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## High long-term survival and asymmetric movements in a reintroduced metapopulation of Cinereous vultures

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3  
4 **Title: High long-term survival and asymmetric movements in a reintroduced**  
5 **metapopulation of cinereous vultures**

6  
7 **Abstract**

8  
9 Post-release mortality and movements are top proximate factors of translocation failure. Yet,  
10 survival and movement reflect different demographic and behavioral processes and may  
11 therefore have contrasted responses to management, although they are often very difficult to  
12 disentangle in animal populations. To provide guidance in animal translocations, we  
13 discriminated the respective roles of survival and movement in the long-term dynamic of a  
14 translocated metapopulation of cinereous vultures (*Aegypius monachus*) in France using  
15 multi-event capture-recapture analyses of reintroduced (n=119) and wild-born individuals  
16 (n=163) observations. Annual apparent survival rates were high and structured in age (>0.8  
17 for young and >0.9 for adults) and did not differ between individuals origin (wild-born or  
18 released), release methods (aviary or hacking) nor between regions (Alps and Causses),  
19 except for those released in the Alps experiencing a reduced survival for one year after  
20 release. In contrast, age structure movements differed between populations and origin  
21 status. Wild-born young from the Causses were more erratic than those from the Alps and  
22 older individuals, whereas vultures reintroduced in the Causses demonstrated restricted  
23 movements during their first year after release. Despite such asymmetric movements, we  
24 overall highlight a strong tropism of individuals whatever the region and their origin. Since  
25 movement and survival were respectively higher and lower in young compared to adults, we  
26 recommend to first release adults in the primary stage of metapopulation translocations for  
27 increasing the establishment success at the release site. Further releasing young and  
28 securing successful breeding into the wild would increase demographic growth and between  
29 population connections.

30  
31 **Keywords :**

32  
33 *Aegypius monachus*, Multi-event capture-recapture modeling, demography, raptors,  
34 scavengers, reintroduction.

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## 1. Introduction

Reintroductions are critical recovery measures to counter biodiversity loss by aiming at re-establishing viable populations over the long term (IUCN/SSC, 2013; Sarrazin and Barbault, 1996; Seddon et al., 2014). Reintroduction outcomes depend on various factors affecting the different phases of reintroduced population dynamic across time-scales: establishment, growth and regulation phase (Sarrazin, 2007). Although reintroduction contributes successfully to species recovery only once reintroduced population has reached the regulation phase (Robert et al., 2015), intermediate progress assessments are crucial for adaptive management (Armstrong and Seddon, 2008; Parker et al., 2013; Sarrazin, 2007). In addition to survival and breeding settlement, post-release movements have been documented as major drivers of translocated population dynamics (Hanski, 1991), especially at the early stages of population establishment when individuals move away from the release site (Le Gouar et al., 2012). Intense dispersal of released individuals within a metapopulation network can indeed lead to local reintroduction failure while reinforcing newly established or remnant population at regional scale (Le Gouar et al., 2008; Mihoub et al., 2011). Therefore, metapopulation restoration is particularly challenging in highly mobile species.

Distinguishing between temporary or permanent dispersal and survival is thus of paramount importance for assessing short-term and long-term viability (Ergon and Gardner, 2014; Newton et al., 2016) of translocated populations. Post-release cost on demographic parameters (Armstrong and Reynolds, 2012), such as decreased local survival, has been reported particularly in birds (e.g. Evans et al., 2009; Sarrazin et al., 1994) as possible results of a lack of personal experience in the wild (Tavecchia et al., 2009) or sub-optimal habitat selection (Mihoub et al., 2009). However, it still remains often unclear whether post-release costs reflect mortality or emigration. In long-lived raptors, survival generally increases with age (Newton et al., 2016). During the first year of life, fledglings need to learn essential skills to become independent from the adults. In the following years, they progressively prospect new areas as immatures and sub-adults before settling in a site for breeding as adults (Reed et al., 1999). Such age-structured processes may affect both movement and survival patterns depending on the respective abilities and requirements of each life-stage. Consequently, the age of individuals to be released need to be considered with care as it has contrasted consequences to the different phases of reintroduced population dynamics and therefore, strongly influence the outcomes of translocations. Specifically, releasing adults can maximize the establishment phase on the short to mid-term in both isolated population (Sarrazin and Legendre, 2000) and metapopulation network (Mihoub et al., 2011) despite higher demographic costs than juveniles, whereas the release of juveniles may benefit to the long-term population viability when genetic inbreeding depression and mutational meltdown occur (Robert et al., 2004).

Taking advantage of the intense individual monitoring in three reintroduction programs of cinereous vultures (*Aegypius monachus*) in France over 25 years, we aimed at quantifying post-release survival and between-population movement rates. After about two centuries of dramatic decline resulting from poisoning, hunting, habitat destruction and decreasing food availability (Donázar et al., 2002; Morán-lópez et al., 2006; Poirazidis et al., 2004), the cinereous vulture has been almost completely extirpated from the western part of its historic range in the late 20th century's (Cramp and Simmons, 1980). Today, the species is slowly recovering in Europe, thanks to intense conservation efforts, including legal protection of the species and its habitat in natural reserves (Moreno-Opo and Margalida, 2013) or translocation programs (Mihoub et al., 2014b). In France, the first reintroduction of cinereous vulture was initiated in the 1992 and 2004 in the Causses region and this program was then followed by two others in Western border of the Alps (Fig. 1), in the Baronnies (2004 to 2018)

111 and Verdon (2005 to 2020). The two Alpine translocations are still in their establishment  
112 phases, hence it is too early to assess their complete demographic success. At this stage,  
113 the individuals released in both Alpine translocations and their descent regularly merged and  
114 interacted. They all constituted an Alpine population. In the Causses, the observed  
115 population growth decelerated since 2011 with 20 to 25 breeding pairs on average, despite  
116 good breeding success. However, it is not clear if this population suffered unexpected  
117 constraints on growth or already reached the regulation phase. Indeed previous assessment  
118 of nesting habitat suitability suggested a 5 fold higher carrying capacity (Mihoub et al.,  
119 2014a) and food availability seemed high over the period.

120  
121 Here we used capture-recapture data from the long-term monitoring following of these  
122 translocations to discriminate the respective roles of survival and movement in the  
123 restoration dynamics of the French metapopulation of cinereous vultures. We particularly  
124 considered the response of survival and movement to: (1) individual factors such as age and  
125 origin (wild-born or released), (2) environmental and social factors related to the local  
126 characteristics of each region (Causses and Alps), and (3) release methods (age at release,  
127 time spent in captivity). First, we aimed at quantifying possible post-release effects on both  
128 survival and movement parameters. Since age at release and/or release method could play a  
129 role on the cost on survival and movement patterns, we predicted a higher release cost on  
130 survival in adults than in juvenile and immatures as previously shown in vulture species  
131 (Mihoub et al., 2014b; Sarrazin et al., 1994). Second, we compared survival and movement  
132 rates within both Causses and Alpine populations in order to understand if the apparent  
133 stagnation of the Causses breeding population was related to mortality or to emigration  
134 toward the Alps. Indeed, since the first release in the Alps in 2004, conspecific attraction  
135 could have led individuals to exhibit two-way movements between the different reintroduction  
136 sites (Mihoub et al., 2011). We focused only on movements within the French  
137 metapopulation to avoid multiplying hypotheses and over-parametrization of our models with  
138 regard to the small number of individuals monitored outside this metapopulation. We  
139 predicted an increase in movements between regions from 2004 onwards, especially among  
140 released juvenile and immatures because adults are mostly sedentary (Donazar et al., 1993)  
141 and possibly higher from the Alps towards Causses, as the latter population was already  
142 established at that time. We discussed the consequences of our results for the viability of  
143 reintroduced population locally and within the restored metapopulation.

## 144 **2. Material and methods**

### 145 **2.1. Species and reintroduction programs**

146  
147  
148 Cinereous vultures are long-lived scavengers. They reach sexual maturity at 4 - 5 years. In  
149 this paper, we considered three age classes: juveniles are 1<sup>st</sup> year, immature and sub-adults  
150 are 2<sup>nd</sup> to 5<sup>th</sup> year, adults are  $\geq 6^{\text{th}}$  year old. Only one egg is laid in February and the chick  
151 fledges in August. Adults are sedentary and territorial, while juveniles and immatures tend to  
152 be erratic (Donazar et al., 1993).

153  
154 Since 1996, the cinereous vulture is Near Threatened globally (Birdlife International, 2020;  
155 IUCN, 1996). At the beginning of the 20<sup>th</sup> century, the species was extinct in France up to its  
156 reintroduction in the Causses and is listed as "Endangered" since 2016 in France (UICN  
157 France et al., 2016). In 2016, 32 pairs bred in France (Causses: n=25; Alps: n = 7).

158  
159 Following the successful reintroduction of griffon vulture (*Gyps fulvus*) in the Causses and  
160 Alps (Terrasse et al., 2004), cinereous vultures were released in three sites in France using  
161 two soft-release methods (Mihoub et al., 2011). The hacking method was used for juveniles  
162 (1<sup>st</sup> year), born in captivity and brought to an artificial nest one month prior to fledging. The  
163 aviary method consisted in keeping immatures and adults ( $\geq 2^{\text{nd}}$  years), mostly originating  
164 from rehabilitation of wild birds, at least 1 year in aviaries at the release site. In 11 cases,  
165 juveniles were released from aviaries, but we pooled them with juvenile released by hacking

166 method as they had the same age at release and likely faced similar post-releases  
167 challenges (e.g. learning skills to fly and forage). Releases of juveniles by the hacking  
168 method occurred from July to November in order to match with the phenology of wild  
169 fledglings. A majority of releases through aviaries occurred between November and May,  
170 which corresponds to pair-formation (November-January) and incubation periods (February-  
171 April).

172  
173 The first reintroduction program was launched in the Causses with 53 individuals released  
174 between 1992 and 2004. Since the first successful breeding in the wild in 1996, 163 juveniles  
175 had fledged by 2016 and the population reached 20 breeding pairs in 2016. The  
176 reintroduction in the Alps began in the Baronnies, c. 150 km east of the Causses, with 43  
177 individuals released between 2004 and 2016; followed by the Verdon, located c. 100 km  
178 south-east from the Baronnies, with 28 individuals released between 2005 and 2016. Since  
179 the first successful breeding in the wild in 2010 in the Baronnies, 21 wild-born juveniles had  
180 fledged by 2016 and a maximum of 10 pairs bred. In the Verdon, three wild-born juveniles  
181 had fledged between 2013 and 2016 and a maximum of two pairs bred.

182  
183 Regular movements of ringed individuals were observed, between these three populations,  
184 thanks to daily flight distance commonly exceeding 100 kilometers in vultures (Duriez et al.,  
185 2019). Based on frequent movements detected in our dataset between Baronnies and  
186 Verdon, and given very similar habitat conditions at both alpine sites, we further considered  
187 the outcome of the two Alpine reintroductions as a single functional demographic population  
188 in our analysis from both biological and methodological reasons (hereafter, Alps).

## 189 190 *2.2. Populations monitoring*

191  
192 Both Causses and Alps populations were similarly monitored. We considered data collected  
193 between 1992 and 2016 for birds released and birds born in the wild between 1992 and  
194 2015. All reintroduced individuals (n = 119, Causses n = 53, Alps n = 66) were marked prior  
195 to release and all (known) wild-born individuals were marked in the nest before fledging (n =  
196 164, Causses n = 145, Alps n = 19). All birds were individually marked with an engraved  
197 metal ring (hereafter “Metal”) for identification at hand or short distances (<20 m), and with a  
198 plastic ring (“Plastic”) allowing long-distance identification (< 400 m). Regarding long-  
199 distance marks used, the early cohort of birds released in the Causses were marked  
200 between 1992 and 2004 with a combination of four different colored rings or/and with a large  
201 white ring engraved black letters, while all other subsequent birds were marked only with a  
202 large white ring engraved with black letters. Released birds were additionally marked with an  
203 individual pattern of bleached remiges or rectrices, allowing flight identification until complete  
204 feather moult two years after release. Finally, 71% of released birds were also equipped with  
205 radio-transmitters with an average life-span of one year. Therefore, feather bleaching might  
206 increase resighting rates in the first two years after release and radiotags might also increase  
207 the recovery rate the first year after release. In the following we have distinguished long-  
208 distance marks (hereafter “LongDist”: plastic ring, pattern of bleached remiges or rectrices  
209 and radio-transmitters) and short-distance marks (“ShortDist”: metal ring).

210  
211 Monitoring was conducted year-round between 1992 and 2016 and consisted in resightings  
212 at supplementary feeding stations and at nests. Visual observations were mostly made using  
213 telescopes, but photo-identifications with camera-trap was also used in Baronnies after 2009.  
214 During the monitoring period, any plastic ring lost and some metal ring lost was reported (i.e.  
215 bird observed with one ring missing, or ring found on ground). Finally, five marked individuals  
216 were definitively recaptured and 44 marked individuals were recovered dead thanks to  
217 transmitters or opportunistically.

## 218 219 *2.3. Building capture-recapture histories*

220

221 We defined resighting occasion over a nine-months period (from January 1<sup>st</sup> to September  
222 30<sup>th</sup>), similarly to previous studies on vulture populations (e.g. Chantepie et al., 2016; Le  
223 Gouar et al., 2008; Mihoub et al., 2014b). Each annual occasion was coded according to the  
224 live or dead status of individuals, the region where the individuals had been seen (Causses  
225 and Alps) and their ringing status (Plastic + Metal, Plastic only, Metal only, No rings).

226  
227 We assigned each observation to a region (Causses or Alps), when they were located within  
228 a radius of 55 km around each release site are located (Fig. 1), allowing a homogeneous  
229 selection of observation data for all reintroduction programs and that include all known nests  
230 until 2016. Because there can only be one information per occasion, we set specific rules for  
231 site attributions: an individual was 1) attributed to the state "Causses" if only resighted there ;  
232 2) attributed to the state "Alps" if only resighted there; and 3) attributed to the state "Mover" if  
233 seen in both regions, i.e. moving within the metapopulation. Due to the low probability of  
234 reading a metal ring, we assumed that an individual wearing only a metal ring could not be  
235 detected as "Mover". Additional details for building capture-recapture histories can be found  
236 in Appendix A.

237  
238 Individuals were grouped by age (from the 1<sup>st</sup> year until  $\geq 6^{\text{th}}$  years), by release status (wild-  
239 born / hacking: released juveniles before fledging / aviary: released immatures, sub-adults or  
240 adults), by origin (Causses / Alps) and if a missing ring was replaced (see Appendix A). This  
241 allowed tracking the age and status of the individuals and the age of the rings (time elapsed  
242 since ringing). The precise age of 14 individuals released by the aviary method was  
243 unknown: we then used plumage abrasion on head and body to attribute them to a likely age.

#### 244 2.4. Multi-event capture-recapture modeling

245  
246  
247 In order to carry out our analyses at local (population) and regional (metapopulation) scales,  
248 we developed two variants of multi-event Capture-Mark-Recapture (CMR) models (Pradel,  
249 2005). A first set of "population" models was used to simultaneously estimate survival  
250 probabilities in each local population (Causses and Alps) considered as isolated (e.g.  
251 movements were disregarded). A second set of "metapopulation" models was used to  
252 estimate movement and survival probabilities within the metapopulation (e.g. between  
253 population movements were considered). Importantly, multi-event models allow for  
254 controlling for heterogeneous detection probabilities, ring loss and a mixture of live  
255 recaptures and dead recoveries (Duriez et al., 2009). Overall, we defined 6 states combining  
256 the different statuses for population models without movements (Appendix B) and 16 states  
257 for metapopulation models with between-population movement (Appendix C).

258  
259 For both population models, we used observations of living individuals only in the region  
260 considered, but we did take into account recoveries of dead individuals wherever they  
261 occurred (e.g. also outside of these areas). For the metapopulation model, we did not use  
262 resightings and dead recoveries outside both studied regions because including these data  
263 would necessitate adding another state "Elsewhere" to account for movements outside the  
264 French metapopulation (see Duriez et al., 2009).

265  
266 As individuals could lose their rings, previously marked individuals may no longer be  
267 observed and may appear as dead. However, those birds should move and survive, and  
268 hence ignoring this possibility may bias the movement and the survival estimates (Badia-  
269 Boher et al., 2019; Tavecchia et al., 2012). Consequently, ring loss probabilities had to be  
270 estimated prior to movement and survival probabilities. Moreover, if an individual was  
271 observed at site 1 and recovered dead later at site 2, it had obviously died after moving. To  
272 account for this possibility, movements were estimated prior to survival in the models. Dead  
273 recoveries were thus site-dependent and the survival probability depended on the site of  
274 arrival.

275

276 Consequently, for both population models, transition probabilities between states were  
277 decomposed into three steps in order to separately model the following parameters in this  
278 order: the probability of plastic ring loss ( $\alpha$ , step 1), the probability of metal ring loss ( $\beta$ , step  
279 2) and the survival probabilities ( $\phi$ , step 3). Similarly, for the metapopulation model, the  
280 transition probabilities between states were decomposed into four successive steps: the  
281 probability of plastic ring loss ( $\alpha$ , step 1), the probability of metal ring loss ( $\beta$ , step 2), the  
282 probability of moving ( $\Psi$ , step 3) and the survival probability ( $\phi$ , step 4). There was a lapse of  
283 one year between transitions and each matrix (i.e. transition probabilities) was conditional on  
284 the previous step. This parameterization allowed separate investigation of the effects of  
285 different covariates or factors on ring loss, movements and survival by fitting different  
286 covariates or factors at each step.

287  
288 We used E-SURGE 2.1.2 software (Choquet et al., 2009b) and we followed (Lebreton et al.,  
289 1992) for model notation (see details in Appendix D). The resighting and the dead recovery  
290 probabilities were denoted respectively  $P$  and  $r$ . For both population models, the model  
291 structure allowed for simultaneous estimates of  $\alpha$ ,  $\beta$ ,  $\phi$ ,  $P$  and  $r$ . For the metapopulation  
292 model, the model structure allowed for simultaneous estimates of  $\alpha$ ,  $\beta$ ,  $\phi$ ,  $\Psi$ ,  $P$  and  $r$ . Due to  
293 the large number of potential models, we examined only models that tested explicit  
294 hypothesis regarding biology and the monitoring of cinereous vulture. A summary of the  
295 hypotheses tested in the population models are given in Table 1 and additional hypotheses  
296 for the metapopulation model in Table 2.

297  
298 Model selection was based on Akaike Information Criterion adjusted for small sample sizes  
299 (AICc, (Burnham and Anderson, 2003)). The best model had the smallest AICc. Delta AICc  
300 ( $\Delta$ AICc) was calculated as the difference in AICc between the model with the smallest AICc  
301 and the other models. Models with  $\Delta$ AICc  $\leq 2$  were deemed to be equivalent. The AICc  
302 weights (wAICc) represent the probability that a particular model is the best among a set of  
303 competing models. We performed a step-wise model selection procedure. At each step,  
304 between all model structures showing  $\Delta$ AICc  $\leq 2$ , we selected the model with the lowest  
305 number of parameters. If several models had the same lowest number of parameters, we  
306 choose the one with the strongest wAICc and used it in further steps.

307  
308 Assessing the goodness of fit of a model to the data is crucial to avoid inflate model  
309 deviances, bias estimates or incorrect model selections (Pradel et al., 2005). All GOF tests  
310 were implemented with the program U-CARE V2.3.4 (Choquet et al., 2009a). All methods  
311 and results are explained in details in Appendix E.

### 312 **3. Results**

#### 313 **3.1. Analyses at population scale**

314 All the hypotheses tested on each parameter are listed in the Table 1 and the model  
315 selections are detailed in the Appendix B.

##### 316 **3.1.1. Causes population**

317  
318  
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320  
321 Whatever the survival hypothesis, the resighting probability for short-distance marks varied  
322 over time, whereas the resighting probability for the long-distance marks was constant  
323 (lowest AICc always supported "ShortDist\*t"; Table B4). Similarly, whatever the survival  
324 hypothesis, the plastic ring loss probabilities followed logarithmic trend with year since  
325 ringing ("tlog"; Table B5). For survival, three models were equally supported (in terms of AICc  
326 and wAICc) with constant survival probabilities for each age class (Table B6). Yet these best  
327 models differed by either no post-release effect, post-release effect on survival for all  
328 reintroduced birds (similar for both release methods, "reintro<sub>s</sub>" effect) and post-release effect  
329 on survival for aviary-released immatures/adults ("aviary" effect), but we could not conclude  
330 about a post-release cost on survival in the Causes.

331  
332 According to the most parsimonious model (model 12, Table 3), the ring loss probability was  
333 higher for plastic ring than for metal ring. Cumulative probabilities of ring loss showed that  
334 from 10 years after ringing nearly 50% of individuals had likely lost their plastic ring, versus  
335 4% for the metal ring (Fig. 2). Annual apparent survival rates were higher for adults than  
336 immatures and juveniles ( $\varphi_1 = 0.804 \pm 0.034$ ;  $\varphi_{2-5} = 0.878 \pm 0.019$ ;  $\varphi_{6+} = 0.945 \pm 0.017$ ; Fig.  
337 3). Long-distance marks yielded high resighting probability ( $0.884 \pm 0.014$ ), whereas short-  
338 distance marks varied between years ( $0$  to  $0.665 \pm 0.181$ ; arithmetic mean:  $0.172 \pm 0.205$ ).  
339 The recovery of dead individuals once reintroduced was high during the 1<sup>st</sup> year after release  
340 ( $0.585 \pm 0.161$ ). Wild born individuals and later reintroduced individuals showed reduced  
341 probability of being recovered as dead ( $0.267 \pm 0.048$ ).  
342

### 343 3.1.2. Alps population

344  
345 Resighting probability of the long-distance marks varied with respect to the use of a camera  
346 trap, whereas the resighting probability of short-distance marks was constant (lowest AICc  
347 always supported "LongDist\*Pcamera"; Table B7). Similarly, whatever the survival  
348 hypothesis, the plastic ring loss probability was constant (Fig 2; Table B8). For survival, three  
349 models were equally supported in terms of AICc (Table B9). The first best model included  
350 constant survival probabilities on each age classes and it considered a short-term post-  
351 release cost in survival for all reintroduced birds (similar for both release methods, "reintro<sub>s</sub>"  
352 effect). The second best model included time-dependence in survival probabilities only for  
353 immatures and sub-adults and considered a short-term post-release cost in survival for all  
354 reintroduced birds ("reintro<sub>s</sub>" effect). The third model supported constant survival probabilities  
355 for each age classes and considered a short-term post-release cost in survival associated  
356 with reintroduction, different for hacking/aviary-released juveniles and aviary-released  
357 immatures/adults (reintro<sub>d</sub> effect).  
358

359 According to the most parsimonious model (model 25, Table 2), the ring loss probability was  
360 higher for plastic ring than metal ring. Cumulative probabilities of ring loss showed that from  
361 10 years after ringing nearly 30% of individuals were likely to have lost their plastic ring,  
362 versus 20% for the metal ring. Annual apparent survival rates were higher for juveniles and  
363 released individuals suffered from a severe post-release cost in survival the first year after  
364 release ( $\varphi_{pre} = 0.570 \pm 0.062$ ;  $\varphi_1 = 0.947 \pm 0.051$ ;  $\varphi_{2-5} = 0.841 \pm 0.044$ ;  $\varphi_{6+} = 0.882 \pm 0.038$ ,  
365 Fig. 3). Resighting rate of long-distance marks were very high with the use of a camera trap  
366 (before camera trap:  $0.732 \pm 0.099$ ; after:  $0.984 \pm 0.011$ ). Resighting rate by short-distance  
367 marks was also high ( $0.651 \pm 0.143$ ). The dead recovery rate of reintroduced individuals was  
368 high during the first year after release ( $0.317 \pm 0.088$ ). Wild-born individuals and later  
369 reintroduced individuals showed reduced probability of dead birds recovery ( $0.211 \pm 0.085$ ).  
370

## 371 3.2. Analysis at metapopulation scale

### 372 3.2.1. Model selection

373  
374 The model selection is detailed in the Appendix C. Ultimately, we selected as the best fitting  
375 model 60 (Table 2 and Table C4). Movements depended on three age classes in interaction  
376 with the region of origin (birth or release site) and a short-term post-release effect on  
377 movement only for individual released in the Causses, regardless of the release method  
378 employed. Survival depended on three age classes and there was only a post-release cost in  
379 survival similar for all reintroduced individuals in the Alps. Plastic ring loss probability  
380 followed logarithmic trend with year since ringing, whereas we assume constant metal ring  
381 loss probability (Fig. 2). The ring loss probability was higher for plastic ring than metal ring.  
382 Cumulative probabilities of ring loss showed that from 10 years after ringing nearly 33% of  
383 individuals were expected to have lost their plastic ring, against 7% for the metal ring.  
384

### 385 3.2.2. Movement between regions

386  
387 Movements of cinereous vultures within the French metapopulation varied according to age  
388 as well as to their region of origin (Fig. 4). Young birds were more erratic than adults. Overall,  
389 vultures moving between regions first demonstrated erratic behaviors within the  
390 metapopulation (“mover state”) before becoming resident in one of the two populations.  
391 Interestingly, vultures released in the Causses showed a strong fidelity to the release site  
392 ( $0.98 \pm 0.02$ ) compared to wild-born birds and to individuals released in the Alps (Fig. 3). In  
393 contrast, birds born or released in the Causses were more erratic than those born or  
394 reintroduced in the Alps and were also more likely to become resident in the Alps than those  
395 originating from the Alps to become resident in the Causses.

### 396 397 3.2.3. Survival probabilities

398  
399 Survival estimates at the metapopulation scale were better assessed since confidence  
400 interval smaller than at local population scale (Fig. 3). When accounting for movements,  
401 survival rates did not differ between regions independent on their movement status (mover or  
402 resident; Table C4). Annual apparent survival rates were higher in adults than in yearlings  
403 ( $\phi_1 = 0.830 \pm 0.029$ ;  $\phi_{2-5} = 0.877 \pm 0.016$ ;  $\phi_{6+} = 0.918 \pm 0.01$ ). Released individuals from Alps  
404 suffered from a 27% reduction in survival the first year after release ( $\phi_{pre} = 0.564 \pm 0.061$ ).  
405 The post-release cost on survival in the Alps was not due to departures of individuals in the  
406 Causses since its value was similar at the metapopulation scale and at the scale of the Alpine  
407 population.

## 408 409 4. Discussion

410  
411 We used long-term CMR data from three reintroductions of cinereous vultures in France to  
412 understand the respective role of survival and movements in the restoration of two  
413 populations in the Causses and the Alps. It is important to notice that the reduction from  
414 three reintroduction to two populations resulted from the fusion of two translocated groups of  
415 individuals more than to a clear extinction of one of them. The differences in survival and  
416 asymmetric movement rates within and among Causses and Alps allowed us to identify the  
417 demographic processes driving the successful settlement of reintroduced populations of  
418 highly mobile birds. Survival did not differ significantly between regions nor between wild-  
419 born and released individuals except for individuals reintroduced in the Alps, which showed a  
420 reduced survival during the first year after release. In contrast, movements differed between  
421 populations and between reintroduced or wild-born birds, with individuals from the Causses  
422 generally exhibiting more erratic behaviours than those from the Alps.

### 423 424 4.1. Survival rates and post-release effect

425  
426 When conducting the analysis at population scale, survival rates varied across regions, with  
427 lower apparent annual survival in the Alps, excepted for yearlings. When considering  
428 observations within both populations at metapopulation scale however, survival rates did not  
429 differ anymore between regions and estimates were more accurate (narrower confidence  
430 intervals). These results suggest that apparent annual survival at local population scales  
431 differed between populations because of asymmetric emigration patterns rather than  
432 mortality. Overall, cinereous vultures reintroduced in France had survival rates consistent  
433 with previous findings in natural and reintroduced populations of other vulture species with  
434 similar life history traits (Badia-Boher et al., 2019; Newton et al., 2016; Schaub et al., 2009).  
435 Survival were constant over time and increased with age, likely reflecting gain of experience  
436 and behavioural changes with maturity before recruitment into a breeding population  
437 (Newton et al., 2016). However, the high juvenile survival rates in the Alps should be taken  
438 with caution as there were only few wild-born individuals there and almost all of them  
439 survived.

440

441 In the Causses, adult survival was lower than shown in a previous study (Mihoub et al.,  
442 2014b). Reduction in adult survival could eventually be related to senescence of individuals,  
443 intraspecific density-dependent regulation or interspecific competition. Senescence is  
444 probably not yet detectable since this process was detected only for griffon vultures older  
445 than 28 years (Chantepie et al., 2016). We would expect that intraspecific competition would  
446 have first impacted survival in juveniles and immatures rather than adults (Le Gouar et al.,  
447 2008). Interspecific competition with other scavenger species such as griffon vultures may  
448 also decrease survival of cinereous vultures and / or make them foraging in places where  
449 competition is lower following interferences in accessing food resources. With respect to  
450 previous survival estimated in the Causses up to 2008 by Mihoub et al. (2014), both  
451 intraspecific and interspecific competition may play a role. Indeed, these processes may  
452 explain higher movements of wild individuals born in the Causses towards the Alps than  
453 released individuals as the population is growing, whereas no effect on survival could be  
454 detected between populations. Interestingly however, the absence of post-release cost on  
455 survival in the Causses is evidenced by both Mihoub et al. (2014) and in the present  
456 analysis.

457  
458 In contrast, we found a strong post-release cost on survival for birds reintroduced in the Alps,  
459 whatever the method of release considered. Such post-release cost was not related to  
460 departures of individuals towards the Causses (local apparent survival due to movement  
461 outside the study area) as both population scale and metapopulation scale analyses support  
462 this effect. Since the release protocol was very similar in both regions, the post-release cost  
463 on survival in the Alps could be explained by lower quality of released individuals, a stronger  
464 negative effect of demographic stochasticity or higher dispersal from the Alps to unmonitored  
465 areas than in the Causses. Yet, these three hypotheses are difficult to assess. Since very  
466 few cinereous vultures have been recorded as emigrant towards established cinereous  
467 vulture populations across Europe (Spain, Portugal or Greece), such low apparent survival is  
468 more likely reflecting mortality than permanent emigration. The origin of the reintroduced  
469 individuals, their body conditions or genetic diversity of released groups could be involved in  
470 individual quality related to mortality causes but could not be tested here due to lack of  
471 statistical power associated with these many and confounding effects on a relatively low  
472 number of individuals.

473  
474 Mortality during the establishment phase of reintroduction is commonly reported to be higher  
475 due to the stress and inexperience in the wild of the released birds (Armstrong and  
476 Reynolds, 2012; Armstrong et al., 2017) and other taxa (Sarrazin and Legendre, 2000). In  
477 griffon vulture reintroduced in the Causses and the Alps, released adults typically suffered a  
478 post-release cost in survival in the first year following release (Le Gouar et al., 2008; Sarrazin  
479 et al., 1994). Here, age class at release or release methods did not affect post-release cost  
480 on survival, as the composition of released groups were very similar between sites while  
481 survival cost only occurred in the Alps whatever the release method. Similarly, differences in  
482 potential threats affecting survival between the two populations or in intrinsic habitat quality is  
483 unlikely, or may have been temporary, as no difference on long-term survival was found.  
484 Therefore, difference between the two populations in terms of post-release cost on survival  
485 most likely from a combination of factors including stochastic effects of environmental and  
486 demographic process as well as heterogeneity or experience of founders.

#### 487 488 *4.2. Pattern of cinereous vultures movements between restored populations and post-* 489 *release effects*

490  
491 As expected, cinereous vultures demonstrated age-structured patterns of movement  
492 according to their life stage, likely reflecting different requirements for foraging or for  
493 breeding. Adults were mostly sedentary while juvenile and immature birds were more erratic  
494 (36% from Causses and 12% from Alps become mover at juvenile stage; 14% from Causses  
495 and 10% from Alps at immature stage against only 0.01% and 0.02% from respectively

496 Causses and Alps at adult stage). Our results are consistent with previous studies on erratic  
497 behavior of immature birds and site fidelity of adults more specifically for vultures (Mundy et  
498 al., 1992) and other raptors (Serrano, 2018). Moreover, our results also indicated that  
499 movements between populations were relatively intense during the erratic phase, as all  
500 moving individuals regularly travelled back and forth before settling permanently into a  
501 population.

502  
503 Another key finding is that movement patterns between both regions were asymmetrical, with  
504 the Alps attracting overall more birds from the Causses than the opposite, which is further  
505 corroborated by recent estimates of gene flows between these two reintroduced populations  
506 (Helsen et al., unpublished). Interestingly however, individuals released in the Causses were  
507 more faithful to their release site than their wild-born offspring's. Although such pattern was  
508 not apparent in the Alps, recalling that the closest populations of cinereous vultures were  
509 located 600 km West (Spain) and 2000 km East (Greece) when the releases started in the  
510 Causses may help interpreting these movement patterns. Asymmetric movements are not  
511 rare among populations of colonial species (Danchin et al., 2004; Serrano et al., 2005) and  
512 reflect complex processes involved in habitat selection. The use of public information such as  
513 conspecific attraction has been evidenced to be a strong driver of habitat selection (Danchin  
514 et al., 2004). Relative isolation from other population of conspecific may therefore promote  
515 establishment to the release site (Mihoub et al., 2011), which may be reflected by the high  
516 fidelity of cinereous vultures released in the Causses before the reintroduction started in the  
517 Alps. Birds released in the Alps might have been attracted by the population already  
518 established in the Causses and movements of wild-born birds would be mostly directed  
519 towards the Causses, whereas our results indicate the opposite. Actually, reduced  
520 connectivity with existing populations may allow the establishment of a newly reintroduced  
521 population even when conspecific attraction is at play, and may even attract individuals from  
522 remnant or previously established reintroduced population and potentially lead them to  
523 extinction (Mihoub et al., 2011). Heterospecific attraction may have both facilitated  
524 establishment and prevented extinctions as population of griffon vultures are established in  
525 the Causses and Alps since the 1980's and early 2000's respectively (Hromada et al., 2008;  
526 Sebastián-González et al., 2010). Nevertheless, the relative decrease of the population  
527 growth of the breeding population of cinereous vultures observed since the late 2000's, when  
528 breeding started in the Alps, may at least partly result from intense movements driven by  
529 conspecific attraction. We cannot assess natal and breeding dispersal as strictly defined by  
530 (Greenwood, 1980) because of the difficulty to identify breeding vultures at nest, but this  
531 interpretation is further supported by our results on survival, showing no significant difference  
532 between regions.

533  
534 It may also be noted that individuals retain a marked tropism towards their site of origin.  
535 Among movers, those originating from the Causses settle mainly in the Causses until age 5  
536 and then exclusively in the Causses when older, those originating from the Alps settle only in  
537 the Alps at all ages. It is also remarkable that among the old individuals established in the  
538 Alps, 11% of those originating from the Causses move back to settle in the Causses while  
539 those originating from the Alps mainly remain there or for a very few (2%) become movers.  
540 These results are very similar to those found on an unrelated species (greater flamingo  
541 (*Phoenicopterus roseus*); Balkiz et al., 2010) and may reflect a more general pattern in bird  
542 species.

#### 543 544 *4.3. Implications for conservation*

545  
546 Detailed and long-term (25 years) monitoring data, allowed us to run complex multi-event  
547 models, to reveal post-release effects on survival and dispersal. Post-release monitoring of  
548 reintroduced individuals is important at short, medium and long-term to allow a rigorous  
549 assessment of the success of reintroduction projects (Griffith et al., 1989; Parker et al., 2013)  
550 and to identify possible causes of failure in order to prioritize management actions adaptively

551 (Sarrazin, 2007). In the case of long-lived scavengers and raptors, ringing data obtained from  
552 visual observation at feeding station provided useful information (Morrison and Baird, 2016).  
553 The high resighting rate of vultures in the Alps promotes the use of camera traps at  
554 scavenger feeding stations, whenever possible, to identify a larger number of individuals.  
555

556 Metapopulation restoration might compromise between the establishment of released  
557 individuals conditional to local viability and sufficient degree of movement among populations  
558 to allow connectivity and metapopulation functioning at larger scales. In raptor, the  
559 underlying movement process by which individuals wander and explore the environment is  
560 still poorly known (Serrano, 2018), especially in reintroduction context for which initial  
561 disequilibrium strongly interact with demographic and behavioral processes (Le Gouar et al.,  
562 2012). Estimating survival of released animals is also crucial for identifying potential threats  
563 (e.g. Ewen and Armstrong, 2007) and for assessing reintroduction success (Robert et al.,  
564 2015). Since release strategies may affect both survival and movements of reintroduced  
565 animals, monitoring and assessing the different effect of release methods on these  
566 demographic processes remain critical for improving reintroduction efficiency (Armstrong and  
567 Seddon, 2008).  
568

569 Our results confirmed that aviaries versus hacking methods did not significantly affect the  
570 reintroduction of cinereous vultures (Mihoub et al., 2014b), whereas the efficiency of the  
571 reintroduction in terms of post-release survival and dispersal was site-specific. We  
572 corroborated that survival of released individuals can be lowered in the short-term even if  
573 environmental conditions allow high survival in the long-term, and that movements can differ  
574 among populations within single species, depending on environmental and social factors  
575 involved in habitat selection (Danchin et al., 2004; Serrano et al., 2001). These asymmetric  
576 erratic movements should not be interpreted as dispersal and do not necessarily imply that  
577 cinereous vultures attracted to the Alps may jeopardize the viability of the Causses  
578 population. Nevertheless, it may explain the decreased in the population growth rate in the  
579 Causses during the last decade. These quantitative results should facilitate the development  
580 of a population model that can predict the probability of population persistence and therefore  
581 provide an indication of longer-term reintroduction success. Since the dispersal is age-  
582 dependent and survival were similar between release methods, we recommend to release  
583 adults to increase the probability of establishment success at the release site (Le Gouar et  
584 al., 2008; Sarrazin and Legendre, 2000).  
585

586 Beyond the case of cinereous vultures, the accurate assessment of survival and movements  
587 within a network of translocated populations underlines the request for a priori defining  
588 spatial and temporal scales for understanding restoration processes and ultimately  
589 translocation success, from local release sites to metapopulation.  
590

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773 **Supplementary material**

774 Appendix A: Additional details for building capture-recapture histories.

775 Appendix B: Multi-event survival modelling for each region at population scale.

776 Appendix C: Multi-event survival modelling for each region at metapopulation scale.

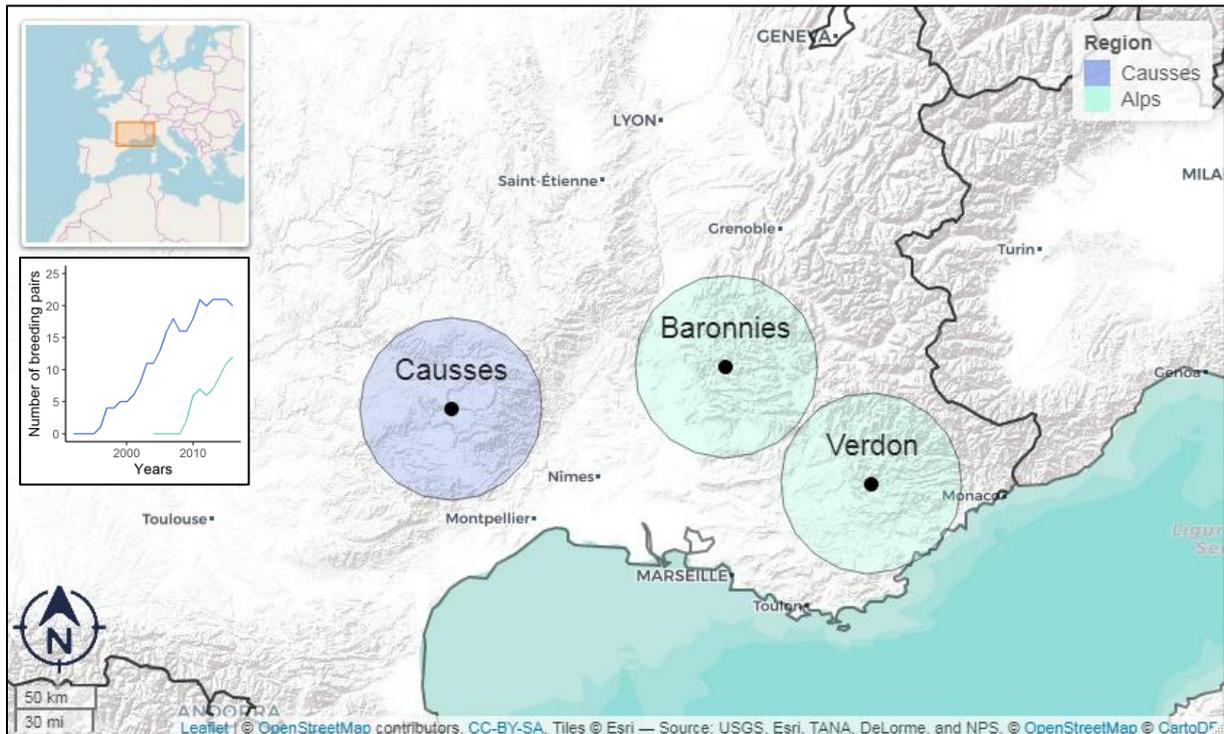
777 Appendix D: Example of Model Definition Languages instructions on E-SURGE software.

778 Appendix E: Goodness-of-fit tests.

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780 **Research data**

781 If the manuscript is accepted, the data supporting the results will be archived in a public  
782 repository and the data DOI will be included at the end of the article.



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Figure 1: Locations of the three reintroduction programs of cinereous vultures in France. Release sites (aviaries) are indicated by dots, surrounded by circles of 55 km radius. Inset: Annual numbers of breeding pairs in the Causses (blue) and in the Alps (green). (2-column fitting image)

792 Table 1: Summary of hypotheses tested in the population models.  
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Parameters	Hypotheses	Abbreviations
<b>Recovery rates (r)</b>	• One year post-release effect	Reintro <sub>1yar</sub>
	• Constant	c
	• Long-distance (LongDist) versus short-distance marks (ShortDist)	2c
	• Time effect on resighting both LongDist & ShortDist	2c*t
	• Time effect on resighting LongDist only	LongDist*t
	• Time effect on resighting ShortDist only	ShortDist*t
	• Effect of absence (1992-2008) and presence (2009-2016) of camera trap	Pcamera
<b>Resighting rate (P)</b>	• Camera trap period effect on resighting LongDist only	LongDist*Pcamera
	• Camera trap period effect on resighting LongDist and time effect on resighting ShortDist	LongDist*Pcamera, ShortDist*t
	• Constant	c
	• Linear effect of time since ringing	tlin
	• Logarithmic effect of time since ringing	tlog
<b>Plastic ring loss (α) and metal ring loss (β)</b>	• Constant	c
	• Time effect	t
<b>Survival (φ<sub>1</sub> / φ<sub>2-5</sub> / φ<sub>6+</sub>)</b> (always with an age effect)	• Age effect only, no post-release effect	-
	• Post-release effect on survival of aviary-released immatures/adults only	aviary
<b>One year post-release effect on survival (φ<sub>pre</sub>)</b>	• Post-release effect on survival of all reintroduced birds	reintro <sub>s</sub>
	• Post-release effect on survival of aviary-released immatures/adults differ from post-release effect on survival of aviary/hacking-released juveniles	reintro <sub>d</sub>
	• Time effect on post-release effect on survival of aviary-released immatures/adults only	aviary*t
	• Time effect on post-release effect on survival of all reintroduced birds	reintro <sub>s</sub> *t
	• Time effect on both post-release effect on survival of aviary-released immatures/adults and post-release effect on survival of aviary/hacking-released juveniles	reintro <sub>d</sub> *t

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796 Table 2: Summary of additional hypotheses tested in the metapopulation model. Some of the hypotheses tested are identical to those of the  
 797 population-scale models; please also refer to the Table 1 for the metapopulation model.  
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Parameters	Hypotheses	Abbreviations
<b>Recovery rates (r)</b>	• Effect of region (Causses versus Alps) and one year post-release effect	Reintro <sub>1yar</sub> *Reg
<b>Resighting rate for long distance marks (P<sub>LongDist</sub>)</b>	• Differ between Causses resident, Alps resident without camera trap, mover without camera trap, Alps resident with camera trap and mover with camera trap	RegStat1*Bcam
	• Causses equivalent to Alps resident without camera trap versus mover without camera trap versus Alps resident with camera trap versus mover with camera trap	RegStat2*Bcam
<b>Resighting rate for short distance marks (P<sub>ShortDist</sub>)</b>	• Time effect in Causses and constant in Alps	CAU*t,ALPS
<b>Initial states</b>	• Effect of reintroduction period: 1992-2003 (reintroduction in Causses only) versus 2004-2016 (reintroduction started in the Alps and breeding population settled in Causses)	Preintro
	• Effect of reintroduction period and release statuses of individuals (wild-born versus reintroduced)	Preintro*reintro
<b>Movement rate (Ψ)</b>	• Age effect (1 <sup>st</sup> year; 2 <sup>nd</sup> -5 <sup>th</sup> years; ≥6 <sup>th</sup> years)	A156
	• Age effect (1 <sup>st</sup> year; 2 <sup>nd</sup> -5 <sup>th</sup> years; ≥6 <sup>th</sup> years) in interaction with the region of origin (birth or release place in Causses or Alps)	A156*Origin
	• Age effect (1 <sup>st</sup> year; 2 <sup>nd</sup> -5 <sup>th</sup> years; ≥6 <sup>th</sup> years) in interaction with the region of origin and dependent of the reintroduction period	A156*Origin*Preintro
	• Age effect (1 <sup>st</sup> -5 <sup>th</sup> years; ≥6 <sup>th</sup> years) in interaction with the region of origin and dependent of the reintroduction period	A56*Origin*Preintro
<b>One year post-release effect on movement (Ψ<sub>pre</sub>) or on survival (φ<sub>pre</sub>) - (See also post-release effect hypotheses in Table 1)</b>	• Differ between the region of origin and dependent of the reintroduction period	Origin*Preintro
	• Post-release effect on survival/movement of aviary-released immatures/adults in Causses (aviary,CAU) or in Alps (aviary,ALPS)	aviary,CAU or aviary,ALPS
	• Post-release effect on survival/movement of all reintroduced birds in Causses (reintro <sub>s</sub> ,CAU) or in Alps (reintro <sub>s</sub> ,ALPS)	reintro <sub>s</sub> ,CAU or reintro <sub>s</sub> ,ALPS
	• Post-release effect on survival/movement of aviary-released immatures/adults differ from post-release effect on survival/movement of aviary/hacking-released juveniles in Causses (reintro <sub>d</sub> ,CAU) or in Alps (reintro <sub>d</sub> ,ALPS)	reintro <sub>d</sub> ,CAU or reintro <sub>d</sub> ,ALPS
	Post-release effect on survival/movement of aviary-released immatures/adults different between Causses and Alps	aviary*origin

- Post-release effect on survival/movement of all reintroduced birds different between Causes and Alps reintro<sub>s</sub>\*origin
- Post-release effect on survival/movement of aviary-released immatures/adults differ from post-release effect on survival/movement of aviary/hacking-released juveniles and differ between Causes and Alps reintro<sub>d</sub>\*origin

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<b>Survival (<math>\varphi_1 / \varphi_{2-5} / \varphi_{6+}</math>)</b>	• Causes resident versus Alps resident versus Mover	RegStat1
(always with an age effect)	• Causes resident equivalent to Alps resident versus Mover	Regstat2

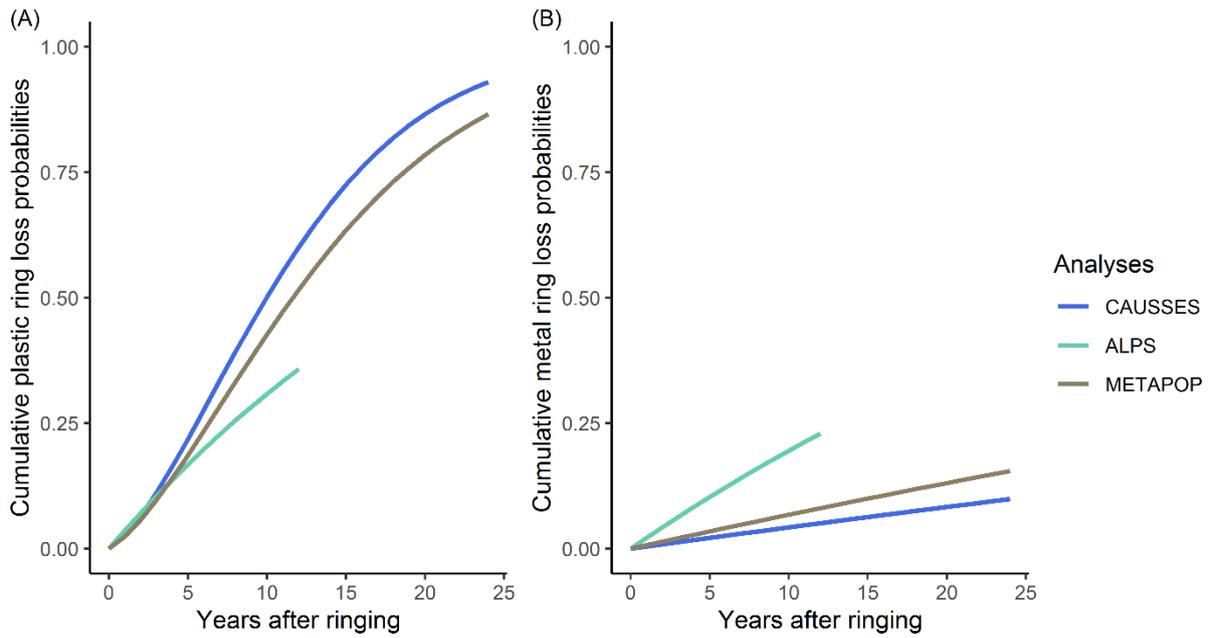
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826 Table 3: Summary of the best supported models for each step. All details about model selection and explanations are given in Appendix B  
 827 (population models) and Appendix C (metapopulation model).  
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	1A: Causes population : model 12	1B: Alps population : model 25	2: Metapopulation : model 60
Resighting probabilities (P)	ShortDist*t	LongDist*Pcamera	$P_{LongDist} : RegStat2*Bcam ;$ $P_{ShortDist} : CAU*t,ALPS$
Recovery probability (r)	Reintro <sub>1yar</sub>	Reintro <sub>1yar</sub>	Reintro <sub>1yar</sub>
Plastic ring loss ( $\alpha$ )	tlog	c	tlog
Metal ring loss ( $\beta$ )	c	c	c
Juveniles survival ( $\phi_1= 1^{st}$ year old)	c	c	c
Immatures and sub-adults survival ( $\phi_{2-5}= 2^{nd}$ to 5 <sup>th</sup> year old)	c	c	c
Adults survival ( $\phi_{6+}= \geq 6^{th}$ year old)	c	c	c
Post-release effect on survival ( $\phi_{pre}$ )	-	Reintro <sub>s</sub>	Reintro <sub>s,ALPS</sub>
Movement rate ( $\Psi$ )			A156*origin
Post-release effect on movement ( $\Psi_{pre}$ )			reintro <sub>s,CAU</sub>

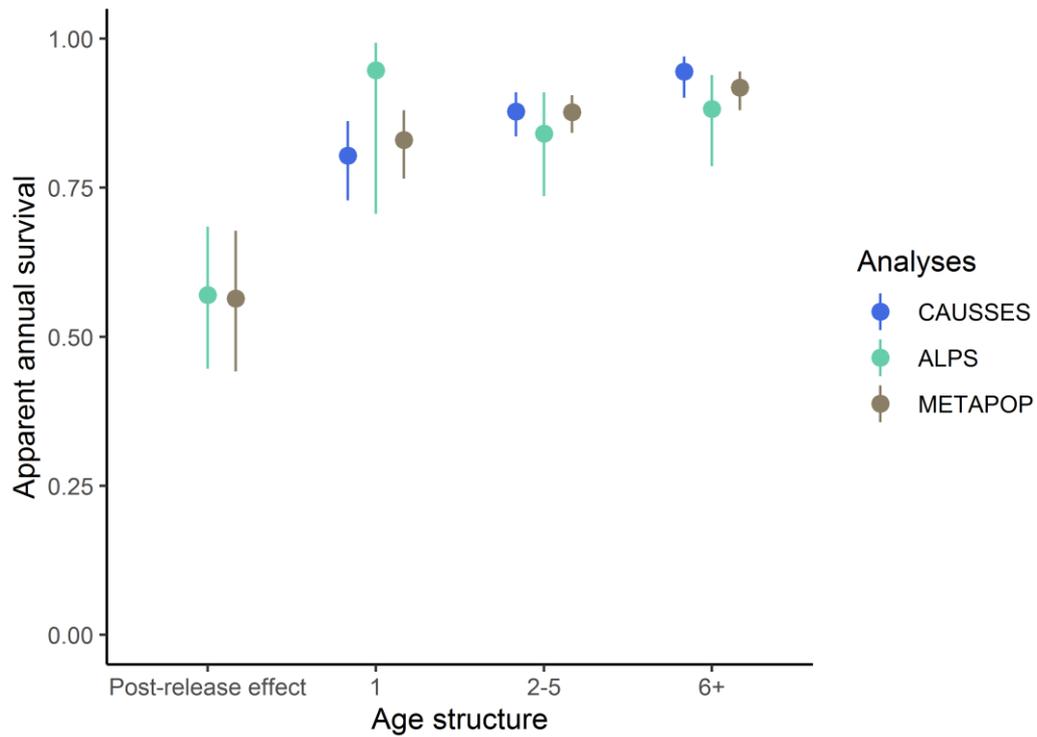
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Figure 2: Cumulative ring loss probabilities (a: Plastic ring loss and b: Metal ring loss) for the analyses at population scale (CAUSSES and ALPS) and at metapopulation scale (METAPOPOP).

(2-column fitting image)

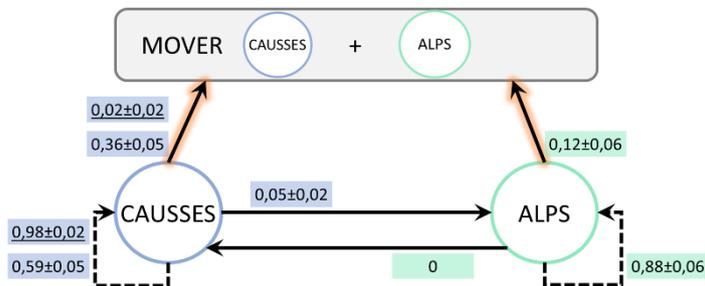


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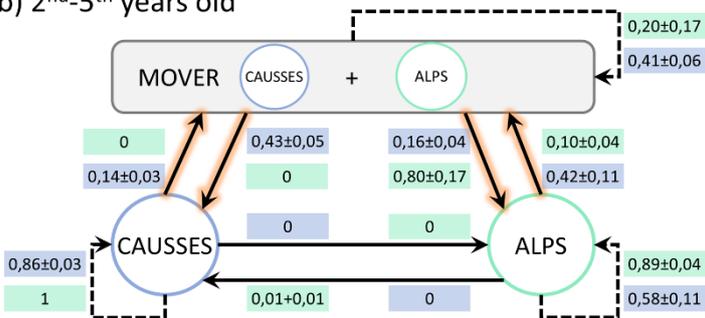
Figure 3: Apparent annual survival rates and 95% confidence intervals for both analyses at population scale (CAUSSES and ALPS) and the one at metapopulation scale (METAPOP), as a function of the three age classes (1, 2-5, 6+ years old) and post-release effect in the Alps.

(1.5-column fitting image)

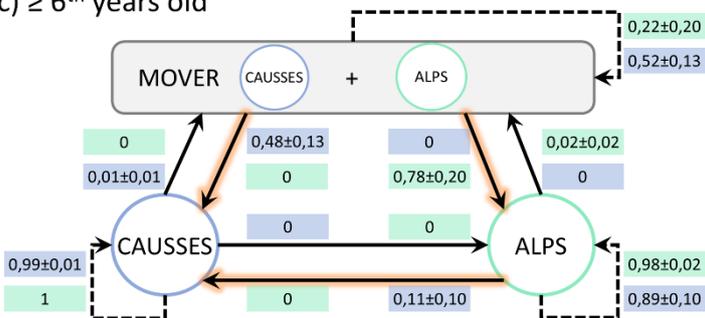
a) 1<sup>st</sup> year old + post-release effect



b) 2<sup>nd</sup>-5<sup>th</sup> years old



c) ≥ 6<sup>th</sup> years old



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 856 Figure 4: Movement/Transition rates (and standard error) between region statuses (Causses,  
 857 Alps, Mover) for the analysis at metapopulation scale, considering three age classes (1, 2-5,  
 858 6+ years old) and post-release effect in the Causses region. The full arrows represent the  
 859 annual probabilities of changing region status (Causses, Alps, Mover). When they are  
 860 orange, it indicates it is the most likely movements. The dashed arrows represent fidelity to  
 861 the region status. Estimates and standard error are: (1) in blue = born or released in the  
 862 Causses, (2) in lightgreen: born or released in the Alps, and (3) in blue and underlined =  
 863 post-release effect for individuals released in the Causses. MOVER represent when an  
 864 individual sailing between both region during an occasion (year).

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 866 (1.5-column fitting image)