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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 :**

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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 1st year, immature and sub-adults
150 are 2nd to 5th 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 20th 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 (1st 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 1st to September
222 30th), 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 1st 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

245 *2.4. Multi-event capture-recapture modeling*

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 (α , step 1), the probability of metal ring loss (β , step
279 2) and the survival probabilities (ϕ , 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 (α , step 1), the probability of metal ring loss (β , step 2), the
282 probability of moving (Ψ , step 3) and the survival probability (ϕ , 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 α , β , ϕ , P and r . For the metapopulation
292 model, the model structure allowed for simultaneous estimates of α , β , ϕ , Ψ , 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 (Δ AICc) was calculated as the difference in AICc between the model with the smallest AICc
301 and the other models. Models with Δ AICc ≤ 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 Δ AICc ≤ 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
319
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_s" 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 ± 0.014), whereas short-
338 distance marks varied between years (0 to 0.665 ± 0.181 ; arithmetic mean: 0.172 ± 0.205).
339 The recovery of dead individuals once reintroduced was high during the 1st year after release
340 (0.585 ± 0.161). Wild born individuals and later reintroduced individuals showed reduced
341 probability of being recovered as dead (0.267 ± 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_s"
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_s" 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_d 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 ± 0.099 ; after: 0.984 ± 0.011). Resighting rate by short-distance
367 marks was also high (0.651 ± 0.143). The dead recovery rate of reintroduced individuals was
368 high during the first year after release (0.317 ± 0.088). Wild-born individuals and later
369 reintroduced individuals showed reduced probability of dead birds recovery (0.211 ± 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 ± 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.

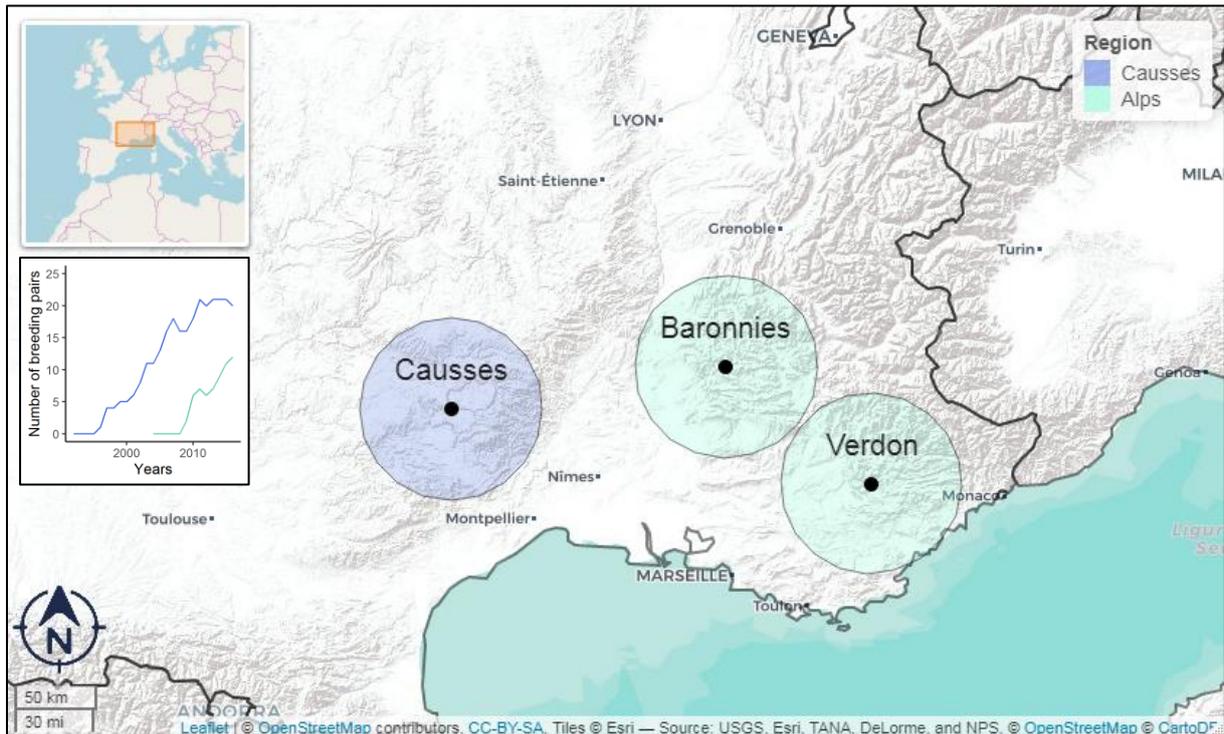
777 Appendix D: Example of Model Definition Languages instructions on E-SURGE software.

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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787 Figure 1: Locations of the three reintroduction programs of cinereous vultures in France.
788 Release sites (aviaries) are indicated by dots, surrounded by circles of 55 km radius. Inset:
789 Annual numbers of breeding pairs in the Causses (blue) and in the Alps (green).
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791 (2-column fitting image)

792 Table 1: Summary of hypotheses tested in the population models.
793

Parameters	Hypotheses	Abbreviations
Recovery rates (r)	• One year post-release effect	Reintro _{1yar}
	• 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
Resighting rate (P)	• 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
Plastic ring loss (α) and metal ring loss (β)	• Constant	c
	• Time effect	t
Survival (φ_1 / φ_{2-5} / φ_{6+}) (always with an age effect)	• Age effect only, no post-release effect	-
	• Post-release effect on survival of aviary-released immatures/adults only	aviary
One year post-release effect on survival (φ_{pre})	• Post-release effect on survival of all reintroduced birds	reintro _s
	• Post-release effect on survival of aviary-released immatures/adults differ from post-release effect on survival of aviary/hacking-released juveniles	reintro _d
	• 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 _s *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 _d *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
Recovery rates (r)	• Effect of region (Causses versus Alps) and one year post-release effect	Reintro _{1yar} *Reg
Resighting rate for long distance marks ($P_{LongDist}$)	• 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
Resighting rate for short distance marks ($P_{ShortDist}$)	• Time effect in Causses and constant in Alps	CAU*t,ALPS
Initial states	• 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
Movement rate (Ψ)	• Age effect (1 st year; 2 nd -5 th years; $\geq 6^{\text{th}}$ years)	A156
	• Age effect (1 st year; 2 nd -5 th years; $\geq 6^{\text{th}}$ years) in interaction with the region of origin (birth or release place in Causses or Alps)	A156*Origin
	• Age effect (1 st year; 2 nd -5 th years; $\geq 6^{\text{th}}$ years) in interaction with the region of origin and dependent of the reintroduction period	A156*Origin*Preintro
	• Age effect (1 st -5 th years; $\geq 6^{\text{th}}$ years) in interaction with the region of origin and dependent of the reintroduction period	A56*Origin*Preintro
One year post-release effect on movement (Ψ_{pre}) or on survival (ϕ_{pre}) - (See also post-release effect hypotheses in Table 1)	• 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 _s ,CAU) or in Alps (reintro _s ,ALPS)	reintro _s ,CAU or reintro _s ,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 _d ,CAU) or in Alps (reintro _d ,ALPS)	reintro _d ,CAU or reintro _d ,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_s*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_d*origin

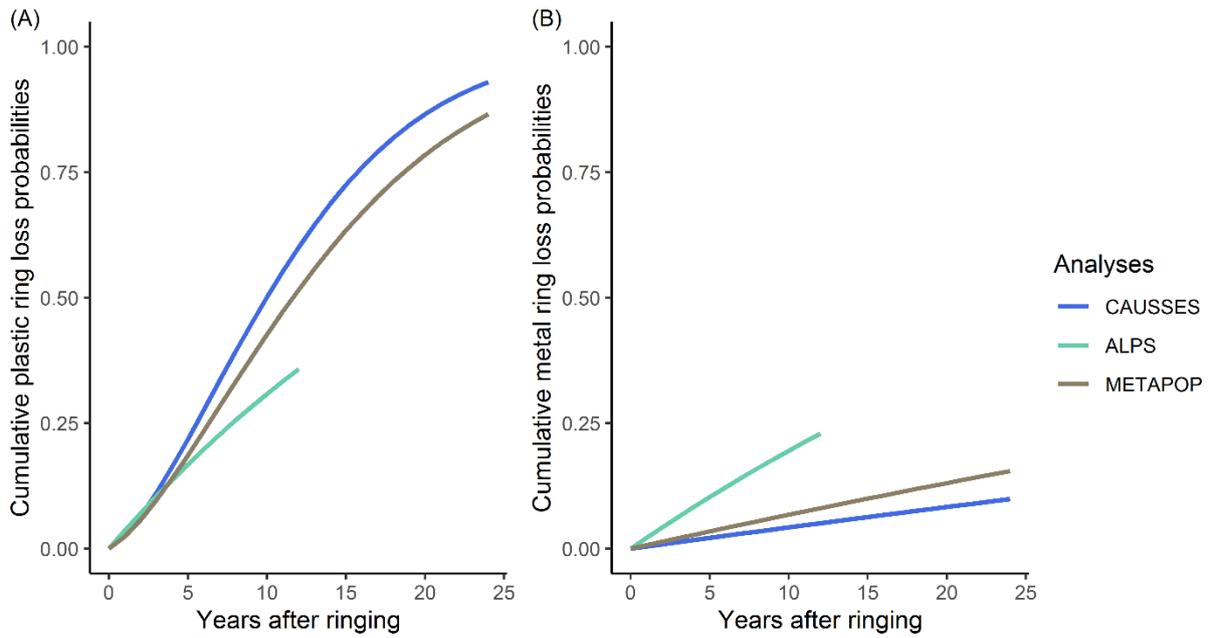
Survival ($\varphi_1 / \varphi_{2-5} / \varphi_{6+}$)	• Causes resident versus Alps resident versus Mover	RegStat1
(always with an age effect)	• Causes resident equivalent to Alps resident versus Mover	Regstat2

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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 _{1yar}	Reintro _{1yar}	Reintro _{1yar}
Plastic ring loss (α)	tlog	c	tlog
Metal ring loss (β)	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 5th year old)	c	c	c
Adults survival ($\phi_{6+}= \geq 6^{th}$ year old)	c	c	c
Post-release effect on survival (ϕ_{pre})	-	Reintro _s	Reintro _{s,ALPS}
Movement rate (Ψ)			A156*origin
Post-release effect on movement (Ψ_{pre})			reintro _{s,CAU}

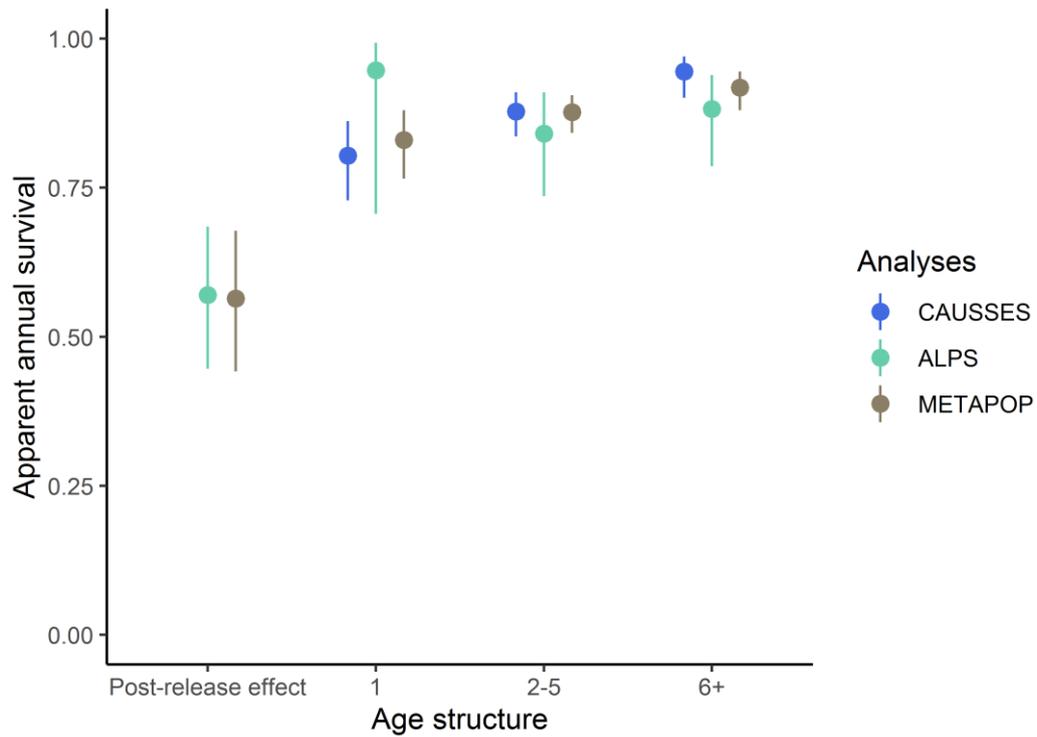
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Figure 2: Cumulative ring loss probabilities (a: Plastic ring loss and b: Metal ring loss) for the analyses at population scale (CAUSSES and ALPS) and at metapopulation scale (METAPOPOP).

(2-column fitting image)

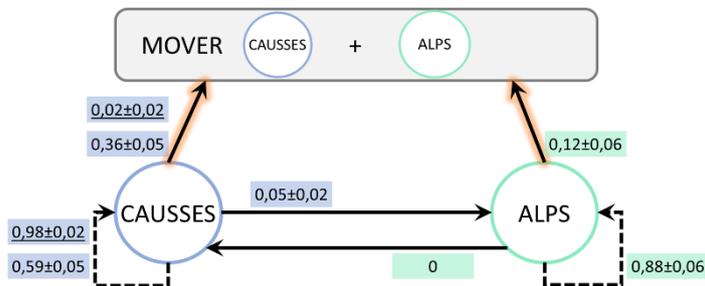


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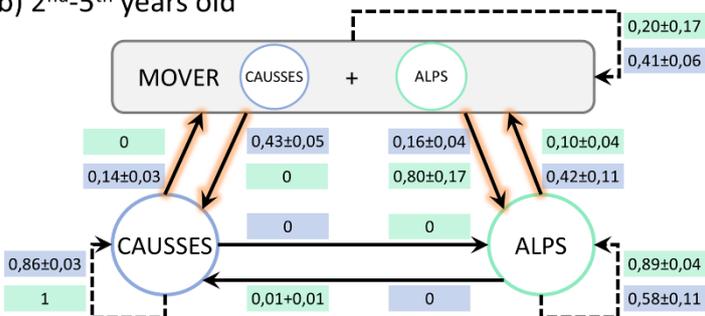
Figure 3: Apparent annual survival rates and 95% confidence intervals for both analyses at population scale (CAUSSES and ALPS) and the one at metapopulation scale (METAPOP), as a function of the three age classes (1, 2-5, 6+ years old) and post-release effect in the Alps.

(1.5-column fitting image)

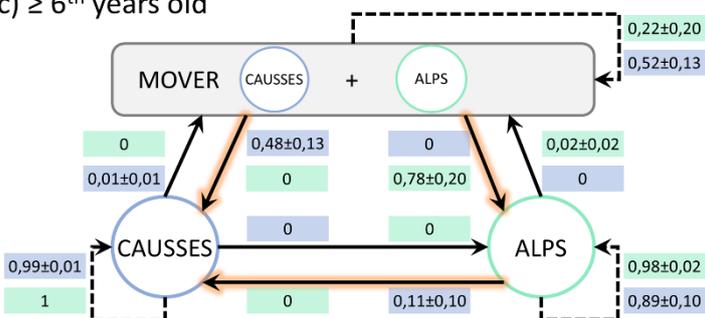
a) 1st year old + post-release effect



b) 2nd-5th years old



c) ≥ 6th years old



855
 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)