

# Sociability leads to instability: A metapopulation model for colonial species

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# 1 Abstract

We present a stochastic metapopulation model for a seasonal colonially breeding species. A key component of the model is the development, at the beginning of each breeding season, of a set of breeding colonies, based on sequential choices by individuals about where to nest. Individuals favor the colony they nested in previously, but are also attracted to colonies that are rapidly establishing, and may switch locations. This positive feedback process destabilises the population dynamics at each location. As a result, a small degree of stochasticity is enough to produce complex population dynamics with frequent “switching cascades” — mass movement of individuals between locations from one breeding season to the next. These dynamics are similar to observed population dynamics from a set of heron and egret breeding colonies in New York Harbor. We discuss the ability of simple, but non-random movement behaviors to dramatically alter the predictions of spatio-temporal models in ecology.

# 2 Introduction

Models of spatiotemporal ecological dynamics must assume something about how organisms move. Most classic models assume, for simplicity, that movement is random in terms of both initiation (e.g., density-independent dispersal), initial or sustained direction (e.g., a random walk), or both (e.g., diffusion models). The first assumption is only appropriate for organisms that are either unable to perceive their surroundings and act upon that information, or that are affected by an external force with a high random component, such as wind. The second assumption may be appropriate if an organism moves: a) passively in response to an external force which varies randomly over time (again, such as wind), b) under its own power but with little control of direction, or c) under its own power and control, but using a random or quasi-random search strategy for a resource because of an

inability to perceive it from a distance.

Obviously, these assumptions fail for many species, including many invertebrates and almost all vertebrates. The navigation abilities of honeybees are well known (see, e.g., Riley 2003; Collet 2006), and even butterflies, whose flight itself can be modelled as a random walk, are making sensible decisions about when to leave a resource patch (Ovaskainen 2004, Hanski *et al.* 2006). Many species of fish, birds and mammals are even more capable. Density-dependent dispersal is another form of goal driven movement, where individuals choose to move into, or out of, areas of high population density. Theoretical studies have shown that these choices very often have fitness benefits, and therefore the ability to make them is likely to evolve (e.g., Travis *et al.* 1999).

An important question, then, is whether such non-random movement significantly alters the behavior of spatio-temporal models. In many cases it does; see Bowler and Benton (2005) for a review of both empirical and theoretical studies. For example, simple metapopulation models assume random dispersal between patches, which has the effect of stabilizing the system as a whole and permitting long-term persistence (Levins 1969, 1970). Sæther *et al.* (1999) showed that density-dependent migration can strongly alter this outcome. In particular, they showed that in presence-absence models, if emigration rate decreases or immigration rate increases with patch density (as in a colonial species), habitat occupancies are reduced compared to a model of random dispersal, and the range of habitat occupancies in which the metapopulation is viable is also smaller. In other words, this combination of density-dependent strategies destabilized the metapopulation. In another example, Russell *et al.* (2006) analysed data on the community dynamics of breeding bird populations on a set of British and Irish islands, and found that some aspects of the system were better explained by the behavioral-based assumptions of optimal foraging, rather than traditional island biogeography. In that case, invocation of choice-based dispersal didn't just explain why the predictions of a model might be incorrect, but suggested a shift from one modeling framework to another.

The present study addresses the metapopulation concept, and was inspired by the dynamics of colonially-nesting heron and egret species in both South Florida and the New York/New Jersey Harbor (NYNJH). Breeding activity in such species is typically distributed across a number of discrete colonies, which can number anywhere from a few to many thousands of nests, depending on the species and the location. A striking characteristic of these colonies is that the number of active nests at any one colony typically fluctuates dramatically from year to year (or even within years). In NYNJH, some colonies have transitioned from being completely unoccupied to hosting over 100 nests in the span of just a few years (Figure 1 — e.g., Kerlinger 2004). In Florida, where colonies are much larger on average, the fluctuations are even more dramatic (Ogden 1994; Russell, unpubl. data). They are much too large to be explained by the processes of birth and death alone, and it is clear, even without marking data, that birds must be switching nesting sites from one breeding season to the next. The Florida system therefore functions as a metapopulation in the general sense (Harrison 1994; Harrison and Taylor 1997). In New York Harbor the maximum recorded colony sizes are much smaller overall, but their dynamics are nevertheless similar, and with the insight provided by the Florida birds, we hypothesise that the NYNJH colonies also function as a metapopulation.

To test this idea, we construct a general stochastic metapopulation model for a colonially breeding species that assumes individuals have the ability to assess a set of possible locations, and choose the ‘best’ one according to simple criteria relating to site fidelity and existing colony size. We show that this simple behavior dramatically affects the dynamics of the model, with a wide variety of possible behaviors that include frequent, dramatic movements of birds from one location to another. We show that there is a good match between the model’s output and census data from the NYNJH colonies described above.

## 3 Material and methods

### 3.1 The model

We constructed a general, stochastic model of a species that breeds colonially, with colonies occupying any subset of a limited number  $P$  of discrete patches. Our model consists of two parts: a submodel of the colony development process (which is where the behavioral element is incorporated) and a submodel of straightforward demographic processes (birth, death, aging). The model is a discrete-time model, with time steps representing sequential breeding seasons. At each step, the colony development process occurs first, and once all individuals are assigned to colonies, only then do demographic activities take place (Figure 2).

Our model shares a number of similarities with one created by Johst and Brandl (1997), who modeled colonies of Black-headed Gull (*Larus ridibundus*). The gull colony dynamics were qualitatively similar to those of the NYNJH heron colonies, but their model differed in a number of details, and we will show that our model actually reproduces their data better than their own model does.

We follow the standard, simplifying convention of modeling individuals, rather than pairs. In demographic models for species with equal sex ratios (as is the case here) it is standard to model females, on the assumption that males represent an unseen population that simply doubles the population sizes. Females are conventionally chosen because they are the ones that actually produce offspring, but in simple models the choice of which sex to model is mathematically irrelevant. In the present case the other component of our model, colony development, arises specifically from the actions of males, as it is males that initiate nest building. In practice it does not matter whether we consider our individuals to be males, females, or ‘pairs.’

## 3.2 Colony development

We assume that colonies develop progressively as individuals arrive one at a time in the general breeding area, and choose a location to breed. Thus the submodel consists of a simulation loop where each iteration describes the arrival and decision of a new individual, and updates one of the colony sizes  $N_1, N_2, \dots, N_P$  by one. The order in which individuals arrive is random, and this represents one of two sources of stochasticity in our model (and the only one that is always present). Each individual chooses a site based on two pieces of information: the site at which it bred (or simply existed without breeding) in the previous season, and the current colony sizes at the various sites (the  $N_i$ ). Each of these contributes to the relative ‘attractiveness’ of each site. The attractiveness based on site fidelity is modeled as a scalar,  $H_i$ , which takes the following values:

$$H_i = \begin{cases} 2 & \text{Nested at patch } i \text{ in previous season} \\ 1.1 & \text{Roosted at patch } i \text{ in previous season (no breeding)} \\ 1 & \text{Roosted or nested elsewhere} \end{cases} \quad (1)$$

The “no previous breeding” option applies to birds that are in their third year of life, which is the age of first breeding. It would also apply to birds that are unable to find a breeding location because all locations are full, but in practice this never occurs because, in keeping with the data, we impose a global limit in the number of breeding pairs that is less than the total capacity of the locations (see Demography below).

The attractiveness based on density is incorporated as the product of two functions that represent an inevitable trade-off:  $d(N_i) = c(N_i) l(N_i)$ . The key component of the model is that individuals like to nest together, so we use a simple, linear attractiveness function,  $c(N_i) = \beta_0 + \beta_1 N_i$ , to represent colonial habit — the more birds already present, the more attractive the location. However, any location must have some kind of carrying capacity for nests, which we can model with a standard density dependence function. For species with fixed territory size (e.g., those which forage within their territory), new nesting locations will be easily available until the site is full, whereupon they will not be available

at all without the significant effort of ejecting a resident — a step-type function. Our model species — egrets and herons — do not forage directly in their nesting colonies, and so territoriality is more flexible and restricted to the immediate space around each nest. We therefore use a theta-logistic function  $l(N_i) = 1 - (N_i/K_i)^{\theta_C}$  with  $\theta_C > 1$  to provide an intermediate functional form between linear density dependence (appropriate for competition for resources) and a step-type function (appropriate for fixed territory size). The product of the two colony size functions is unimodal, with a peak somewhat to the left of the ‘nest capacity’  $K_i$  of each site (Figure 3). In other words, the most attractive colony size at a given location for an incoming bird is one that has as many birds as possible while still leaving space to build another nest. The overall product of the fidelity and density attractiveness values generates an overall attractiveness value  $A_i$  for each site

$$A_i = H_i d(N_i). \quad (2)$$

After calculating the attractiveness of each location to a given arriving individual, we then assign that individual to a patch. This where the second source of stochasticity in our model comes in. We assign the individual probabilistically, with the probability of choosing a particular site proportional to its attractiveness function raised to the power  $s$ . The variable  $s$  therefore determines the overall ability of the bird to both evaluate the locations and choose the best one. When  $s = 0$ , all sites appear equally attractive, and a location is therefore chosen at random. When  $s = 1$ , the probability of a site being picked is directly proportional to its attractiveness, meaning the the best location is more likely to be picked than any other, but that likelihood may still be low (especially if there are many other locations). This represents a moderate ability to choose. As  $s \rightarrow \infty$  (in practice,  $s > \sim 8$ ) the individual tends to always pick the best location. In the rare event of an exact tie, the location is chosen at random from the set of ‘best’ locations. Thus  $s$  lets us introduce the key behavioral trait of these species at any level of ability we choose.

### 3.3 Demography

A striking characteristic of the NYNJH data is that only a fraction of the locations which have ever contained colonies are occupied in any given year — often less than half. This implies either a combination of high extinction and low colonization rates, or some limit to the overall number of nesting pairs other than the total number of available nest sites. While a key feature of the data is indeed the rapid collapse of local populations, often to zero, the fact that this is caused by the wholesale movement (rather than death) of individuals implies that the colonization rate is also high, and that the existence of many ‘empty’ sites is therefore due, at least in part, to a global limit on the number of breeding pairs  $K_G$ , where  $K_G < \sum K_i$ . We suspect that for the NYNJH birds, this limit is food quality and/or availability. Many of these birds are believed to forage in the NJ Meadowlands (Nagy 2005), which is a highly altered ecosystem containing large amounts of toxic chemicals, some of which enter the food chain (see Kiviat and MacDonald 2002 for a review), although the cause of the limit does not affect the model.

The demographic submodel is simple. Once the colonies have formed, individuals are born by assigning a Poisson-distributed number of offspring to each individual.  $\lambda$ , the parameter of the Poisson distribution, is the same for all individuals in a season, and is given by a second theta-logistic density-dependence function  $\lambda = r(1 - \sum N_i/K_G)^{\theta_G}$ , where  $\sum N_i$  is the total number of individuals,  $K_G$  is the global carrying capacity for breeding pairs, and  $r$  is the maximum reproductive rate. On the assumption that the global limit is a result of competition for food, we use  $\theta_G = 1$ . Following births, individuals die with probability  $d$ , except those that have reached the age of 15, which always die. Finally, individuals are ‘aged’ one year.



### 3.4 Model exploration

For this paper, we ran our models for anywhere from 300 to 1000 breeding seasons, depending on the kind of data required. Each model was initialised with the same, plausible age distribution (an exponential decay across age classes 0–15) and an even distribution across sites. Model behavior was insensitive to these starting conditions, and settled down into self-consistent behavior after just a few seasons. We ran two kinds of models. The first had five locations, all with equal nesting capacity  $K_i$  of 50 nests (250 nests in total). This model was used to explore the effect of various parameters, such as the global carrying capacity  $K_G$  and the ability to choose  $s$ , on the dynamics of the model. The other kind of model had sixteen locations whose nesting capacities were based on the maximum observed nesting populations of great egrets from the sixteen locations in the NY dataset. This model had a global capacity taken as the maximum observed total number of nests in the data.

In addition to the  $K_i$  values described above, we used the following set of parameters except where noted:  $\theta_C = 2.2, \theta_G = 1.0, \beta_0 = 0.1, \beta_1 = 0.009, K_G = 140, s = 5, r = 0.5, d = 0.1$ . We mainly explored the effect of varying  $s$  and  $K_G$  on the model's dynamics.

## 4 Results

### 4.1 The effect of the ability to choose

The parameter  $s$  determines the ability of the birds to select the best location for breeding. Figure 4 shows a range of dynamics. When  $s \leq 1$ , birds are choosing sites almost at random, and the timeseries of population densities for each site therefore resembles white noise. As  $s$  increases, the amplitude of the dynamics also increases, and structure begins to emerge. At  $s = 4$ , we see the emergence of a bimodal distribution of population densities, with three sites typically having densities near their nesting capacities and three being empty or almost

empty. However, the identity of the ‘full’ sites changes frequently, with dramatic population booms and busts in which large numbers of birds switch from one site to another. We call these ‘switching cascades,’ and they are a key feature of the real world dynamics of heron colonies (and gull colonies — see Johst and Brandl 1997).

To explore the interaction of individual movements and site dynamics, we ran a series of ten 1000-year simulations for a sequence of values of  $s$ , and for each simulation we calculated the mean fraction of individuals switching locations in each year, and also the rate of switching cascades. (We defined a cascade as any sequence of population sizes that progressed from the top 25% of all recorded population sizes to the bottom 15%, or vice versa. The rate is the total number of such progressions in the simulation divided by its length, and the result is then divided by two to account for the fact that every bust is accompanied by a boom, creating a single ‘switch’.) Figures 5A and 5C show the mean and 95% interval for the ten simulations at each value of  $s$ .

The overall rate of location switching is clearly greatest when birds have no ability to value sites, as there is consequently no site fidelity (Figure 5A). In the limit, with five sites chosen at random, birds will switch in four out of every five years on average. This fraction decreases sigmoidally as choosing ability increases, to a minimum value close to 0.1. Even with  $s = \infty$ , there is always some degree of movement. In large part this is due to young birds (ages 0–2), which have low site fidelity and are much more likely to switch from the site in which they were previously merely roosting.

The rate of switching cascades, by contrast, is strongly unimodal, with a peak around  $s = 3$  (Figure 5C). Detailed examination of many colony development histories shows that this peak represents an interaction between the positive feedback of the choosing process (birds are attracted to sites that already filling up) and the randomness introduced by the occasional sub-optimal decision by individual birds. For example, early in the colony development cycle, when few birds have arrived, one or two ‘mistakes’ can cause a previously

almost-empty site to gain a small colony that is enough to make it the most attractive. Subsequent birds have enough choosing ability to switch to this colony, and the more it grows, the more attractive it becomes (until it fills up). But when  $s$  is very large, the initial mistakes become less frequent, and the rate of large-scale switching drops again.

## 4.2 The effect of the global carrying capacity

An intermediate level of choosing ability is necessary, but not sufficient, for complex dynamics with frequent switching cascades. For the model with equal site carrying capacities, the dynamics also depend crucially on the global carrying capacity. Figures ?? and 5B and D show that both the rate of individual switching and the rate of switching cascades is periodic with respect to  $K_G$ . In fact, the rate of switching cascades is maximized when the global carrying capacity is approximately  $n.7 \times K_i$ , where  $n = 1, 2, \dots$  etc. When  $K_G$  is an integer multiple of the (identical in this case)  $K_i$ , then one, two, three, etc. sites are almost completely full all the time, and the remainder almost completely empty, a condition which is not favorable to the series of ‘mistakes’ (see above) necessary to produce a switching cascade. At intermediate values of  $K_G$ , the constant presence of at least one site which is partly full promotes the frequent switching of dominance.

## 4.3 Matching the data

Having shown that simple colonial behavior can, under the right circumstances, give rise to complex dynamics with rapid switching cascades, we return to the data on heron nesting colonies in the New York/New Jersey Harbor to see if our model can match those data more precisely. To do this, we ran the model with sixteen locations, and gave each location a different carrying capacity based on the maximum observed colony size for a particular species on each of the sixteen islands in our dataset. We assigned our  $K_i$  as the observed maximum multiplied by 1.2, because the optimal attractiveness for a colony is somewhat

below its theoretical capacity, as shown in Figure 3 and borne out by the simulations. We chose the global carrying capacity as the maximum total number of nests (including all colonies) across all years. In the absence of data on growth rates and choosing ability, we ran the model with a variety of values of  $r$  and  $s$ , to see whether a particular combination would produce dynamics similar to those observed.

We present results for two species, plotting the same span of time for the model and the data (25 years). Figures 6A and 6AB show the data for Great Egret, plus one run of the model with  $s = 2.5$  and  $r = 2.5$ . With the obvious difference that the data show an overall population increase from 1982, the dynamics are qualitatively very similar, with both the data and model showing rapid declines and expansions over a timescale of 2–3 years, as well as more gradual changes. The maximum population sizes achieved by the various model colonies are also very similar to their counterparts in the data.

Figures 6C and 6D show the same for the more abundant Black-crowned Night Heron (*Nycticorax nycticorax*), with  $s = 2.5$  and  $r = 1.5$ . In this case, the match is not so good. In particular, the highest carrying capacity (574 nests) is 45% larger than the next highest (396 nests), and in most simulations this population persists for long periods at a fairly stable level of  $\sim 500$  nests. As the example shows, the population can still crash, but it rarely shows the yearly fluctuations seen in the data. Almost certainly these are the result of environmental stochasticity, which does not appear in the model.

## 5 Discussion

Our simulations clearly validate the main hypothesis of this paper, which is that simple colonial behavior, implemented as a positive feedback process, can dramatically alter the dynamics of a metapopulation model by amplifying minor stochastic variation into large-scale population instability. They also show that such behavior could potentially explain a large

part, if not all, of the observed dynamics of a number of the heron and egret species nesting in one particular system. At a larger scale, we have provided another example of the more general conjecture (see Introduction) that even well-studied spatial-temporal models in ecology are highly sensitive to assumptions about individual behavior, and may give substantially incorrect predictions when applied to organisms capable of directed movement and at least a moderate level of decision-making ability.

For the herons and egrets of the New York/New Jersey Harbor, the practical consequences of this finding should be a renewed focus on the complete system of colonies. As this article is being written, a number of locations which supported large colonies in the past (Parsons 1994) have been empty for one or more years. A number of concerned organisations and individuals have put forward hypotheses as to the cause of specific colony collapses, including the introduction of predators (e.g., racoons, rats), disturbance by human visitors, or vegetation changes caused by invasive species such as Japanese Honeysuckle (*Lonicera japonica*) or Asiatic Bittersweet (*Celastrus orbiculatus*) (pers. obs.). While it is indeed possible that such disturbances played a role, our model shows that they are not necessary — the drastic declines could be caused entirely by the intrinsic dynamics of the colonies. This is not a trivial point; if specific disturbances are at fault, then a location may be regarded as unsuitable until some form of remediation takes place. Such efforts are typically expensive and time-consuming, and clearly a waste if they occur unnecessarily. On the other hand, if they don't occur, the location may be 'written off' as unsalvageable, and other genuine disturbances (such as development) allowed. Our model implies that sort-term absences of a few years are not, *in themselves*, cause for alarm or immediate action.

These issues came to prominence recently when the invasive Asian Long-horned Beetle *Anoplophora glabripennis* (ALB) was found on Prall's Island, located in the Arthur Kill which separates Staten Island and New Jersey. Prall's has been unoccupied by nesting colonies since 2003 but once was home to large colonies of Great Egrets, with various other species also present (Parsons 1994). The USDA, in cooperation with the New York City

Department of Parks and Recreation, quickly implemented their quarantine plan. This involved clear-cutting all the trees in a 0.5km radius around the infestation site — a loss of approximately 3000 trees on the island itself and 8000 on neighboring Staten Island. Many of these trees were of species, such as Gray Birch (*Betula populifolia*), that had previously hosted nests, with the result that Prall’s island has effectively been eliminated as a colony site. At a recent meeting between stakeholders and the USDA to discuss the potential impact of ALB on the heron and egret colonies in this area, the possibility was raised of preventative measures — such as pesticide application — for sensitive sites such as the colonies. What our model shows is that important sites are not restricted to those currently occupied by birds.

Our model does fail to capture key aspects of the data for certain species (see Figures 6C and 6D), and the most obvious omission is environmental variability in either or both of the nesting capacities of the sites (which reflect local disturbance and can vary independently), and the global capacity (which should cause synchronized fluctuations across locations). Another possibility is that larger breeding colonies progressively reduce the quality of the very vegetation on which they depend (Lemmon *et al.* 1994; Ellis 2005). Such variability, or time-delayed site quality effects, could easily be added to the model, but before making it more complex, the next step should be to examine whether the hypothesised underlying switching behavior actually occurs. If we were able to track the movements of a reasonable sample of the overall population on a daily basis, then over the course of a few breeding seasons we would obtain rates of movement between locations, as well as the timings of those movements in the context of the colony development process. These could be compared to the model output, which predicts, among other things, that individual switches, especially to a previously unoccupied site (‘mistakes’), should be more common early in the colony development process and for young birds. A good match between model and data would further support the behavioral hypothesis, and justify further development of the model for this particular system.

Intriguingly, the technology to collect such data (e.g., programmable, ID-coded radio tags and detectors) is now in the marketplace and becoming less expensive. We foresee an explosion of studies that collect detailed data on organism movements, thereby shedding new light on some of the fundamental principles of spatial ecology.

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## 8 Figures

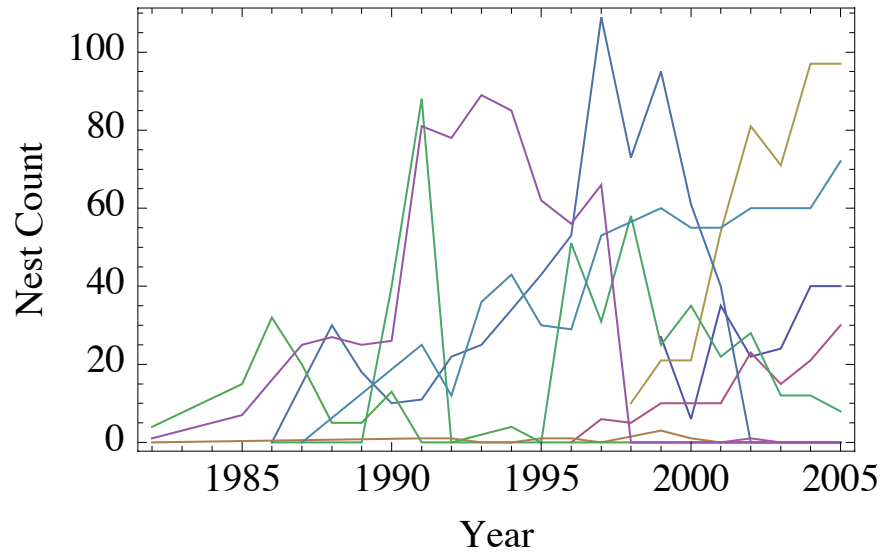


Figure 1: Number of nests of Great Egrets (*Casmerodius alba*) on various islands in New York Harbor and Long Island Sound. Colors represent different islands.

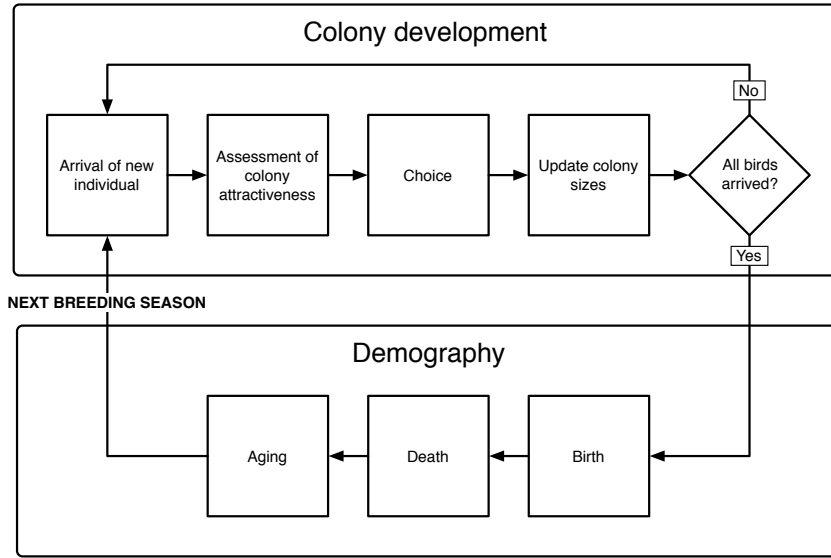


Figure 2: Components of the model.

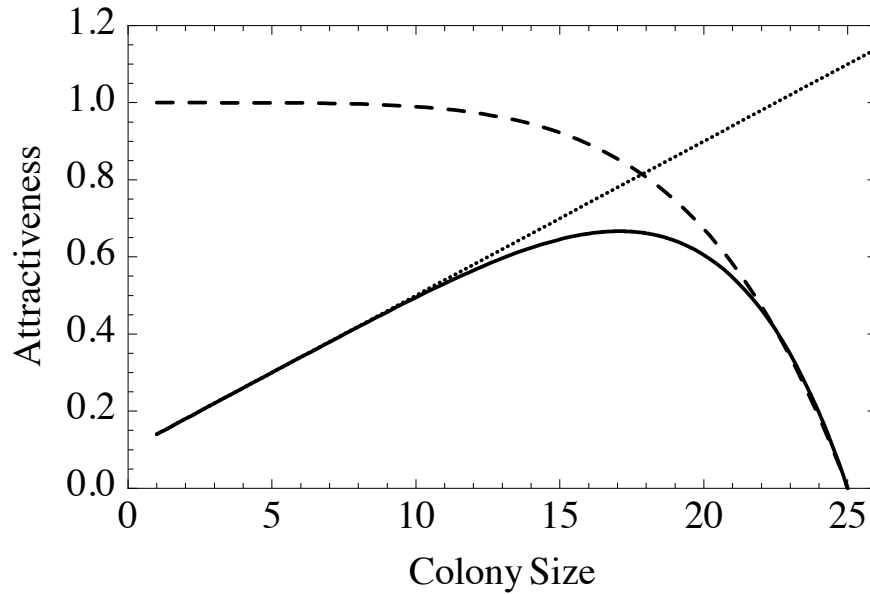


Figure 3: The attractiveness of a location ( $d(N_i)$ , black line) to an arriving individual as a function of the current colony size at that location. It is the product of the attractiveness based on colonial attraction ( $c(N_i)$ , dotted line) and the attractiveness based on space availability ( $l(N_i)$ , dashed line).

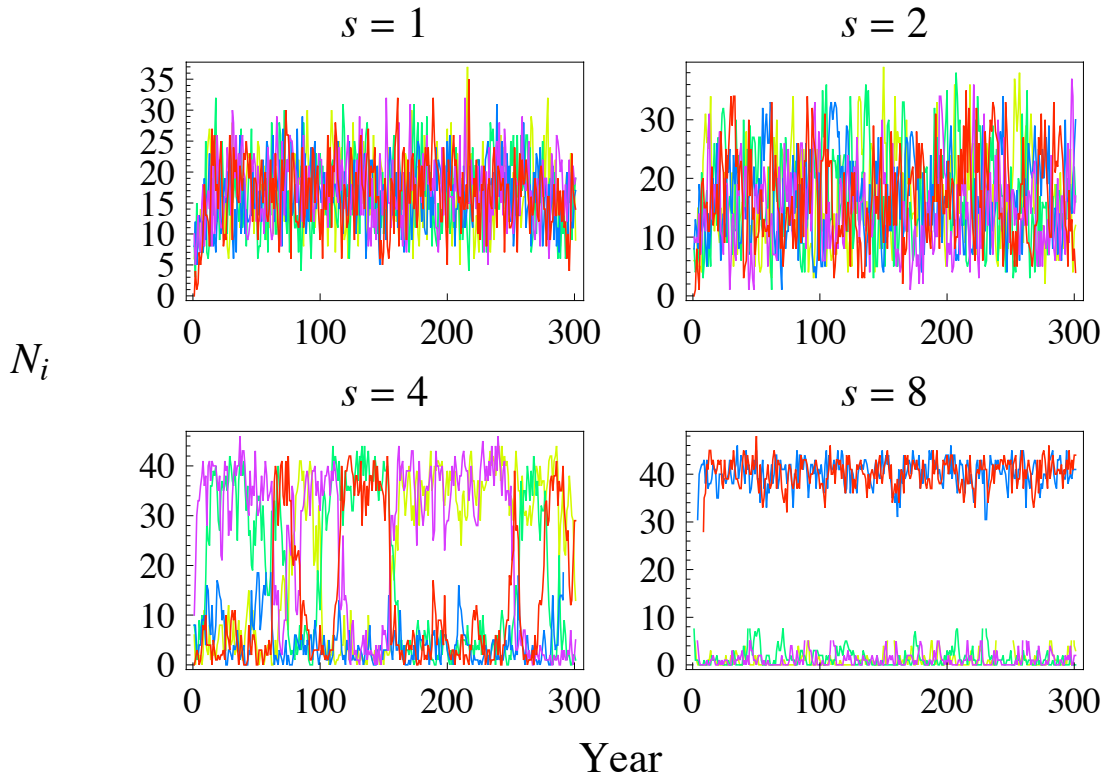


Figure 4: Varying  $s$ , the ability to choose, in the ‘five equal-capacity locations’ model produces a variety of dynamics from white noise through complex dominance-switching to complete dominance by a subset of locations.

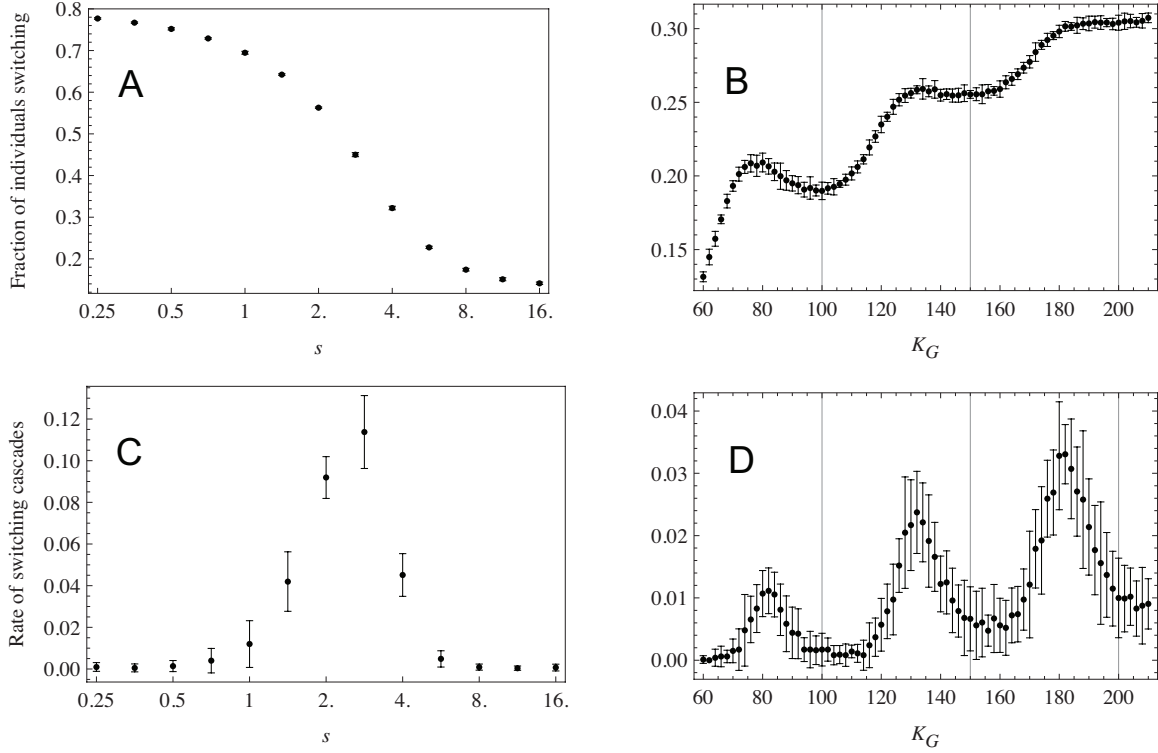


Figure 5: Increased choosing ability  $s$  reduces the rate of site switching by individuals (A), but intermediate levels of choosing ability cause the maximum rate of large-scale switching cascades that alter the set of ‘full’ patches (C). The rate of both individual switching and switching cascades is periodic with respect to the global carrying capacity  $K_G$  (B and D). Vertical lines indicate integer multiples of the site capacity ( $K_i = 50$  for all  $i$ ). Each point is the mean of ten simulations of 1000 seasons; error bars indicate 95% bounds.

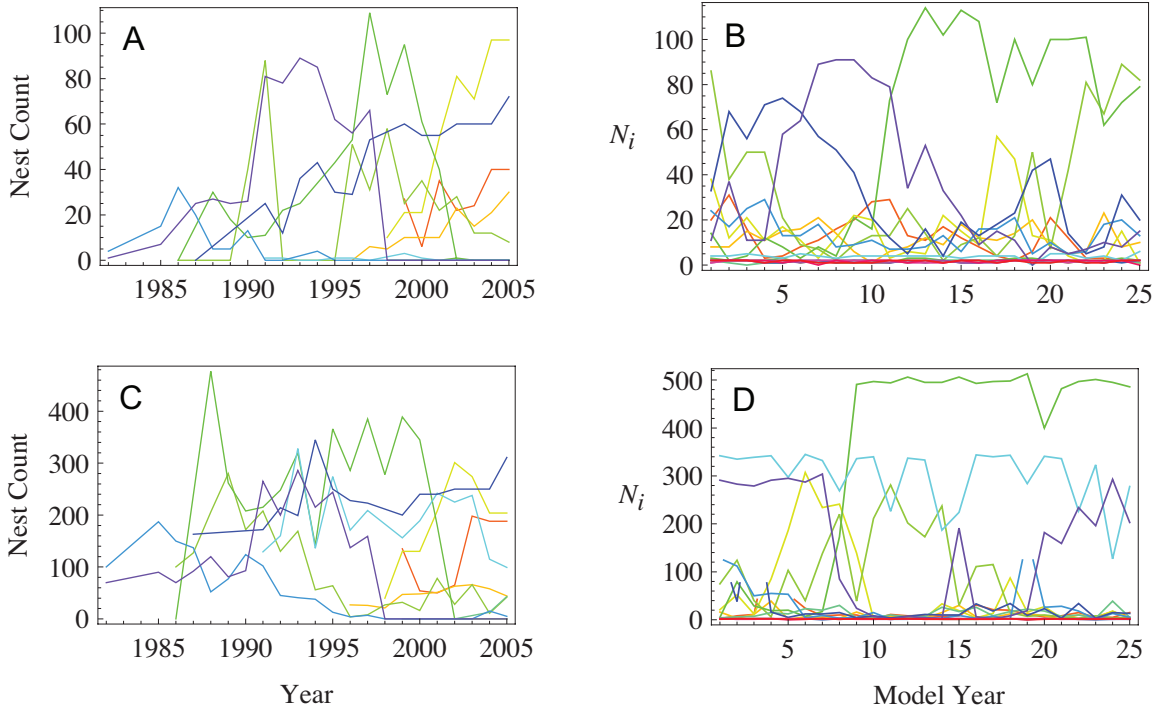


Figure 6: A comparison of the observed nesting populations of Great Egrets (A) and Black-crowned Night Herons (C) with single runs of our stochastic simulation model with global and nesting capacities estimated from the data (B and D). Colors indicate corresponding locations between the simulations and the data. In terms of amplitude and frequency, the Great Egret simulations closely resemble the data. (Some locations with zero population size are not shown in the data plot.) The Black-crowned Night Heron simulations, however show long periods of dominance by the location with the highest nesting capacity, whereas the data show high-frequency fluctuations even of this colony, presumably attributable to external sources of variability not included in the model.