# PNAS

# Social copying drives a tipping point for nonlinear population collapse

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**Sudden changes in populations are ubiquitous in ecological systems, especially under perturbations. The agents of global change may increase the frequency and severity of anthropogenic perturbations, but complex populations' responses hamper our understanding of their dynamics and resilience. Furthermore, the long-term environmental and demographic data required to study those sudden changes are rare. Fitting dynamical models with an artificial intelligence algorithm to population fluctuations over 40 y in a social bird reveals that feedback in dispersal after a cumulative perturbation drives a population collapse. The collapse is well described by a nonlinear function mimicking social copying, whereby dispersal made by a few individuals induces others to leave the patch in a behavioral cascade for decision-making to disperse. Once a threshold for deterioration of the quality of the patch is crossed, there is a tipping point for a social response of runaway dispersal corresponding to social copying feedback. Finally, dispersal decreases at low population densities, which is likely due to the unwillingness of the more philopatric individuals to disperse. In providing the evidence of copying for the emergence of feedback in dispersal in a social organism, our results suggest a broader impact of self-organized collective dispersal in complex population dynamics. This has implications for the theoretical study of population and metapopulation nonlinear dynamics, including population extinction, and managing of endangered and harvested populations of social animals subjected to behavioral feedback loops.**

tipping points | runaway dispersal | nonlinear population dynamics | social behavior | feedback

Understanding abrupt declines in a populations' response to environmental perturbations is crucial for the theoretical study of population extinction and for managing harvested and endangered species, especially under the impacts of global change (1–3). Under the conceptual framework of the logistic model, the transition from a population level near carrying capacity to collapse in populations subjected to perturbations should occur through a negative exponential decay (4–6). However, the logistic model has several limitations because it assumes both a linear association between density and growth rate and a lack of time lag in the response of individuals to changes in density (5). Time-lagged responses may generate transient phenomena, which can explain abrupt regime shifts that are not directly associated with environmental changes (7, 8).

A crucial driver of the dynamics in animal populations is individual behavior, which influences relevant demographic parameters such as dispersal and the evolution of life histories (9). Information theory frames how populations may persist in stochastic environments when behavior is targeted for gathering information and reducing environmental uncertainty for making optimal decisions (e.g., to be philopatric or to disperse) (10). Individuals living in social groups have two sources of information for making decisions that may have fitness consequences: The first is private information that each individual gathers and stores on its own, and the second is public information in the form of decisions and performances others make. Examples of public information are flight from a predator approaching the group or average fertility in a particular patch indicating its suitability to a prospecting individual (11–13). The use of public information may generate density-dependent behavioral responses, such as runaway dispersal from a patch to escape from a perturbation. This is why dramatic sudden collapses in populations are likely to occur in social organisms. Social groups are complex systems in which the number of interactions within a group is not additive but grows in a factorial manner resulting in behavioral feedback loops, such as those arising for information gathering, social copying, and group cohesion. These feedback loops are autocatalytic, meaning that as more individuals perform a particular behavior, more other individuals will decide to follow suit. The density of conspecifics drives individual decision-making for staying or dispersing in a patch when the trade-off between the benefits of foraging and the risks of predation are considered (14). This is linked with collective behavioral loops that trigger informational cascades

## Significance

Among the complex dynamics arising in all living systems, sudden population collapses are one of the most fascinating. Understanding the mechanisms that may cause these collapses is fundamental to the conceptual study of population dynamics. We fit dynamical models to population fluctuations over 40 y in a social bird that showed an unexpected collapse after a perturbation press that progressively eroded environmental conditions at the world's most suitable breeding patch. We demonstrated that the density-dependence feedback related to the simple behavior of social copying for dispersal to other patches explained the collapse. The significance of our study lies in showing that stochastic perturbations may trigger a tipping point by runaway dispersal, driving populations to a state of quasi-extinction.

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used in the locating resources and threats (15). Collective behavior may influence complex population responses such as tipping points for regime shifts, boom-bust dynamics, and chaotic dynamics, all of them having potential consequences for population extinction (16–19).

A key process linking individual and collective behavior to a demographic trait with consequences for populations is decision-making for dispersal (19). How dispersal is influenced by copying behavior in social animals, including humans, remains unexplored, but empirical and theoretical studies show that copying is favored under perturbations (4, 15). Less is even known about the consequences of that copying in dispersal and other behavioral feedbacks for the occurrence of tipping points and the collapse of populations. The main reason for this is that theoretical population dynamic models including a mathematical expression of dispersal, such as coupled logistic equations, mostly consider dispersal as simple passive diffusion and not as

a density-dependent, nonlinear process (20, 21) (Fig. 1). Determining how populations of social organisms may collapse and diagnosing what behavioral mechanisms are involved is hampered by the challenges of collecting long-term data on both population fluctuations and environmental changes, including perturbations (22). Perturbations may have different temporal features, such as stochastic pulses and presses, but these dynamics are crucial to understanding the impact and responses they may generate on populations.

An unprecedented opportunity to investigate the effects of social feedback on population nonlinear collapses is afforded by 40 y of population and environmental data of the colonial long-lived Audouin's gull (*Ichthyaetus audouinii*) breeding seasonally at Punta de la Banya (Ebro Delta, western Mediterranean) (Fig. 2) (23). Despite being a species that has evolved a slow life history, the patch held almost 50% of the total world population after only 6 y since colonization, due to its habitat suitability allowing
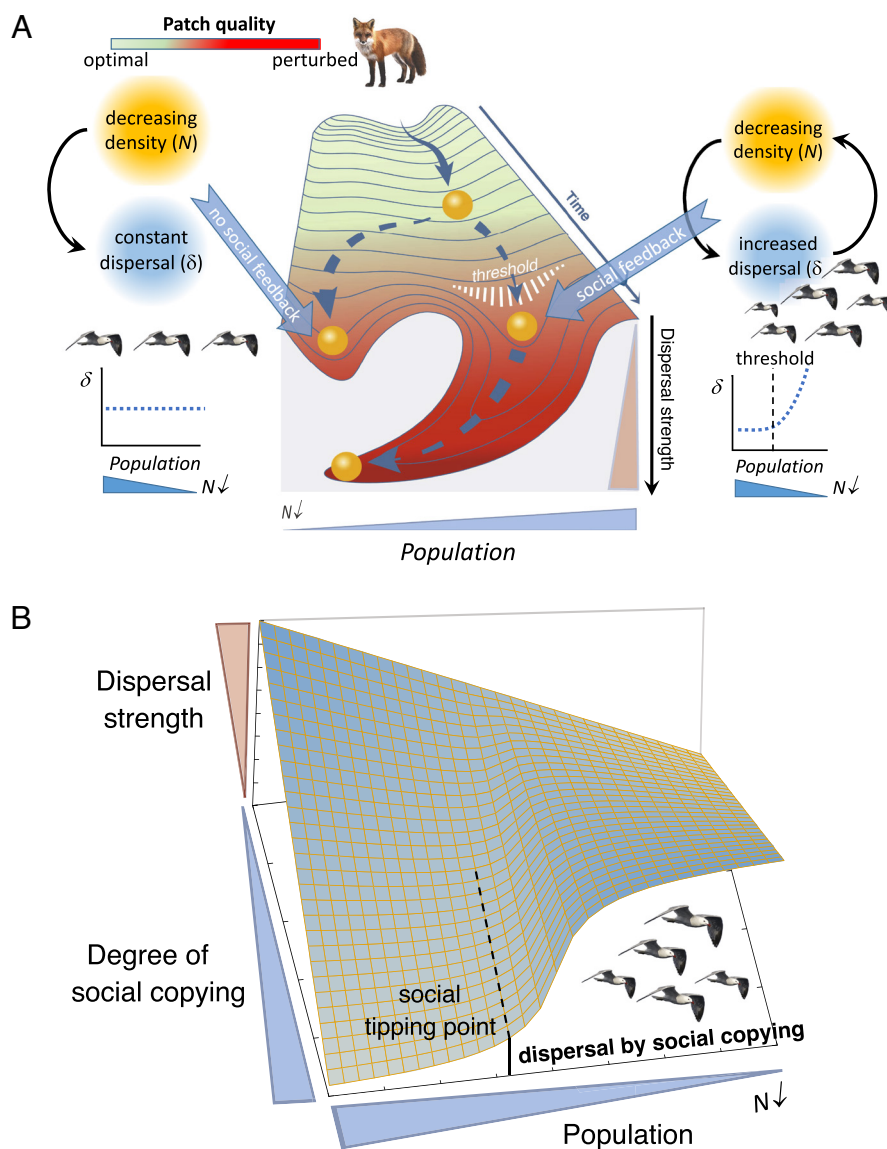


**Fig. 1.** (*A*) Schematic diagram of dispersal represented as a dynamic landscape. Depending on the patch quality (here represented as a perturbed patch with the presence of predators), individuals may undergo different dispersal dynamics (represented by δ) depending on population density (expressed as decreasing values over the *x* axis), e.g., density-independent (*Left*) or dispersal by social copying (*Right*). For social copying, a low population threshold may be found, accelerating such a dispersal. (*B*) Conceptual surface of dispersal strength as a function of population size and social copying feedback. In this study, we tested whether dispersal made by a few individuals induces others to leave the patch in a behavioral cascade once a tipping point is exceeded. This social copying for dispersal should be mimicked by a negative density-dependent function, where dispersal increases at a decreasing population density.
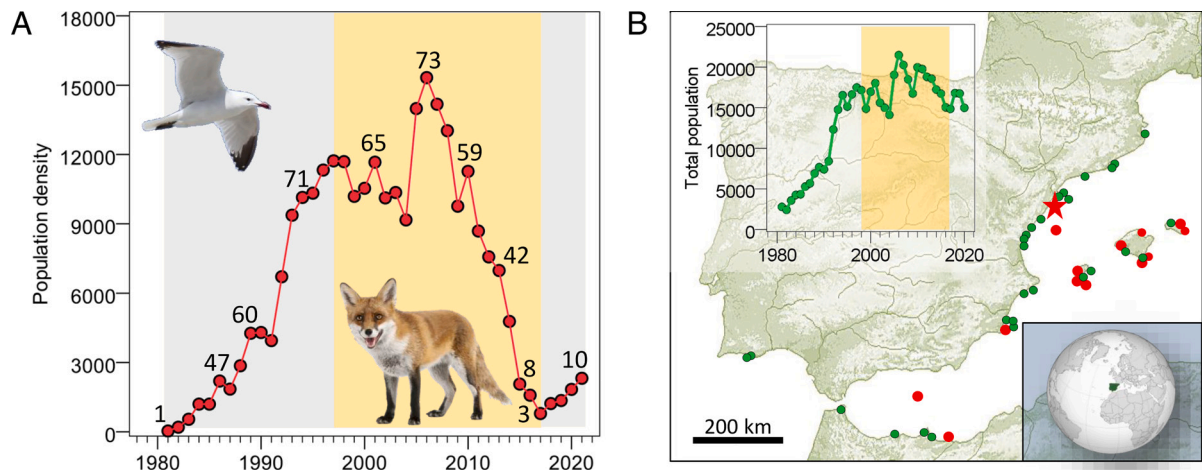
**Fig. 2.** (*A*) Population dynamics of gulls breeding at La Banya since colonization (1981 to 2021), expressed as density of reproducing females. The orange areas show the duration of the perturbed regime caused by the arrival of carnivores. In the final years, the population showed a slow recovery after predators were removed for conservation purposes. Numbers over the line are percentages of the total world population breeding here. (*B*) Spatial distribution of breeding patches, where 90% of the total world population breeds. Red star shows La Banya, red dots are the patches occupied before the perturbed regime, and green dots are the patches colonized since then. (*Inset*) Population dynamics for the same period 1981 to 2021 of the whole metapopulation, which holds ca. 45 breeding patches. Fluctuations in metapopulation density were greatly influenced by the dynamics of La Banya, but they did not show an abrupt decline because dispersed individuals were redistributed over the colonized patches.

for extremely high rates of survival, fertility, and immigration from other patches (24, 25). Low interference competition with other sympatric species of the same ecological guild and the absence of terrestrial predators enhanced these rates (26, 27). The population continued to increase through a rapid transition, ending in a seemingly dynamic equilibrium state, which occurred when predators invaded the patch (Fig.2*A*). Predator densities were very low and did not vary over the years, but a perturbation was pressing over the breeding seasons eroding habitat quality and causing not only a slight decrease in adult survival but also a high dispersal to other occupied patches, especially to empty patches for colonization (28–30) (Fig. 2*B*). Because we accurately monitored the metapopulation at a large spatial scale, we quantified dispersal processes of emigration and immigration among the different patches, including extinction and colonization events over the years (Fig. 2*B*). Just after peaking at a maximum density due to a stochastic increase in food availability during 2005 to 2006, holding 73% of the total world population, the local population underwent a sustained decline leading to collapse, where it held only 3% of that total world population (Fig. 2*A*). In summary, we tested the hypothesis that the arrival of predators triggered a tipping point by runaway dispersal driven by social copying behavior that caused the population to collapse.

To test our hypothesis, we first built a population model that described the local population dynamics as a single-patch system and considered immigration and dispersal of individuals within the metapopulation, which was not explicitly considered. The model also took into account other ecological processes, such as intraspecific competition for resources and density-independent death rates. In previous studies, we accurately estimated death rates by capture-recapture modeling of +30,000 banding birds and +28,000 resights over 32 y encompassing 69 local patches of the metapopulation (+90% of the total world population) (27, 29). Metapopulation dynamics and most dispersal processes, in terms of the density of individuals, were governed by the dynamics of the study patch, because it held a large percentage of the total world population (Fig. 2) (29). Most importantly, for modeling the dispersal out of the study patch in our model, we included different forms of dispersal to assess which one played a major role

in explaining the population dynamics observed after the arrival of predators. One dispersal form was positively density-dependent, whereas the other was negatively density-dependent mimicking the behavior of social copying (4). To assess how population density influenced dispersal, we used an Elliot sigmoid function, which allowed us to test for different shapes of negative density-dependence, including the extreme case of density-independent dispersal. This function typically increases at decreasing population values (i.e., dispersal would increase with decreasing population density), but it allows some other forms, such as sigmoidal shapes and sudden nonlinear changes (*SI Appendix*, sections S2 and S4, Figs. S8–S10). For instance, nonlinear shapes with a drastic increase in dispersal beyond a threshold value of population density would fit with a tipping point for runaway dispersal by social copying (4, 31). On the contrary, an Elliot function fitting density-independent dispersal would suggest that dispersal occurred only after using private information. Finally, we developed an optimization technique to fit the population models to our field data using artificial intelligence algorithms.

## Results and Discussion

The geometric mean of the population growth rate over the whole study (expressed as $x_{t+1}/x_t$, being $x_t$ the size of the population at time $t$ since colonization, $t_0 = 1,981$) was high, and it showed large fluctuations (mean = 1.106; SD = 0.835), likely due to the influence of large rates of both immigration and dispersal (*SI Appendix*, Fig. S1). The model for the initial phase before the arrival of predators (1981 to 1997) given by Eq. 1 with $\rho = \lambda = 0$ (i.e., with no dispersal) clearly showed a logistic behavior with an initial exponential growth, an average growth rate = 0.349 $y^{-1}$ and carrying capacity = 18,828 birds (least-squares LS = 2,593.05, coefficient of determination $R^2$ = 0.976, $N$ = 17) (*SI Appendix*, section S3.2.2) (Fig. 3). During this initial phase, the population was in a transient state, and it did not reach the predicted equilibrium value even though the patch already held a large proportion of the total world population. This was due to the arrival of predators (Fig. 3*B* and *SI Appendix*, Fig. S6). We confirmed this after we fitted field data with the logistic model from 1981 to 2004 to test
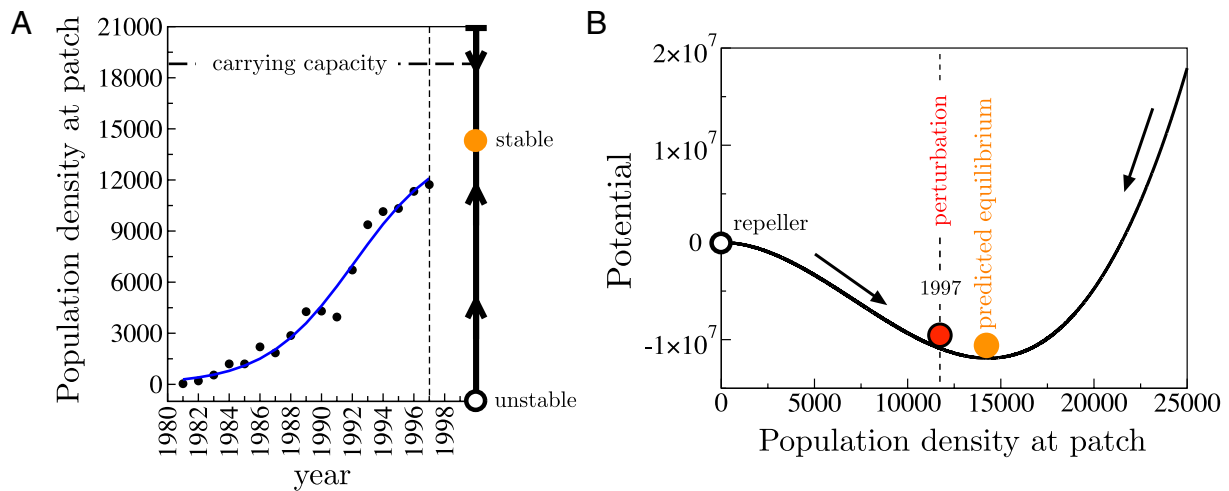
**Fig. 3.** (*A*) Population dynamics from patch colonization in 1981 to the arrival of predators in 1997 and the fit of the logistic model displayed with a blue line, which shows an exponential increase in density (*SI Appendix*, section S3). The fitted parameters suggest that the population was approaching the expected equilibrium value when predators were established at the patch. The estimated carrying capacity is shown with a dashed line, in conjunction with the location of the equilibrium points (stable in orange, unstable in white), predicted by the estimated parameters (*SI Appendix*, section S3.2). (*B*) Potential function of the logistic model showing the predicted equilibrium (orange marble), which was not achieved due to the perturbation starting in 1997 (red marble) (*SI Appendix*, Eq. **S3.2** and Fig. S5).

whether the model performed well without considering the impact of predators, but the fitting was worse (LS = 5,639.34, R² = 0.928, *N* = 24) (*SI Appendix*, section S4.3 lines 669 to 688, *SI Appendix*, Figs. S16 and S17).

After the onset of perturbation phase in 1997, population fluctuations likely increased due to an increase in demographic noise, caused by the negative density-dependent dispersal found in our model. The population also showed a slight decrease between 1998 and 2004 (Fig. 2*A* and *SI Appendix*, Figs. S1 and S18). This decrease could not be attributed to a deterioration in environmental conditions, because none of the environmental parameters influencing resource availability and predators (densities and killing rates) changed significantly (*SI Appendix*, Fig. S1.2, sections S1.2, S1.3, and S4.3) (4, 29). Despite the low amount of data for this phase, the parameters estimated in our model using the results obtained for the full collapse phase (see below) indicated that the dominant dispersal was social copying, whereas positive density-dependent dispersal was negligible (*SI Appendix*, section S4.3, lines 689 to 716 *SI Appendix*, Fig. S18).

For the final phase of population collapse (2006 to 2017), the full model given by Eq. 1 fitted the population decline with high accuracy (LS = 2,566.99, R² = 0.975, *N* = 12) (*SI Appendix* lines 646 to 668, *SI Appendix*, Table S4). The model considered a negative density-dependent dispersal mimicking social copying for dispersal (4) (Fig. 4). Contrarily to what is predicted by simple theory (32), models considering only density-independent or positive density-dependent dispersal had a worse fit for the full collapse phase (LS = 3,391.96 and R² = 0.957 for the former model, *SI Appendix*, section S5). For the positive density-dependent dispersal model, no optimum exists, but rather a sequence of progressively better positive density-dependent functions with quadratic errors converging to LS = 3,300. These functions were essentially indistinguishable from the density-independent case (*SI Appendix*, Fig. S21), showing that the positive density-dependent dispersal played no role in reproducing the field data for the full collapse phase (*SI Appendix*, section S5.2). Therefore, models considering standard dispersal modes did not improve the fit of the model with dispersal by social copying. The set of parameters that better fitted field data for describing the negative density-dependence dispersal function showed that dispersal varied non-linearly with population density over three different phases (Fig. 4).

During the first years of the collapse period (initial slow phase, Fig. 4*B*), dispersal increased slightly with a decrease in population density. Interestingly, dispersal accelerated once a tipping point of population density was crossed (acceleration phase, Fig. 4*B*). After attaining its maximum rate, dispersal decreased with lower population densities (slowing down phase, Fig. 4*B*). These results contrast with the simple linear dispersal process assumed in simpler models.

We used a mathematical technique for fitting a population model to real data to explore which type of dispersal could explain the collapse of a local population at a metapopulation level. Our capacity to study how perturbations may cause population collapses has increased in recent decades, thanks to the greater availability of long-term data on both populations and environmental variability (33–35). Furthermore, more detailed population models are considering the complex nature of population dynamics by incorporating simultaneously density-dependent mechanisms and the different types of stochasticity (mainly environmental and demographic) (36–39). Nevertheless, disentangling the role of endogenous (e.g., density-dependence) and exogenous (density-independent, environmental perturbations) drivers on population declines remains a challenge, especially when environmental changes are not accurately monitored (40). Further challenges include modeling dispersal processes explicitly to understand local and metapopulation dynamics and to assess the role of density-dependence on those processes, which may be particularly crucial during phases of colonization and declining population (i.e., immigration and emigration, respectively) (24, 41). Here, we built a mechanistic population model to explain the population dynamics from colonization through collapse in a social bird subpopulation that went from holding 73% of the total world population to only 3% in just 10 y. The results show that the collapse was caused by a nonlinear negative density-dependent dispersal, suggesting the behavior of social copying. The generality of copying in social animals is supported by the bulk of theoretical studies and empirical evidence showing the importance of social information exchange when making decisions (15, 28, 42, 43). Copying also occurs in human behavior when decision-making is at play and it is studied under the framework of the theory of conformity (44). Other than primates, social copying has been found in a broad range of animals, even in simple organisms, and
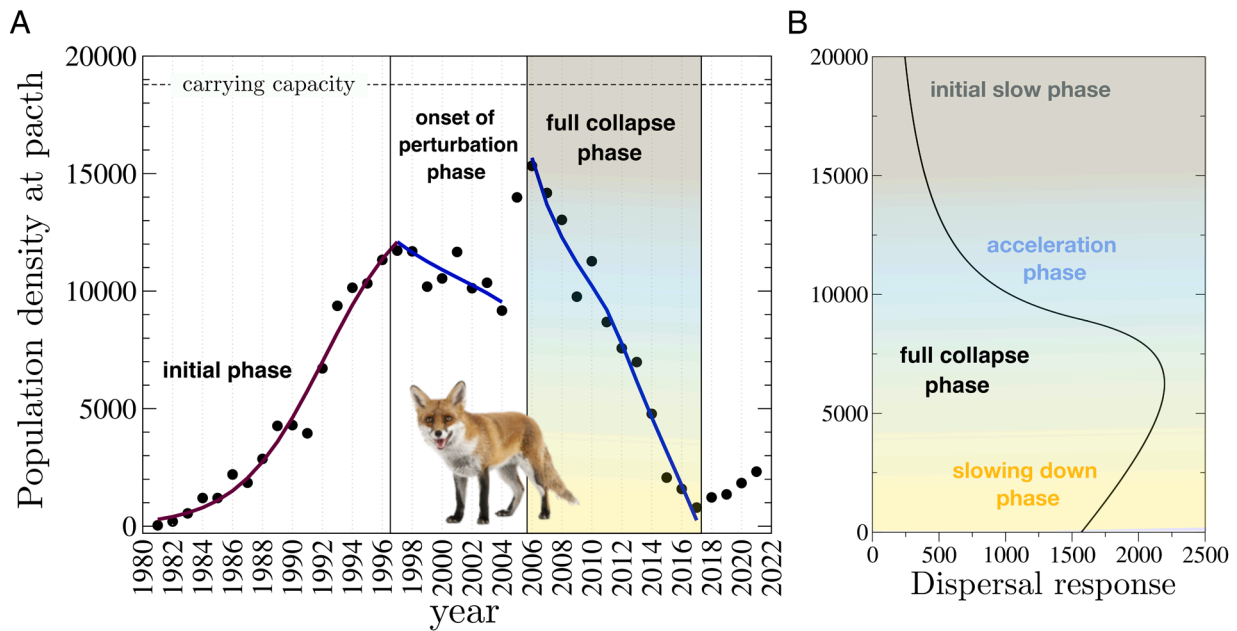
**Fig. 4.** (*A*) The entire population dynamics since colonization to collapse obtained from the field data (solid dots) and the fit of the model without (brown line) and with (blue lines) dispersal. The initial phase (from 1981 to 1997) was fitted using Eq. 1 with $\rho = \lambda = 0$ (i.e., with no dispersal). Here, the population showed a logistic growth before the arrival of predators in 1997. Later, the field data showed a first slight decline after this arrival, and a very abrupt decline from 2006 to 2017, when predators were removed. These two declining phases were fitted with the full model given by Eq. 1 including asocial and social dispersal terms. (*B*) Dispersal of individuals in the full collapse phase varied nonlinearly with population density, showing three phases: an initial slow phase (gray area), an acceleration of dispersal with a social tipping point (blue area), and a slowing down phase found at a low population size (yellow area).

it may have important consequences for the individual, e.g., for mate choice and thus for its fitness (45, 46). In an ecological context, theoretical models exploring how individuals weigh private and social information to make decisions showed that the tendency to follow the majority option is enhanced by deteriorating environmental conditions (e.g., the presence of a predator) (15).

Beyond the behavioral consequences that social copying may have for individual fitness, very little attention has been devoted to the potential effects that copying may have for generating nonlinear density-dependence dispersal and population dynamics (4, 47). In colonial, long-lived species with spatially structured populations, individuals dispersing may use inadvertent social information available at each patch (in the form of conspecific density and the fertility of conspecifics) to assess its suitability and make decisions about where to settle each reproductive season (11, 48, 49). Thus, social copying would influence the decision-making in the trade-off between staying in the patch and dispersing to other patches, which could also affect dispersal at the level of the group and the dynamics of local populations and metapopulations (e.g., periodic dynamics, boom-bust, rescue effects, source-sink dynamics). Furthermore, some individuals of the population (e.g., specific ages, sexes) may be more prone to disperse and generate demographic heterogeneity among patches, thus increasing stochasticity and spatial variability in extinction risk (30, 37).

The first nonlinear response of the studied population was related to social processes that occurred after the onset of a perturbation. Population fluctuations increased mainly due to an unexpected sharp and short increase in the population leading to a maximum density, and this corresponded to what resilience theory calls demographic compensation (50). Compensation was likely caused by high local recruitment and a decrease in interspecific competition favored by a pulse of higher food availability recorded at the patch (Fig. 2*A* and *SI Appendix,* Fig. S2) (27, 50, 51). The transient arrival of predators in the beginning of the

collapse phase lasted nearly a generation. The time elapsed under the perturbation press regime was consistent with predictions of the transient theory for fast–slow dynamics: While population growth after colonization of new patches can be extremely fast (4), it only occurs once individuals gather enough information about the suitability of alternative patches for what is termed "informed dispersal" (12, 42). This behavioral process of prospecting to gather information may be slow in empty patches due to the lack of public information, which is used as a cue for assessing the quality of occupied patches (*SI Appendix,* Fig. S2) (4, 28, 43, 52). When predators first invaded La Banya, only a few small other patches in the metapopulation were occupied and their local population growth was constrained by competition for breeding sites. Therefore the dispersal to these patches, where social information was available, was challenging (Fig. 2*B*) (28, 29). However, little is still known about how individuals copy others in the process of dispersal and whether they are able to track a decreasing density at the actual patch (53). Interindividual behavioral synchronization for collective dispersal has been seldom described (54). Group dispersal may occur at different temporal scales and using several alternative, nonexclusive, behavioral mechanisms. First, previous studies show that individuals use public information by tracking density at some patches at a metapopulation scale, and density is a clue for patch suitability and therefore decision-making on where to settle for breeding (24, 29, 48, 55). Patches with larger population densities generate higher conspecific attraction due to the advantages of grouping (e.g., risk dilution, social cohesion, and collective vigilance). Individuals inhabiting patches subjected to press perturbations and decreasing densities may disperse to avoid the costs of living in small groups (e.g., incurring in Allee effects) (56–58). We also know that birds and mammals may follow others while foraging and commuting between feeding patches (59, 60). This process might also operate while individuals are prospecting different breeding patches for gathering information

about where to disperse (4, 52). We have some lines of evidence of Audouin's gulls copying each other when leaving to go on patch prospecting trips (52).

It is clear that population dynamics of social organisms in deteriorating environments may be more influenced by transient phenomena and density-dependent mechanisms than solitary, territorial species (7). Empirical data on declining populations of nonsocial organisms suggest their dynamics should follow a density-independent decrease toward extinction (61, 62). The existence of social behavioral feedback, from very simple (e.g., social copying) to more complex (e.g., cooperation, hierarchies), may increase stochasticity in local population processes like abrupt extinctions and the appearance of tipping points for collapses (4, 14, 17, 63, 64). Nevertheless, disentangling the processes that, alone or in interaction, may drive population nonlinear declines, and the mechanisms behind those processes that may cause the tipping point to appear, remain a challenge (14, 65, 66). Outside of mesocosmos experimental studies, interpreting complex local population dynamics in empirical studies needs accurate monitoring of both metapopulation dynamics and environmental stochasticity. The exceptional fitting of our population model during the phase of collapse is an example of how an environmental stochastic perturbation (i.e., the arrival of predators) triggered a tipping point by runaway dispersal, i.e., a negative density-dependent accelerating dispersal caused by positive behavioral feedback that drove the population to a state of quasi-extinction. This type of tipping, which occurs by the progressive loss of the resilience of the current population state, can potentially be anticipated when using the tools of early warning signals (67).

## Conclusions

The critical significance of our results is that social copying, a simple behavioral mechanism operating in all social organisms, may generate nonlinear population collapses by the occurrence of tipping points in dispersal processes. These dynamics fit well with what has been observed in populations of social animals subjected to press perturbations, such as superabundant species subjected to culling and humans during warfare (4). Under these circumstances, there is an initial reluctance to leave the patch due to a large availability of information, the force of social cohesion, and the evolutionary advantages of being philopatric as opposed to being disperser, which is riskier in terms of fitness prospects (28, 68, 69). In humans, this is reinforced by a sunk-cost effect, which prevents people from abandoning their ways of living, cultures, and beliefs (70). However, once a threshold for deterioration of the quality of the patch has trespassed, there is a tipping point for a social response of runaway dispersal corresponding to social copying feedback. Finally, dispersal decreases at low population densities, which is likely due to the unwillingness of some individuals to disperse after occupying a suitable patch for extended periods. At an ecoevolutionary scale, this corresponds to the individual heterogeneity for dispersal within populations, with some individuals being extremely philopatric. This phenomenon may generate long queues of quasi-extinction states observed in some populations of social animals, and that would boost immigration by conspecific attraction once environmental conditions at the patch are recovered (4). Our study emphasizes the value of combining long-term demographic and environmental data with mathematical modeling to uncover the behavioral mechanisms driving nonlinear responses of populations of social organisms under perturbations. Our results suggest a broader impact of self-organized collective dispersal in complex population dynamics, such as tipping points and transient phenomena. This may have implications for the theoretical study of population and metapopulation nonlinear dynamics, including population extinction and resilience, predator-prey dynamics, and the management of endangered and harvested populations of social animals subjected to behavioral feedback loops.

## Materials and Methods

**Study System and Species.** Demographic population monitoring of Audouin's gulls (*Ichthyaetus audouinii*) at Punta de la Banya (Ebro River Delta: 40°34010:8900N, 0°39034:2800E) started in 1981 when the patch was colonized, and it has been monitored constantly for the last four decades (1981 to 2021). La Banya is a 2,500-ha sandy peninsula formed by sandy dunes covered by halophilous vegetation. The site, once effectively protected in the early 80s, held extremely suitable environmental conditions for breeding ground-nesting waterbirds (i.e., large availability of food and reproductive habitat free of predators). Audouin's gulls are long-lived social birds with a bet-hedging life history. They have evolved to cope with ephemeral habitats typical of Mediterranean marshes (71, 72). Consequently, Audouin's gulls have nomadic behavior between breeding seasons. When patch conditions change or worsen, then individuals are more prone to disperse to other occupied sites, but in recent years, and after the arrival of invasive carnivores in the late 90s, colonization rate of new patches has largely increased. Ground-nesting gulls have not developed evolutionary defenses to cope with terrestrial predators like carnivores. This is why they select breeding patches isolated and protected against carnivore invasions. The long-term monitoring at the metapopulation scale allowed reliable knowledge of the system in terms of population fluctuations (Fig. 2*B* and *SI Appendix*, Fig. S1), interference competition with species of the same ecological guild, demographic parameters (e.g., survival, fertility, recruitment, and dispersal), and environmental stochasticity, including the invasion of predators, the occurrence of other perturbations, and fluctuations in food availability over the years (*SI Appendix*, lines 4 to 26) (24, 26, 27, 29).

**Fieldwork Methods.** Results regarding the methods used to monitor demographic parameters and population size were published previously (27), and exhaustive details concerning the fieldwork protocols and sites can be found in the previous literature and in *SI Appendix* (lines 27 to 74). Briefly, population density, which corresponded to the number of breeding females, has been estimated since colonization in 1981 by counting the nests containing eggs just before hatching, when biases due to the variance in laying dates were minimal. Errors at counting nests were quantified and were small and constant over the years (<5%). The same procedure was followed to estimate the population density of the main competitor of Audouin's gull, the larger yellow-legged gull (*Larus michahellis*). The density of carnivores (mostly foxes, *Vulpes vulpes*) and the number of killings were estimated every year since their arrival in 1997 thanks to the tracks in the sand and the intense monitoring of roosting and breeding dens. Other impacts affecting demographic parameters, such as mortality by fishery bycatch, were also duly monitored. Finally, we used the statistics of landings on trawling boats in the harbors close to the study site. Landings are highly correlated with the amounts of fish discarded, which represent up to 70% of biomass ingested by the gulls and greatly influence their fertility. We showed that the population collapse was not caused by a deterioration of environmental conditions but by the stochastic fluctuations of carnivore densities (*SI Appendix*, Fig. S2, lines 75 to 97).

**Mathematical Model and Data Fitting.** To analyze population dynamics from colonization through collapse, we used an ordinary differential equation logistic population model and density-dependent migration terms (*SI Appendix*, lines 98 to 139). Due to the very low number of predators and their negligible effect on predation (28), we did not consider predator–prey dynamics explicitly as an ecological process causing population decline by direct mortality. The model, which describes the population dynamics in a single-patch system, but considers immigration and dispersal of individuals, is given by

$$\frac{d}{dt}x(t) = (\vartheta + \omega)x(t)\left(1 - \frac{x(t)}{K}\right) - \varepsilon x(t) - [\rho x(t) + \lambda D(x(t), \mu, \sigma, \delta)],$$
[**1**]

where *x(t)* denotes population density at time *t*, $\vartheta$ is the intrinsic reproduction rate, $\omega$ is the immigration rate from other patches, and $\varepsilon$ is the annual death rate estimated from field data [0.11 y$^{-1}$, estimated from long-term monitoring (1988 to 2015) using capture–recapture modeling (27)]. The model introduces

intraspecific competition for resources constrained by a logistic function with carrying capacity $K$, and importantly, it includes two distinct dispersal terms. The first dispersal term $\rho$ is the linear (exponential) dispersal to other patches, which corresponds to a positive density-dependent dispersal. The second dispersal term is represented by the function $D(x(t), \mu, \sigma, \delta)$, which is an Elliot sigmoid function (see below and *SI Appendix*, lines 250 to 355). This function introduces a negative density-dependent term of dispersal (i.e., the fewer individuals at the patch, the faster the dispersal, see Fig. 1), which mimics social copying of individuals leaving the patch, with dispersal rate $\lambda$. We applied the model in Eq. 1 to fit empirical population fluctuations separately for three phases in which we divided the dynamics of the population (*SI Appendix,* lines 123 to 139, *SI Appendix,* Fig. S3). The first phase goes from the patch colonization to the arrival of predators (initial phase: 1981 to 1997). In the absence of predators, we expected this initial phase to be characterized by an early exponential growth and a logistic behavior when approaching the carrying capacity. Here, we did not consider dispersal triggered by the perturbation because predators were not present in the patch during that phase, and previous studies showed that population dynamics were dominated by high immigration rates from outside (24). Thus, we used Eq. 1 and removed the two dispersal terms (i.e., $\rho = \lambda = 0$). For fitting the population model to this phase, we used a standard trust region method and the Levenberg–Marquardt algorithm (*SI Appendix,* lines 232 to 249, *SI Appendix,* Fig. S6).

Second, we analyzed the two phases in which predators were present at the patch. One phase (onset of perturbation phase) encompassed from the establishment of predators in 1997 to 2004, before population density suddenly increased due to a stochastic pulse of food availability in the years 2005 to 2006 (*SI Appendix*, Fig. S3). The last phase encompassed the maximum density attained to the full collapse phase between 2006 and 2017 (Fig. 2 and *SI Appendix*, Fig. S3, sections S4.2 and S4.3). For these two phases, we used the full Eq. 1, which included the two distinct dispersal terms (*SI Appendix*, Eq. **S4.1**). We tested whether there was a negative density-dependent term of dispersal by social copying using different values of the parameters contained in function $D(x(t), \mu, \sigma, \delta)$. The parameters of this function drove the sharpness of the jump and its smoothness in the relationship between density and dispersal: $\mu$ reflects the tendency of dispersal for small population sizes, $\sigma$ defines the sharpness and smoothness of the dispersal function, and $\delta$ models the transition between small and large population sizes (*SI Appendix*, lines 266 to 305). The Elliot sigmoid function has two features that make it suitable for testing what type of dispersal would explain the population collapse. First, the function typically increases at decreasing population values, and second, different combinations of those parameters correspond to different nonlinear types of negative density-dependent dispersal, all indicating that dispersal occurred by social copying (*SI Appendix*, section S4.1, Figs. S7–S9). Interestingly, we note that for some special conditions (e.g., $\sigma$ close to 0), the Elliot function represents a density-independent dispersal, which would mimic individuals dispersing only using private information (*SI Appendix*, Remark S4.2, Figs. S7, S9, and S10). We searched for the model parameters that matched our population data using artificial intelligence methods (*SI Appendix*, lines 520 to 645). Because the number of years for the full collapse phase was larger than for the onset of the perturbation phase, we used the longer period to fit the parameters of the Elliot sigmoid function (*SI Appendix*, section S4.2). Then we used those parameters to fit the model to the onset of perturbation phase (*SI Appendix*, lines 689 to 716, *SI Appendix,* Fig. S18).

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