impacted both the subordinate survival and dispersal estimates but also the mean dispersal distance (fig. S2). Because the number of territories available for settlement were over-estimated when the landscape was assumed homogeneous, residency probabilities were artificially under-estimated and subordinate survival, dispersal and mean dispersal distances were in turn over-estimated. The over-estimation was up to 25%, 18% and 10% for the subordinate survival, dispersal probability and mean dispersal distance, respectively. Note that the lower bias of the mean dispersal distance estimator was associated with a large variance. In addition, the standard error of the mean seems to slightly decrease when the proportion of unsuitable habitat increases, and that both for the homogeneous and heterogeneous models.

These results demonstrate the importance of taking into account the structure of the landscape outside the study area when using spatial capture-recapture models. Indeed, if the landscape structure

is unknown and assumed homogeneous, the ND models will over-estimate true demographic parameters for potential dispersers (*i.e.* subordinates). This can have important consequences, especially in applied studies with population management purposes where misestimating dispersal or survival probabilities can lead to deleterious management decisions being taken. Although these models have great potential as they allow to estimate otherwise unattainable estimates of true survival and dispersal parameters, they still rely on strong assumptions about the shape of the dispersal distance distribution (Gilroy *et al.* 2012, Ergon & Gardner 2014, Schaub & Royle 2014, Dupont *et al.*, *in press*) and the structure of the landscape outside the study area (this study). The validity of these assumptions can be cumbersome to assess. Whilst the shape of the dispersal distance distribution may be assessed from the data if the study area is large enough to observe a large number of dispersal events (but further studies are required to thoroughly explore this), the structure of the landscape requires additional information collected outside the study area.

As a conclusion, although we strongly support using the Natal Dispersal model (or other spatially explicit capture-recapture models) because of their ability to estimate true demographic parameters, we also recommend being cautious. In particular, we advise users to fully acknowledge what information is available to them and what are the assumptions they have to make when fitting the model to their data.

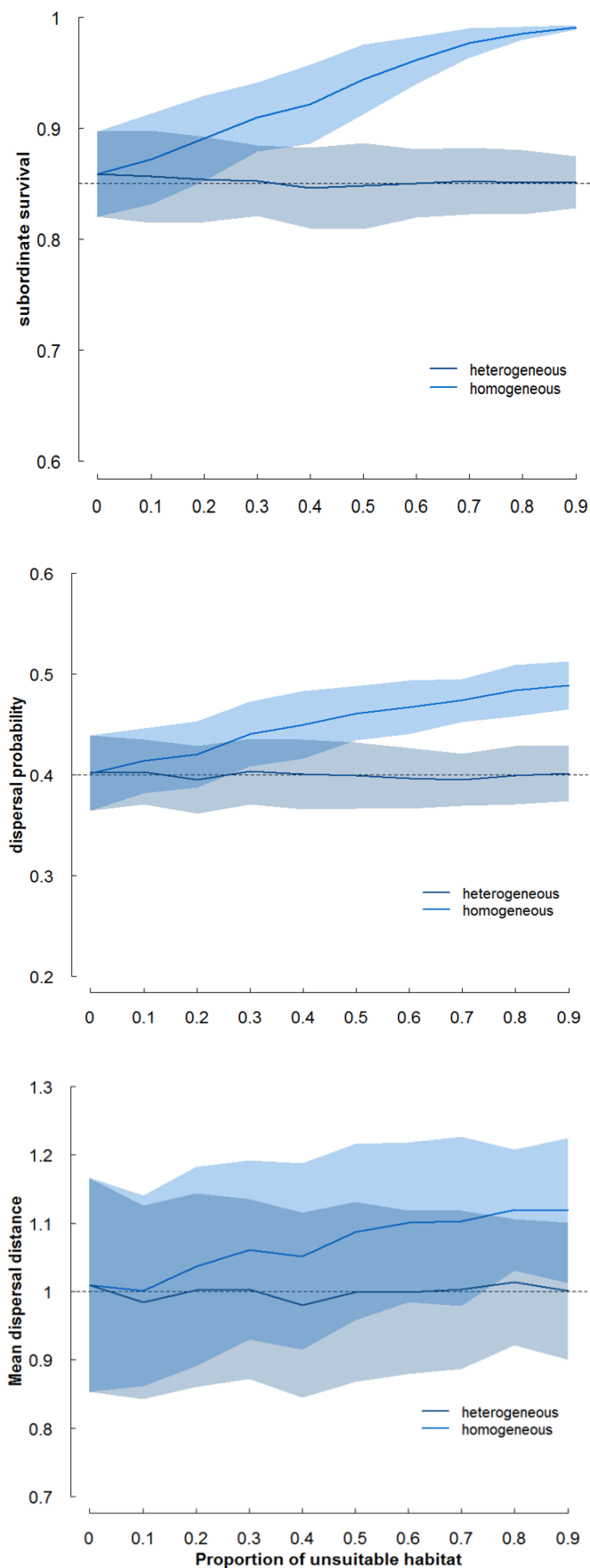


Figure S2. Subordinate survival (upper panel), dispersal (middle panel) and mean dispersal distance (lower panel) estimates with increasing proportion of unsuitable habitat outside the study area returned by the Natal Dispersal model under the assumption of homogeneous (light blue) or heterogeneous (dark blue) landscapes. Shaded areas represent the associated standard error of the mean.