Adaptive learning and coloniality in birds

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We introduce here three complementary models to analyze the role of predation pressure in avian coloniality. Different explanations have been proposed for the existence of colonial breeding behavior in birds, but field studies offer no conclusive results. We first propose a learning model in which the decision of birds are taken according to the collective performance. The properties of the system are then studied according to a model in which birds choose according to their individual experience, and the agreement of the introduction of spatial structure with field data are then shown.

I. INTRODUCTION

In the last few years there has been an increasing interest in the understanding of learning processes of collective behavior, specially in systems of interacting agents. The aim of these studies is to reproduce qualitatively features of economic or biological systems [1, 2].

Colonial breeding behavior in birds has been extensively studied [3, 4, 5]. During the breeding season vertebrate social systems can be behaviorally classified into three main groups: territorial, cooperative and colonial. This classification is according to the genetical relationship with the other members of the colony, and to the spatial organization. While territorial and cooperative behavior are evolutionary understood, colonial behavior remains an open question. Different hypotheses have been put forward in order to explain this behavior, like minimizing the distance required for foraging [6], observation of conspecific foraging groups [7, 8, 9], information transfer at the colony [10], shortage of nests [11, 12], or predation pressure [8].

One of the difficulties in verifying the previous hypotheses is that present day conditions need not to coincide with those which lead to colonial behavior in the first place. Thus, modelling of bird populations using reasonable assumptions for bird behavior can be useful in the elucidation of possible scenarios favorable towards the evolution of coloniality.

Some theoretical studies give support to the hypothesis that information transfer at the colony increases the tendency towards colony formation [13, 14, 15]. However this hypothesis requires the previous existence of a group or colony, and therefore it cannot explain by itself the evolution towards colonial behavior.

Predation can induce colonial habits in many ways. The simplest passive mechanism is the dilution effect provided by a colony of sufficiently large size [16, 17, 18]. In addition, the detection and defense capabilities are enhanced in colonies [16, 18, 19, 20, 21]. On the other hand, the lack of significant predation pressure on some colonial species has been used as evidence against the predation hypothesis [17, 22], although a phylogenetic analysis of coloniality across bird species shows a strong correlation with exposure to predation in the past [1].

The present work analyzes the role of predation on the formation of colonial habits by means of a mathematical model which incorporates some of the known facts about the response of birds to attacks by predators, and makes simple assumptions about the memory and learning processes at play.

II. MODELLING LEARNING PROCESSES IN SOCIAL SYSTEMS

A. Minority Game and Individual Minority Game

We model birds experience in a similar way to that used in the “Minority Game” (MG) model [24, 25, 26, 27, 28]. The minority game was introduced in the analysis of decision making by agents with bounded rationality, derived from “El Farol” bar problem [23, 29]. The model describes N agents which must make a choice between two alternatives (originally defined as {0, 1}, later on described as {−1, 1}). Agents make choices using as input the preceding collective performance. A successful choice for an agent is that which no more than half the total of agents choose. The bounded capacity of each agent is modelled assuming that agents can only remember the last m rounds of the game. This time span defines 2m possible outcomes which each agent needs to consider. Hence, the number of strategies that the agents can use is 2m, each of which is a set of choices for each possible previous outcome. To keep the assumption of bounded rationality, agents have a limited number s of strategies, taken at random (in most studies, s = 2). Each strategy has an independent score, which is updated after each move, according to its performance.

The game is defined by three parameters: N, the number of agents, m, the number of time steps agents use to determine the next decision, and s, the number of strategies available to each agent. Depending on the ratio α = 2m/N, a phase transition has been
The model has been generalized in different directions (see [27]). There are different versions in which the agents are allowed to evolve. The strategies with which each agent is endowed can be considered its “genotype”, and can be allowed to change. Alternatively, each agent can have an extra character, which allows it to favor a given strategy or its opposite [4].

The main objective of the present work, as described previously, is the modelling of processes which lead to individual or collective behavior and which are determined by responses to unexpected events, like predation. While the generic pattern of response can be genetically defined, we will concentrate on the adaptation to the habitat which takes place during the lifetime of each individual, using the agent’s past experience only. Hence, our starting point will be a variation of the minority game in which the information used by each agent is not taken from the collective history, but from the agent’s own choices and performance [28]. We define this version of the minority game as the individual minority game. Previous studies show that the use of different sources of information by different agents change significantly their behavior in the $\alpha \ll 1$ region, where some of the “herding” effects described in this section are avoided. On the other hand, the fact that the information used by each agent cannot be considered a random input [15], makes it difficult to use analytical techniques.

### III. Results

#### A. Collective scoring model

We first study a scoring scheme in which the collective traits used in the standard minority game are combined with the use of information private to each individual. The scores are updated according to the following rules: i) The scores corresponding to strategies which lead to the outcome not chosen by the bird are updated according to their average success among the birds which have followed them, ii) The scores corresponding to the strategies which lead to the actual choice taken by the bird are updated according to the success obtained by the bird their previous nesting site. Birds choose a colony or an isolated nest depending on their previous experience.

Each season, birds can be predated with probability $p$. We take as our unit a breeding couple. A predation event does not imply the birds which form the predated pair are removed from the population, but that the nest suffers predation from small animals (rats, snakes, etcetera) which eat or damage the eggs. Therefore, the reproductive success of the couple is zero or small, and they learn from the experience. These “small” predation events are much more common in nature than those which involve big predators, such as mammals, which can destroy the whole colony. The birds have a finite lifetime, which limits their ability for learning (see below), which is not related to predation. The objective of the present work is the study of simplified learning schemes by which birds can aggregate in colonies, and this learning mechanism can only occur when birds survive to predation. Hence, “big” predation events are irrelevant for this purpose.

Each bird has, as already mentioned, $s$ strategies (see table I for example of a strategy of memory $m = 2$). Each of these strategies has a score, which reflects the innate preferences of each bird, or the degree of reproductive success that the bird would have had if it had followed it.

We consider different scoring mechanisms, as the available biological data can be interpreted in different ways. We first assume that this score is updated using collective information from the performance of all individuals. Next, we analyze the case when each bird updates the scores of its strategies using information from its own success in previous occasions. Hence, each bird uses information different from that used by other birds, and the model departs from the minority game usually analyzed in the literature, where the score of strategies is the same for all agents.

The finite lifespan of the birds is modelled with a probability of setting the scores of the strategies of a bird to zero $p = \frac{1}{v}$ at each time step, where $v$ is the average lifespan of the birds. This is equivalent to introduce a new bird with no previous experience, and allows us to keep the population size constant.

#### B. Coloniality by predation

In our approach to colonial behavior we assume that the available choices to birds are limited to two possibilities each breeding season: they can either form an individual nest, or join an existing colony. Therefore we find a binary system of decisions, equivalent to the MG model.

Successful breeding individuals tend to be faithful to

| Signal | Decision |
|--------|----------|
| 11     | 1        |
| 10     | 1        |
| 01     | 0        |
| 00     | 1        |

**TABLE I:** Example of strategy, for $m = 2$
| Choice        | Success | $\Delta_i$ | $\Delta_c$ |
|--------------|---------|------------|------------|
| Individual   | Predated| 0          | $1 - 2 \times p/N$ |
|              | Not Predated | 2          | $1 - 2/n_c$ |
| Colonial     | Predated| $2 \times (1 - p)$ | $1 - 2/n_c$ |
|              | Not Predated |          | 1          |

TABLE II: Collective scoring, where $N$ is the number of birds, $p$ is the predation probability and $n_c$ is the number of colonial birds. $\Delta_i$ is the increase on the score of an individual strategy and $\Delta_c$ is the increase on the score of a colonial strategy.

at that season. We assume that, in the absence of predation, the innate tendency of the birds is such that the score assigned to strategies leading to individual behavior is twice that for colonial behavior.

This choice of scores takes into account the innate tendency of many birds towards an individual behavior [18]. The dilution effect, which favors colonial behavior in the presence of predation, is included in two ways: i) birds which choose an individual behavior update the scores of the strategies leading to colonial behavior taking into account the dilution effect which exists in a large colony which includes all the birds and ii) birds which choose a colonial behavior are predated less often, depending on the size of the colony to which they are in, which we assume to include all colonial birds.

We have studied this model for different values of the parameters, and we have found that the same qualitative features as we vary the number of strategies $s$ available to each bird or its memory $m$. Typical results are shown in fig. 1.

It is interesting to consider the case of infinite lifespan, although biologically unrealistic, shown in fig. 2. Then, the population reaches a stationary state where all birds behave individually or colonially, with a sharp phase transition at $p = 0.5$. This result can be obtained by estimating the balance between costs and benefits of each type of behavior for the whole population. Thus, the learning scheme described by this model is guaranteed to lead to the optimal behavior if the learning ability, or the memory, of the birds was infinity. Near $p = 0.5$ we find a very long lived transient, which tends to become a power law decay, in line with the critical slowing down near a second order phase transition [36]. In this sense, one consider the stationary distribution at finite lifespans (fig. 1) as the equivalent of finite size effects near a continuous phase transition.

**B. Individual scoring model**

It is equally or more consistent with existing field data to assume that each bird makes all choices according to its own experiences. This requires to modify the scoring assigned to the strategies not followed by each bird, defined in table II. The simplest choice is to assume that, when unsuccessful (predated), the bird assigns to the

FIG. 1: Results for $m = 2$, $s = 5$, $N = 1000$ and $v = 9$. Top, temporal evolution of the model for different predation pressures, from $t = 1$ to $t = 16384$, Bottom, distribution of colony sizes for the same temporal evolution.

FIG. 2: Results for $m = 2$, $s = 5$, $N = 10000$ and $v \to \infty$. Top, temporal evolution of the model for predation pressures for different predation pressures, from $t = 1$ to $t = 16384$. Bottom, distribution of colony sizes for the same temporal evolution. Note the change in the range of values of $p$ studied with respect to those shown in fig. 1.
Choice & Success & $\Delta_i$ & $\Delta_v$ \\ Individual & Predated & 0 & 1 \\ & Not Predated & 2 & 0 \\ Colonial & Predated & 2 & 0 \\ & Not Predated & 0 & 1 \\

TABLE III: Scoring in a Individual Model. $\Delta_i$ is the increase on the score of a strategy that gives an individual outcome and $\Delta_v$ is the increase on the score of a strategy that gives a colonial outcome.

strategies leading to the option not followed the score corresponding to the benefit of that behavior in the absence of predation, as shown in table III. A bird who made a successful choice (not predated), updates only the scores of those strategies which lead to that choice. Finally, we assume that the predation pressure is not the same for all colonial birds, as they form colonies of different sizes. In order to take this into account, we distribute the colonial birds into colonies which sizes follow a power law distribution. The number of colonies of size $w$ is proportional to $w^{-1}$. This is the expected behavior if the relative fluctuation of colony sizes is random. The distribution is normalized to the number of colonial birds.

At each time step, which corresponds to one breeding season, there is a finite probability $p$ that a nest will be predated. Unless otherwise stated, the predation probability, $p$ is constant in time, though the inclusion of variable probability does not change the results qualitatively.

As in the previous case, individual strategies, when successful, obtain a larger score than colonial strategies (2 vs. 1), reflecting the innate (or genetic) preference of successful, obtain a larger score than colonial strategies (2 vs. 1), reflecting the innate (or genetic) preference of birds to individual breeding in the absence of predation.

We have studied the temporal evolution of the number (or frequency) of colonial breeders, for different values of $n$, $s$ and $v$, performing simulations for each combination of these three parameters from $p = 0.01$ to $p = 0.99$. In fig. 3 we can observe that the qualitative features are equivalent for $v = 3$ and $v = 15$, however with longer lifespan, birds can learn more, and therefore the adaptation process is clearer for $v = 15$. These results are in agreement with field studies [18].

### C. Modelling colony distributions

Finally, we will consider explicitly the influence of the colony size distribution, which is not taken as given. We start with a population of individual birds, $n_b$, distributed among $n_s$ sites, where $n_b \ll n_s$. Birds have two possible strategies or behaviors, individual or colonial, which have a score which reflects the reproductive success that a bird would have if it would have followed it. Note that we do not make use here of the set of the strategies of the MG (such as in table II), but only these two strategies, as well as the information of the previous time step. These birds are predated, and use scoring rules similar to those described in the previous subsection, and given in table II. Birds which, at a given time step, choose to follow colonial behavior, join an existing colony. At the beginning, as no colonies still exist, birds which acquire this behavior are paired among them. A given colonial bird has the same probability of joining any one of the existing colonies [37]. Otherwise the bird (couple) nests in one of the available empty sites. When the score of a bird is taken to zero, the (new) bird has an innate tendency towards individual behavior. Finally, and guided by field observations, we have considered the case where birds make new choices every season, and the case where birds which have not been predated repeat the previous choice, and only consider their possible choices if they have been predated.

The model leads to different colony distributions. In general, after some transients, large colonies appear and grow indefinitely, leading to distributions skewed towards large sizes. In this respect, the model differs from the two cases considered previously. In the model discussed in III A, the growth of large colonies was arrested because birds were able to appraise the collective performance of colonial birds. For the individual model in III B, we assumed a fixed distribution of possible colony sizes. By combining an individual scoring procedure and not imposing constraints on the distribution of colony sizes, we find that the average size drifts towards large values, induced by the dilution of predation pressure for large colonies.

This tendency towards large colony sizes, for arbitrar-
FIG. 4: Fit to the average colony distribution for a population of approximately 300 couples of lesser kestrel in Los Monegros (Spain) [18]. The number of couples is 300, and the number of available sites where colonies can be formed is 15000. The predation pressure is $p = 0.08$, and there is a finite probability of catastrophic events, $p_{\text{cat}} = 0.01$, which limits the maximum colony size to $\sim 100$.

FIG. 5: Colony distributions obtained for a population of 3000 couples, and $p = 0.06$, left, $p = 0.08$, center, and $p = 0.10$, right.

fily small predation may help to explain the existence today of species which form very large colonies, like penguins and other sea birds. In many cases, however, there is an upper limit to the maximum size that a colony can have, because of the different disadvantageous effects of colonies, such as parasitism, transmission of diseases, lack of food on the vicinity of the colony and the attraction of big predators to big colonies. We have incorporated this possibility by assuming that there are catastrophic events which act on all members of a colony, and which probability increases with the size of the colony. Similar effects are obtained if the probability of predation includes the possibility that there are events where a whole colony is predated.

The present model, including (few) catastrophic events which limit the maximum colony size, allows us to fit observed colony distributions [18]. A fit to results for colonies of lesser kestrels in Los Monegros (Spain) is shown in figure 4. The predation pressure is $p = 0.08$, the average lifetime is $v = 5$, and the ratio between the success of individual birds and colonial birds, in the absence of predation, is $\Delta_i/\Delta_c = 2$. We also assume a catastrophic predation $p_{\text{cat}} = 0.01$. This implies that colonies cannot grow to sizes much larger than 100.

When we introduce an upper cutoff the maximum colony size, the numerical results are very suggestive of a rounded second order phase transition, as in the cases discussed in [II A] and [II B]. We find a regime where most birds choose individual strategies, for low predation pressure, and a regime where most birds form colonies. The main difference with the previous cases is that the critical predation pressure, $p_c$, at which this transition takes place, is now lower. Our results suggest that, in the present case, $p_c \approx 0.08$. This reduction in the value of $p_c$ is consistent with the enhanced tendency towards coloniality in this version of the model. The evolution towards a stationary state is very slow, and, for the parameters used, at least $10^3$ time steps are required.

It is interesting to note that the best value of $p$ which fits the observed broad distribution of colony sizes is close to the critical value which separates the two regimes described earlier. This is best appreciated in fig. 5, where we have repeated the calculations which lead to fig. 4, $p = 0.08$, and also $p = 0.06$ and $p = 0.10$, for a population of 3000 birds, and leaving all other parameters unchanged. These results suggest that the assumption of a power law distribution of colony sizes, made in [II A] and [II B] is consistent.

IV. CONCLUSIONS.

Our results suggest that colonial behavior can arise as a natural response to predation pressure. Note that we made a number of conservative assumptions, in order to avoid any bias towards colonial behavior: i) The birds have an innate tendency towards preferring individual nests, ii) The only protection provided by the colony
is the dilution effect, iii) The distribution of colonies is such that small colonies are more abundant, and, in some variations of the model, iv) predation pressure fluctuates strongly from year to year, allowing for the existence of periods of low predation.

The number of colonial birds increases with increasing lifespan, as birds accumulate experience for a longer period. This evidence is in agreement with the observation that birds make use of their long term breeding experiences [38, 39, 40, 41].

The models used here are inspired in the minority game model, and use similar definitions of allowed choices and strategies. On the other hand, agents use their individual experiences in order to update the scores of the different strategies, and the payoffs are related to a random event, the chance of being predated.

Our results suggest that simple mathematical models of predation pressure on colonial birds can lead to a dynamical phase transition, in which a majority of birds change from colonial to individual breeding behavior. This transition is smoothed due to the finite lifespan of the birds, which limits the ability to learn new behaviors. Note, however, that the models used in the present work cannot be expressed in terms of the minimization of a benefit function.

Finally, it is intriguing that field observations [13] can be fitted by the model in [11] by tuning the parameters to be close to the critical point discussed above, suggesting some kind of self critical organization [42].

V. ACKNOWLEDGEMENTS.

We are thankful to F. Hiraldo, J. A. Donázar, M. G. Forero, J. Cartwright, J. M. García Ruiz and F. Otálor for helpful discussions. We acknowledge financial support from grants PB96-0875 (MCyT, Spain), 07N/0045/98 (C. Madrid), and Caja de Ahorros de Granada “La General”.

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