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1 **Decrease in social cohesion in a long-lived species under a perturbation**

2 **regime**

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14

15

16 **Abstract**

- 17 1. Environmental perturbations may have a strong impact on the dynamics of a  
18 population and their understanding may help to mitigate the effects of global  
19 change. In social animals, social interactions can influence behavioural  
20 processes and can play an important role on populations' resilience. However  
21 little is known about the effects of perturbations on the strength of social  
22 cohesion that keep group-living animals connected.
- 23 2. To explore the strength of social cohesion and its dynamics under perturbations,  
24 we studied an ecological system involving a colonial, long-lived species living  
25 in a site experiencing a shift to a perturbed regime. This regime, caused by the  
26 invasion of predators, led an Audouin's gull *Larus audouinii* colony to hold  
27 from 70% to only 3% of the total world population in only one decade (32%  
28 mean annual decline). Birds breed aggregated in discrete and annually changing  
29 patches within colonies, which allowed us to disentangle whether annual  
30 aggregations were random or resulted from social ties among individuals. Our  
31 goals were 1) to uncover if there were long-term social ties between individuals  
32 and 2) to examine whether the perturbation regime affected social cohesion.
- 33 3. We explored social cohesion by means of contingency tables and by modeling  
34 interdependencies among observations within the Social Network Analysis  
35 framework, using additive and multiplicative effects (AME) and accounting for  
36 missing data. We analysed 25 years of monitoring with an individual capture-  
37 recapture database of more than 3,500 individuals.
- 38 4. We showed that there are social ties between individuals over the years.  
39 Furthermore, social cohesion strongly decreased after entering the perturbation  
40 regime. We propose that sociality and individual behavioural heterogeneity play

41 a major role driving dispersal between sites and thus population dynamics in  
42 social animals.

43 5. Perturbations may lead not only to changes in individuals' behaviour and fitness  
44 but also to a change in populations' social cohesion. The demographic  
45 consequences of the breaking down of social ties are still not well understood,  
46 but they can be critical for population dynamics of social species. Further studies  
47 considering individual heterogeneity, sociality and different types of  
48 perturbations should be carried out to improve our understanding on the  
49 resilience of social species.

50

51 Keywords: Audouin's gull, colonial species, decision-making, non-linear response,  
52 perturbations, resilience, social cohesion, social network analyses.

## 53 **Introduction**

54 Ecosystems are subject to perturbations, both natural and human induced, affecting  
55 individuals, populations and communities. When they are strong or are maintained  
56 through time, these perturbations may cause a shift between stable states at the level of  
57 both individual and population and even lead to population collapses and extinctions <sup>1,2</sup>.  
58 Understanding how individuals and populations will respond to these perturbations is  
59 critical both from a ‘pure’ ecological standpoint and also from an applied point of view  
60 to mitigate the effects of global change <sup>3-5</sup>. Population dynamics may be directly  
61 affected by these perturbations through a decrease in demographic parameters such as  
62 survival or fecundity, or by a change, immediate or delayed, on individual behaviour,  
63 such as an increase in dispersal <sup>6</sup>. We define population resilience as the maximal pulse  
64 perturbation a population can tolerate or absorb without going extinct <sup>1,7</sup>. In social  
65 animals, social behavioural processes, such as information sharing and decision-  
66 making, add another dimension to understanding the resilience of populations facing  
67 perturbations. For instance, the amount of social information can be enhanced not only  
68 by positive density-dependence, but also by social cohesion <sup>8-11</sup>. Social cohesion favor  
69 the exchange of private information and consequently reduce uncertainty in resource  
70 acquisition (e.g. shelter against predators, food, mates) or in decision-making in the face  
71 of disturbances, such as dispersal to non-perturbed or less perturbed sites <sup>6,12-14</sup>. Thus,  
72 the structure of a group may affect social interactions, information transfer, and  
73 collective decisions <sup>15</sup>. Some recent studies also show that spatial cohesion may be risk  
74 sensitive, and that responses may differ depending on the risk and the social group <sup>16</sup>.  
75 However, little is known about the effects of environmental perturbations on the  
76 cohesion of social groups in empirical studies of social animals <sup>17</sup>.

77 The analysis of social relationships in animal populations may include a range of social  
78 dynamics, from simple and ephemeral contacts, to permanent and strong bonds between  
79 individuals <sup>11,18-20</sup>. Coloniality is a life-history strategy where individuals show a social  
80 link among conspecifics by breeding in large and dense groups <sup>21,22</sup>. However, many  
81 colonial species are philopatric, thus this link may not necessarily reflect individual  
82 social ties but a shared tendency to breed in the same birthplace. This tendency may  
83 result from the need to share information about resources, especially when they are  
84 patchy and more unpredictable, or it may result from the advantages of social defence  
85 against predators <sup>23,24</sup>. A challenge lies in disentangling whether annual association  
86 between individuals is only due to philopatry, or also due to the existence of a social ties  
87 within groups of individuals over time <sup>25</sup>. Social ties between neighbouring pairs in  
88 breeding colonies are rarely considered in behavioural and ecological studies <sup>26</sup> and, if  
89 true, such associations may suggest the evolution of social cohesion for exploiting the  
90 evolutionary advantages of social living (including social information sharing) for  
91 individual fitness prospects.

92 Social network theory, which originated in sociology to study human relationships and  
93 social organization <sup>9,27,28</sup> now provides both a conceptual framework and the analytical  
94 tools to explore social cohesion and social processes in animal populations <sup>29-33</sup>.

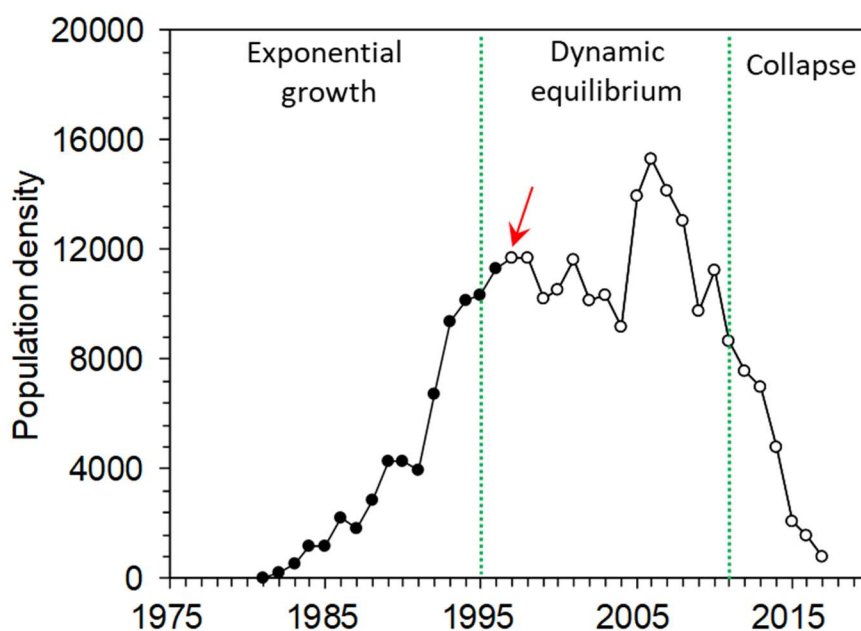
95 Network theory is now being simultaneously developed in a number of fields, including  
96 statistical physics, sociology, molecular biology, and computer science. As a result, the  
97 field is changing at a rapid pace. While not all developments can or should be applied  
98 toward the study of animal societies <sup>34</sup>, this rush of novel ideas from outside disciplines  
99 is enriching behavioural ecology <sup>35</sup>.

100 To assess the existence of social cohesion and its dynamics under perturbations, we  
101 studied an ecological system involving a colonial, social vertebrate (the Audouin's gull

102 *Larus audouinii*) living in a site experiencing a shift to a perturbed regime. Interestingly  
103 from a social point of view, the species breeds aggregated in spatially-discrete patches  
104 within large colonies. Each breeding season, some patches go extinct and some are  
105 colonized <sup>36</sup>, forcing individuals to breed in patches different from the ones they were  
106 born in or they bred in the previous year. These colonization-extinction processes may  
107 allow us to disentangle whether social aggregation among individuals is an annual  
108 random association, or it rather results from social cohesion among individuals over the  
109 years.

110 An extensive long-term individual monitoring program has been carried out since 1988  
111 at the Ebro Delta, including the main breeding site for the species, the Punta de la  
112 Banya <sup>37</sup>. At the study site, population dynamics has undergone different phases: an  
113 initial growing phase after site colonization, a stable phase of dynamic equilibrium, and  
114 a final transition phase to population collapse <sup>17,38</sup> (Figure 1). This collapse was due to  
115 the arrival of terrestrial predators, and led this colony to hold from 70% to only 3% of  
116 the total world population in only a decade (32% mean annual decline) <sup>36,37</sup> (Figure 1).  
117 Most predators were foxes, but also badgers and other mesocarnivores. Predators  
118 invaded the site likely due to their increasing densities in recent decades <sup>39</sup> and the  
119 attractiveness of the site in terms of food availability and lack of competition. The  
120 perturbation regime caused changes in the spatial distribution of patches at the site,  
121 changes in age structure, decrease in fecundity and a progressively increase of dispersal  
122 to other sites <sup>6,36</sup>. The response of this population to predators has been not immediate  
123 probably due to strong philopatry, high site-suitability inertia and social behavioural  
124 processes, such as conspecific attraction <sup>17</sup>. This raise in dispersal was caused by social  
125 processes, as social copying <sup>17</sup>, however it remains to assess how social cohesion among  
126 individuals, if occurred, was affected by dispersal processes. One possibility is that

127 dispersal would broke social cohesion by individual heterogeneity in the willingness to  
 128 disperse <sup>40</sup>. In contrast, social cohesion can be maintained over time when dispersal  
 129 occurs collectively at the scale of social groups to the same sites <sup>25,41</sup>.  
 130 Taking advantage of the long-term monitoring of this long-lived species, the knowledge  
 131 of its population dynamics, and the use of tools recently developed in the Social  
 132 Network Analysis (SNA) framework, we specifically addressed the following  
 133 questions: 1) is there any long-term social ties between individuals breeding in the same  
 134 patch? and 2) have perturbations, in this case a perturbation regime, affected social  
 135 cohesion? We finally discuss the role and consequences of social cohesion in population  
 136 dynamics and resilience in social species.  
 137



138  
 139 **Figure 1.** Number of breeding pairs in the Punta de la Banya colony from colonization  
 140 in 1981 to 2017. The observed phases in the population dynamics (growth, dynamic  
 141 equilibrium and collapse) are separated by green lines, which are identified by  
 142 chronological clustering analysis <sup>38</sup>. Red arrow indicates the arrival of predators to the



143 colony (open dots for the time series). We compared the period 2002-2010 with the  
144 period 2011-2017 corresponding to the dynamic equilibrium and collapse phases  
145 respectively.

146

## 147 **Results**

148 We analysed a total of 1,610,922 dyadic interactions during the first period (2002-2011)  
149 and 368,142 during the second period (2012-2017).

150 When assessing the social ties with the contingency table approach during the period of  
151 stability, the assumption that breeding aggregations in Audouin's gull were at random  
152 was rejected, and those individuals that bred together during the sub-period 2002-2006  
153 had a higher probability of breeding together during the sub-period 2007-2011 ( $\chi^2_1 =$   
154 64.685,  $P < 0.0001$ ). When randomly reducing sample size of the data set, results were  
155 still statistically significant in more than 95% of the cases (1000 randomizations).

156 Accordingly, when assessing the social ties with dependent regression terms in the  
157 AME function, we showed that the probability of breeding together during the second  
158 sub-period (2007-2011) depended on whether they have bred previously together in the  
159 first sub-period (2002-2006), with a statistically significant coefficient of regression  
160 parameter (Table 1; Figure 2). When analysing this data set with permuted data, we  
161 concluded that there was indeed a non-random association of individuals within the  
162 patches, with our statistic being among the 5% extreme values.

163 When we analysed the social ties during the transition to collapse phase, we observed  
164 that the probability of breeding together during the period 2012-2017 did not depend on  
165 whether they have bred together the five previous years ( $\chi^2 = 1.957$ , p-value = 0.162)  
166 and we could not reject the hypothesis of a random association between individuals. In  
167 addition, the SNA approach showed that breeding aggregations in Audouin's gull

168 during the transition phase did not depend on whether they have bred together the five  
 169 previous years (Table 1; Figure 2).

170

171

	Stable period				Transition to collapse period			
	pmean	psd	z-stat	p-value	pmean	psd	z-stat	p-value
<b>intercept</b>	-1.467	0.087	16.808	0.000	-0.231	0.018	-12.629	0.000
<b>.dyad</b>	6.420	0.328	19.576	0.000	-0.004	0.022	-0.188	0.851

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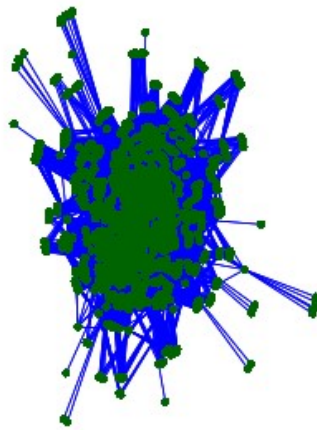
173 **Table 1.** Results of the AME regression function to test if there were social ties between  
 174 individuals while breeding during the stable period and during the transition phase to  
 175 collapse period. The alternative hypothesis is that individuals aggregate annually at  
 176 random for breeding. “.dyad”: coefficient of the dependent regression term considering  
 177 the previous dyadic relationship between individuals; “pmean”: posterior mean  
 178 estimate; “psd”: posterior standard deviation; “z-stat “: nominal z-score.

179

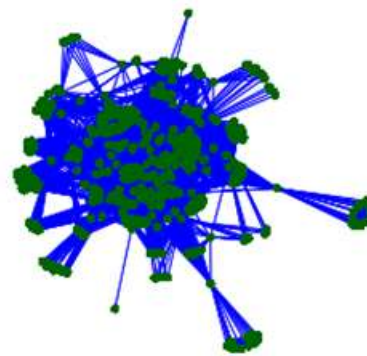
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181

a)



b)



182

b) **Figure 2.** Graphical representation of social networks by the association

183

between individuals of Audouin's gulls in breeding patches comparing a) the

184

stability phase (2002-2011) and b) the transition phase to colony collapse (2012-

185

2017) (see Figure 1). Each node represents an individual and each edge links

186

those individuals that have bred together in the same patch. We used the half-

187

weight association index (HWI) to estimate the strength of relationship between

188

pairs of individuals an index more suitable when not all individuals within each

189

group have been identified <sup>42,43</sup>.

190

191

## 192 **Discussion**

193

By studying a particular ecological system of a colonial long-lived species that

194

experiences a perturbation regime, we showed that social ties among individuals persist

195

over unperturbed years and that perturbations may decrease social cohesion in animal

196

populations.

197 The characteristic breeding behaviour of the study species that aggregates in patches  
198 that change annually, allowed us to show that individuals do not annually breed  
199 aggregated at random but rather there is some group stability, with individuals  
200 establishing social ties that persist over time. Our study system resembles what it was  
201 recorded for Slender-billed gulls (*Chroicocephalus genei*), a colonial breeder with weak  
202 inter-annual breeding-site fidelity: some individuals bred together across breeding  
203 seasons and some social groups showed tenacity despite the colony often moving every  
204 year<sup>41</sup>. Group stability can emerge as a product of network self-organization, but may  
205 provide the necessary conditions for the evolution of other social processes<sup>44,45</sup>. Our  
206 results would support the idea that social aggregation during breeding would provide  
207 other advantages than the mere defence against predators<sup>46,47</sup>, such as social  
208 information sharing (e.g.<sup>48,49</sup>). Social information sharing is crucial for decision-making  
209 in risky behaviours, such as dispersal, and previous studies showed that the perturbed  
210 regime in our study site caused dispersal to other sites, including colonization of new  
211 habitats<sup>36,50</sup>. In our case study, sociality may have played a major role driving dispersal  
212 and thus population dynamics, both during the exponential growth after colonization  
213 and the collapse after the perturbation regime. This idea is also reinforced with a  
214 mechanistic dynamical model that shows that population dynamics of Audouin's gulls  
215 at the study site can only be explained by dispersal runaway caused by social copying  
216<sup>17</sup>.

217 The importance of social information compared to private information increases under  
218 perturbations, even when the quality of social information does not increase compared  
219 to a non-perturbed regime<sup>51,52</sup>. For instance, Maldonado et al.<sup>53</sup> show that experimental  
220 disturbances applied to a social bird may impact its foraging efficiency by social  
221 instability caused by the split of social groups. In colonial birds, breeding failure, which

222 is a proxy of environmental stress, may trigger splitting of the social groups (e.g. <sup>41</sup>). At  
223 demographic level, the alteration of social network structure may affect the behaviour of  
224 populations. For instance, under stress conditions, sociality may operate through  
225 feedback loops such as social copying for dispersal, causing non-linear population  
226 dynamics and playing a critical role on the resilience of populations (e.g. <sup>17</sup>). We  
227 showed here that after a perturbation, not only the number of individuals in the  
228 population may decrease (by increased mortality or dispersal) but also its social  
229 cohesion, likely reducing but also altering the information transfer within the social  
230 network composed by those individuals that remain in the site where perturbation  
231 occurs. Among other demographic processes, dispersal may alter social connections of  
232 both individuals remaining and those dispersing, with consequences for social network  
233 structure <sup>40</sup>. The perturbation regime suffered by the study population has likely  
234 triggered a social transition <sup>54</sup> in collective behaviour from philopatric to dispersal and  
235 with the fast diffusion of innovations such as the colonization of harbours by large  
236 number of individuals, a habitat safe from predators never occupied before <sup>50</sup>. Previous  
237 studies have shown that responses of populations to perturbations may also depend on  
238 individual personalities in the population <sup>55-57</sup>. For example, dispersers are different  
239 from non-dispersing individuals for a suite of phenotypic traits, including their  
240 behavioural profile <sup>58-60</sup>. Heterogeneities in personalities for dispersal decision-making  
241 may have also played a role in our studied population, with most individuals dispersing  
242 to other sites after a period of disturbance, while some individuals remaining  
243 philopatric. This change may have also further consequences for social network  
244 stability, as performance in social groups may improve with heterogeneity in individual  
245 personalities <sup>60,61</sup>.

246 Our study opens new research avenues about resilience of social populations under  
247 perturbations; if perturbations affect social cohesion and heterogeneity in personalities  
248 in the population, we may wonder whether this population would be equally resilient to  
249 future perturbations. Additionally, in our study population, sociality seemed to operate  
250 not right after the first perturbation episode but after cumulative maintained perturbation  
251 <sup>50</sup>; would the type of perturbation, either pulse or in regime <sup>62</sup> influence the response of  
252 social groups? We have shown here that a regime perturbation may decrease social  
253 cohesion in animal populations, but further studies should be carried out to improve our  
254 understanding on the demographic consequences of the breaking down of social ties  
255 under perturbations for population dynamics and resilience in social species.

256

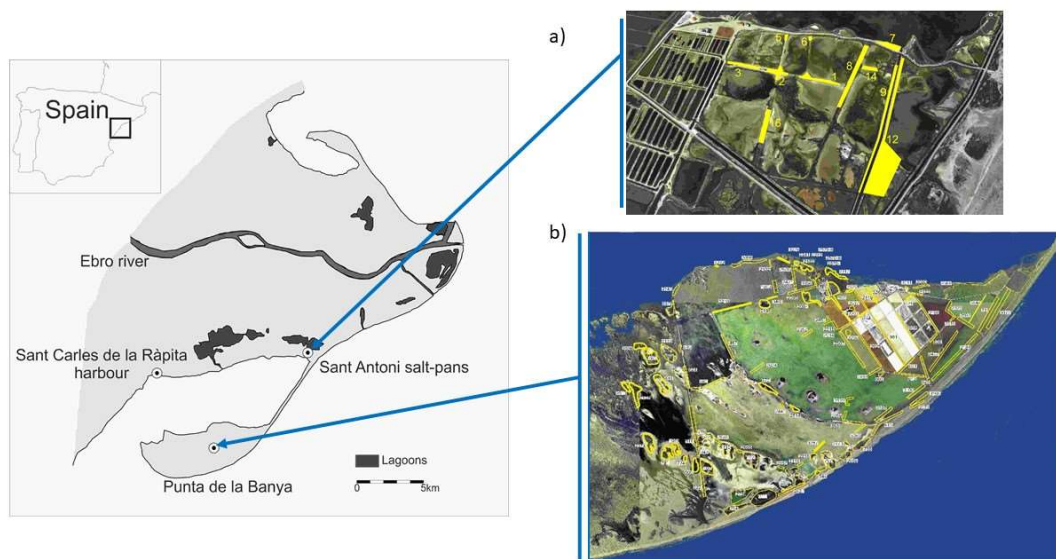
## 257 **Material and Methods**

### 258 Study species and study area

259 The Audouin's gull is a long-lived seabird with more than 80% of the global population  
260 breeding in the western Mediterranean

261 (<http://www.iucnredlist.org/details/22694313/0>;<sup>37</sup>. The species was critically  
262 endangered until the early 80's, when it colonized a new site, the Punta de la Banya in  
263 the Ebro Delta (Figure 2). Here, the large availability of both suitable breeding habitat  
264 and food resulted in a rapid and exponential growth, ending with the site holding more  
265 than 70% of the total world population in 2006. The global population dynamics was  
266 mainly driven by this colony and after the exponential growth, the species was  
267 downgraded to a conservation category of "least concern" <sup>63</sup>. However, the Punta de la  
268 Banya colony is now collapsing and even if the species is colonizing new sites, the  
269 global population is decreasing at a 5% annual rate <sup>37</sup>. In 1997, first carnivores (mainly

270 foxes, but also badgers, beech martens and least weasels) arrived at Punta de la Banya,  
271 and since then the site has been perturbed by the presence of carnivores.  
272 Annual censuses of breeding pairs at every patch within colonies at the Ebro Delta area  
273 have been carried out since colonization in 1981 to 2017 (Figure 1, 3 and Table S1). In  
274 the Ebro Delta there are three colonies: Punta de la Banya, colonized in 1981 and  
275 occupied throughout the study period, Sant Carles de la Ràpita harbour, occupied since  
276 2011 to 2015, and Sant Antoni, occupied from 2013 up to now (Figure 3, Figure S1).  
277 Within colonies, individuals are distributed in patches<sup>64</sup>. As patch location may change  
278 from one year to another, we annually geolocalized, mapped and defined the breeding  
279 patches (Figure 3 and S2).



280  
281 **Figure 3.** Map of the study area comprising the 3 main colonies and the distribution of  
282 patches within colonies during the study period at a) Sant Antoni and b) Punta de la  
283 Banya. Sant Carles de la Ràpita colony is considered to have only one patch.

284  
285 The species is monogamous, there is assortative mating by age, and from an  
286 evolutionary point of view is a bet-hedger, laying commonly 3 eggs, although few

287 chicks survive, except in years with high food availability, when the strength of density-  
288 dependence is low <sup>65</sup>.

### 289 Individual data

290 During 1988-2017 a total of 30,290 individuals were captured and ringed as chicks at  
291 the Punta de la Banya <sup>66,67</sup>. From 2002 to 2017, resightings were made using spotting  
292 scopes from a distance all over the western Mediterranean with a total of 63,106  
293 resights in the study area and 5,593 different individuals resighted. Each year we  
294 recorded the breeding patch for each individual. To make sure that individuals were  
295 breeding and that they did so in a particular patch, we only selected those individuals  
296 seen during the breeding season in a particular patch showing unequivocal breeding  
297 behaviour. Specifically, individuals making alarm calls, incubating eggs or with chicks.  
298 After this selective filter, our final database included 3,548 individuals.

### 299 SNA framework

300 Our social network, defined as the observed pattern of breeding association, was  
301 constructed taking individuals (N=3548) as the nodes of the network and each edge  
302 dyad (i.e. pair of individuals) representing the fact that individuals breed in the same  
303 patch. We ended with a global sociomatrix, i.e. the matrix representation of the dyadic  
304 relationships among individuals, of 3,548\* 3,548. Edges showed if two individuals bred  
305 in the same patch at least once in a certain period (see below). The network was not  
306 directional. Based on previous results on population dynamics, and on the population  
307 size of this species and colony <sup>37,50</sup>, we divided our dataset in two main periods: a period  
308 defined as “stable phase” from 2002 to 2011, and a period of “transition phase to  
309 collapse”, from 2012 to 2017 (Figure 1).  
310 We used the recently developed AME function from the AMEN package <sup>68,69</sup>, that can  
311 be applied to binary, ordinal, and continuous network data. This new approach is a



312 random-effects regression model; uses an iterative Markov chain Monte Carlo (MCMC)  
313 algorithm that provides Bayesian inference of the parameters in the social relations  
314 regression model (SRM;<sup>70</sup>) using additive and multiplicative effects and combining the  
315 linear regression model with the covariance structure of the SRM<sup>69</sup>. The AME method,  
316 not currently used in research on animal social networks is also able to cope with  
317 missing and censored data, our data set complying with the assumption that individuals  
318 are missing at random. Coping with missing data is highly relevant when analysing  
319 sociality on wild populations, as detection rate for individuals is almost always  
320 imperfect, and properly controlling for missed observations is a very important step in  
321 social network analysis<sup>71,72</sup>. To create and visualize our networks we used the packages  
322 Amen<sup>68</sup>, Asnipe<sup>73</sup>, gdata<sup>74</sup> and igraph in R<sup>75</sup>.

### 323 Are there social ties that persist over time?

324 We investigated if individuals create social ties that persist over time longer than one  
325 breeding occasion by means of two approaches: i) contingency tables and ii) the  
326 inclusion of time dependent regression terms in the AME modelling framework<sup>68</sup> (see  
327 previous section). We used both methods because this is the first application of the  
328 AME approach in an ecological context. We analysed data of the period of stability,  
329 from 2002 to 2011, dividing this period into two sub-periods of five years (2002-2006  
330 and 2007-2011). In the contingency table approach, we tested if the probability of  
331 breeding together at least once during the second sub-period was independent of having  
332 bred together at least once in the first period. We built a 3x3 table of frequencies,  
333 showing the frequencies of two individuals breeding or not together at least once during  
334 the second sub-period depending on whether they bred together or not at least once  
335 during the first sub-period, and pulling apart those dyads with missing data. We then  
336 tested for deviation of random frequencies by Chi Square test.

337 With the SNA approach, we analysed the social ties between individuals using the AME  
338 function provided in the Amen package in R and including data from the first period  
339 (five previous years) as predictors of association during the second sub-period. We  
340 considered that this time window was not too large to include important death events,  
341 but large enough to account for the imperfect detection of individuals. To achieve  
342 convergence, we increased the number of iterations to 100,000 from the default value of  
343 10,000 and lengthened the burn-in period to 500.

#### 344 Had perturbations affected social cohesion in this species?

345 To assess if perturbations affected social structure in this species, we analysed as  
346 previously, with both the contingency table approach and the SNA approach, the social  
347 ties during the period of “transition phase to collapse” (2012-2017). To do so, we tested  
348 if the probability of breeding together in this phase (2012-2017) was independent of  
349 having bred together during five previous years (2007-2011). We then compared these  
350 results from those previously observed during the “stability phase”.

351 A potential concern was the reduced power during the collapse period because the  
352 number of individuals decreased from the stability period. In order to have a similar  
353 power in both analyses, we performed the contingency table analysis during the stability  
354 period by drawing at random a number of observed associations equal to the number of  
355 observed associations during the collapse. We did this repeatedly (1000 times) and  
356 calculated which percentage of times the resulting chi-square was significant at the 5%  
357 level.

358 Regarding the SNA approach, it is advised <sup>76</sup> to do permutations on the raw data prior to  
359 the analysis and compare the result of some relevant statistic obtained with the original  
360 data to the distribution of the same statistic over the permutations. We chose the  
361 regression coefficient of the association of a dyad on the previous association of the

362 same dyad as our statistic of social cohesion. This statistic is provided by the function  
363 ame of the package amen<sup>68</sup>. We calculated this statistic on the original data. Then,  
364 within each year, we rearranged randomly the individuals among the patches, keeping  
365 the same number of individuals within each patch. We did this 200 times and calculated  
366 each time the regression coefficient. Then, we situated the value of the regression  
367 coefficient from the original data among the distribution of regression coefficients from  
368 the permutated data and examined how extreme it was. If it was among the 5% extreme  
369 values, we concluded that there was indeed a non-random association of individuals  
370 within the patches.

371

372

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### 385 **Authors' contributions**

386 MG conceived the idea; MG, OG, RP and RC designed methodology; MG, DO and AB  
387 collected the data; MG analysed the data; MG led the writing of the manuscript. All  
388 authors critically contributed to the drafts and gave final approval for publication.

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#### 391 **Data accessibility**

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393 Data is available via CSIC repository.

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