Decrease in social cohesion in a colonial seabird under a perturbation regime

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Decrease in social cohesion in a long-lived species under a perturbation regime

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Abstract

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

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

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

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

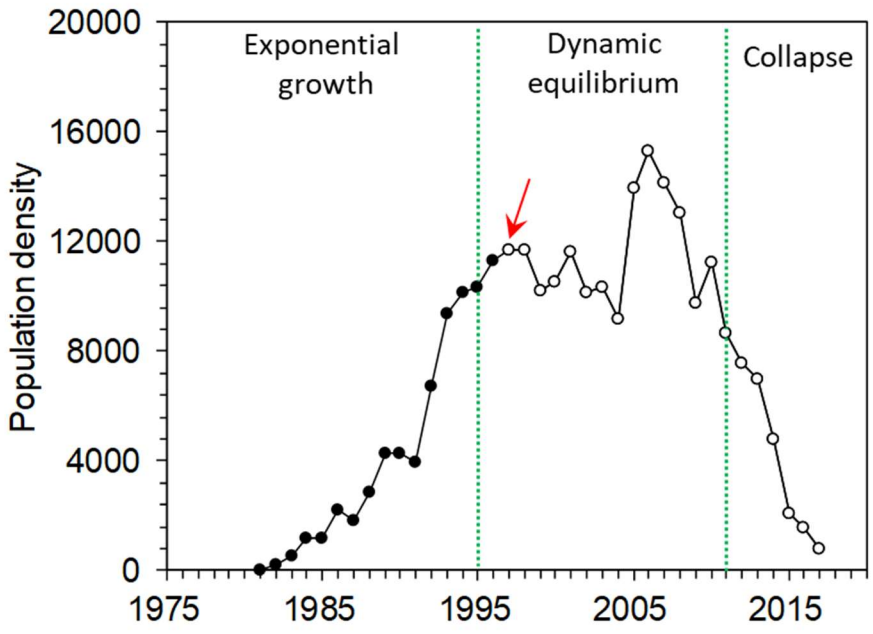
Introduction

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

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 [11,18–20]. Coloniality is a life-history strategy where individuals show a social
80 link among conspecifics by breeding in large and dense groups [21,22]. 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 [23,24]. 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 [25]. Social ties between neighbouring pairs in
88 breeding colonies are rarely considered in behavioural and ecological studies [26] 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 [9,27,28] now provides both a conceptual framework and the analytical
94 tools to explore social cohesion and social processes in animal populations [29–33].
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 [34], this rush of novel ideas from outside disciplines
99 is enriching behavioural ecology [35].
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 [36], 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 [37]. 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 [17,38] (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) [36,37] (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 [39] 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 [6,36]. 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 [17]. This raise in dispersal was caused by social
125 processes, as social copying [17], 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 [40]. In contrast, social cohesion can be maintained over time when dispersal
129 occurs collectively at the scale of social groups to the same sites [25,41].
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 [38]. 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**

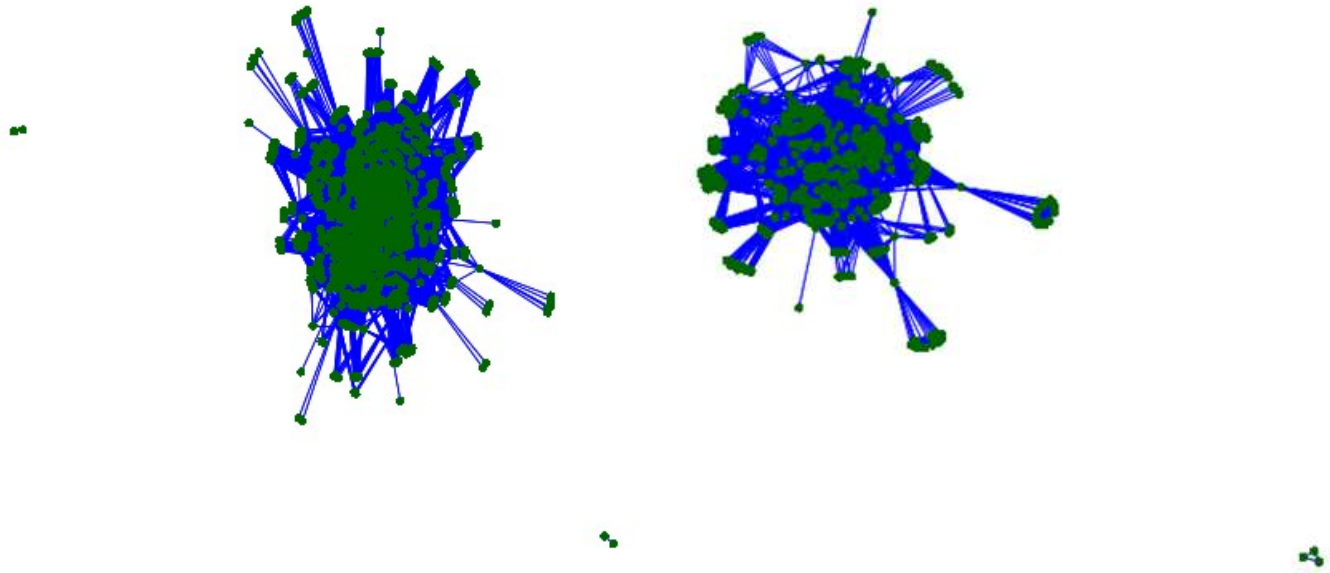
148 We analysed a total of 1,610,922 dyadic interactions during the first period (2002-2011)
149 and 368,142 during the second period (2012-2017).
150 When assessing the social ties with the contingency table approach during the period of
151 stability, the assumption that breeding aggregations in Audouin's 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 (χ_1^2=
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 permutated 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 (χ^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

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

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

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

a) b)



b) **Figure 2.** Graphical representation of social networks by the association between individuals of Audouin's gulls in breeding patches comparing a) the stability phase (2002-2011) and b) the transition phase to colony collapse (2012-2017) (see Figure 1). Each node represents an individual and each edge links those individuals that have bred together in the same patch. We used the half-weight association index (HWI) to estimate the strength of relationship between pairs of individuals an index more suitable when not all individuals within each group have been identified [42,43].

Discussion

By studying a particular ecological system of a colonial long-lived species that experiences a perturbation regime, we showed that social ties among individuals persist over unperturbed years and that perturbations may decrease social cohesion in animal 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 [41]. 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 [44,45]. Our
206 results would support the idea that social aggregation during breeding would provide
207 other advantages than the mere defence against predators [46,47], such as social
208 information sharing (e.g.[48,49]). 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 [36,50]. 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 [17].
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 [51,52]. For instance, Maldonado et al. [53] 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. [41]). 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. [17]). 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 [40]. The perturbation regime suffered by the study population has likely
234 triggered a social transition [54] 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 [50]. Previous
237 studies have shown that responses of populations to perturbations may also depend on
238 individual personalities in the population [55–57]. For example, dispersers are different
239 from non-dispersing individuals for a suite of phenotypic traits, including their
240 behavioural profile [58–60]. 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 [60,61].

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

Material and Methods

Study species and study area

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

foxes, but also badgers, beech martens and least weasels) arrived at Punta de la Banya, and since then the site has been perturbed by the presence of carnivores.

Annual censuses of breeding pairs at every patch within colonies at the Ebro Delta area have been carried out since colonization in 1981 to 2017 (Figure 1, 3 and Table S1). In the Ebro Delta there are three colonies: Punta de la Banya, colonized in 1981 and occupied throughout the study period, Sant Carles de la Ràpita harbour, occupied since 2011 to 2015, and Sant Antoni, occupied from 2013 up to now (Figure 3, Figure S1). Within colonies, individuals are distributed in patches [64]. As patch location may change from one year to another, we annually geolocalized, mapped and defined the breeding patches (Figure 3 and S2).

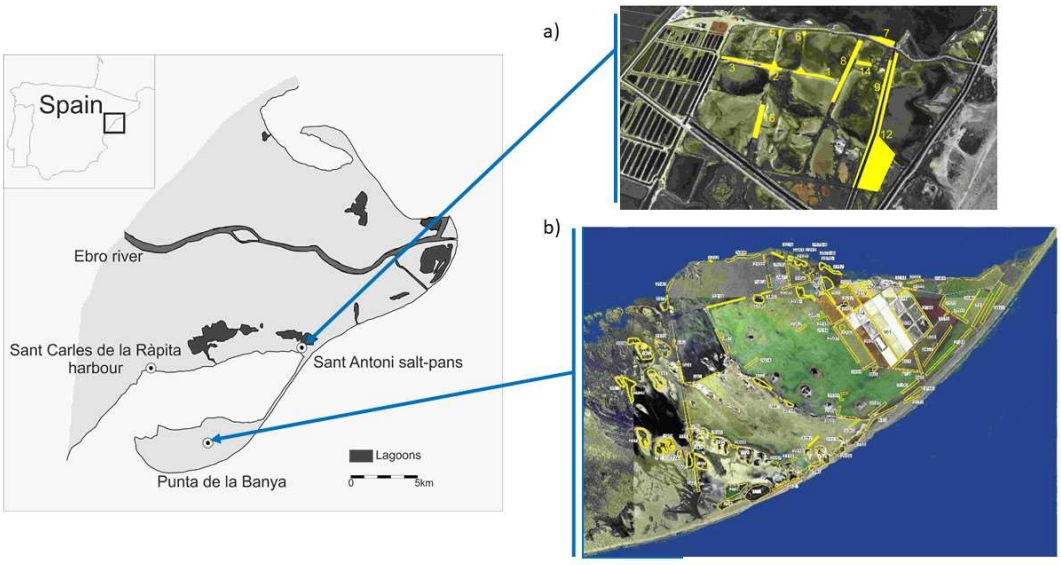


Figure 3. Map of the study area comprising the 3 main colonies and the distribution of patches within colonies during the study period at a) Sant Antoni and b) Punta de la Banya. Sant Carles de la Rápita colony is considered to have only one patch.

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

chicks survive, except in years with high food availability, when the strength of density-dependence is low [65].

Individual data

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

SNA framework

Our social network, defined as the observed pattern of breeding association, was constructed taking individuals (N=3548) as the nodes of the network and each edge dyad (i.e. pair of individuals) representing the fact that individuals breed in the same patch. We ended with a global sociomatrix, i.e. the matrix representation of the dyadic relationships among individuals, of 3,548* 3,548. Edges showed if two individuals bred in the same patch at least once in a certain period (see below). The network was not directional. Based on previous results on population dynamics, and on the population size of this species and colony [37,50], we divided our dataset in two main periods: a period defined as "stable phase" from 2002 to 2011, and a period of "transition phase to collapse", from 2012 to 2017 (Figure 1).

We used the recently developed AME function from the AMEN package [68,69], that can 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;[70]) using additive and multiplicative effects and combining the
315 linear regression model with the covariance structure of the SRM [69]. 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 [71,72]. To create and visualize our networks we used the packages
322 Amen [68], Asnipe [73], gdata [74] and igraph in R [75].
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 [68] (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.

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

Had perturbations affected social cohesion in this species?

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

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

Regarding the SNA approach, it is advised [76] to do permutations on the raw data prior to the analysis and compare the result of some relevant statistic obtained with the original data to the distribution of the same statistic over the permutations. We chose the regression coefficient of the association of a dyad on the previous association of the

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

Acknowledgements

We would like to thank all the people who have helped with the fieldwork in the Ebro delta over the years, particularly Julia Piccardo, Toni Curcó and the technical staff and volunteers at the Ebro Delta Natural Park. We would also like to thank Peter Hoff, for his advices and solving an analytical problem we encountered while using the AMEN R package. We also thank the Regional Government of Catalonia, for permits to access the study sites. Elisabeth Rochon corrected the English. Funding came from the Spanish Ministry of Science (CGL2017-85210), grant PICS INTERACT n°07699 (2016, CSIC-CNRS). MG was partially supported by the European Union (MINOUW Project, H2020-634495) and the Spanish Ministry of Science (CGL2017-85210). We have no conflict of interest to declare.

Authors' contributions

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

Data accessibility

Data is available via CSIC repository.

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