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Sociability leads to instability

Site-switching cascades in a colonial species

Gareth J. Russell · Abraham Rosales

Abstract We present a general stochastic model showing that colonial breeding can lead to complex multi-colony population dynamics when combined with nothing more than (inevitably) imperfect decision-making by individuals. In particular, frequent "switching cascades"—mass movement of individuals between locations from one breeding season to the next—arise naturally from our model, bringing into question the need to invoke a separate, fitness-based explanation for this commonly observed real-world phenomenon. A key component of the model is the development, at the beginning of each breeding season, of a set of colonies, based on sequential choices by individuals about where to breed. Individuals favor the colony they bred in previously, but are also attracted to colonies that are rapidly establishing, and may switch locations. This provides a positive feedback that leads to switching cascades. We examine the effect on the dynamics of individuals' access to (and ability to act on) information, as well as the overall size of the colony system and of individual colonies. We compare the model's dynamics to the observed population dynamics of a set of heron and egret breeding colonies in New York Harbor.

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Introduction

Models of spatio-temporal 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 passively in response to an external force which varies randomly over time (again, such as wind), under its own power but with little control of direction, or 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 are inappropriate for many species, including many invertebrates and almost all vertebrates. The navigation abilities of honeybees are well known (Riley et al. 1996; Collet et al. 2002), and even butterflies, whose flight itself can be modeled 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 the ability to make them is therefore likely to evolve (Travis et al. 1999).

In many cases, such non-random movement significantly alters the behavior of spatio-temporal systems [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), but density-dependent dispersal can strongly alter this outcome. In particular, 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 (Sæther et al. 1999). In other words, this combination of density-dependent strategies destabilizes the metapopulation. In another example, Russell et al. (2006) analyzed 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 behavorial-based assumptions of optimal foraging, rather than traditional island biogeography. In that case, invoking choice-based dispersal did not just explain why the predictions of a model might be incorrect, but suggested a shift from one modeling framework to another.

Colonial dynamics

The present study 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, separated from nearest neighbor colony sites by distances of 300 m to a few kilometers, and which can contain 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 (Fig. 1—e.g., Kerlinger 2004). In Florida, where colonies are much larger on average, the fluctuations are even more dramatic (Ogden 1994, Russell et al., unpubl. data). They are much too large
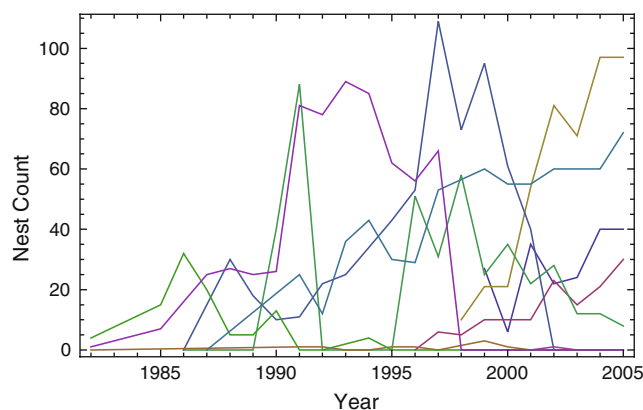
Fig. 1 Number of nests of Great Egrets (*Casmerodius alba*) on various islands in New York Habor and Long Island Sound. *Colors* represent different islands

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.

[Note that while such a system might be considered a metapopulation in a very general sense (Harrison 1994; Harrison and Taylor 1997), and other colonially nesting birds have been identified as having metapopulation structure (e.g., Feare and Lesperance 2002), the system we describe is far enough removed from the "classic" definition that we do not use the term here.]

Traditionally, there have been two explanations for large-scale site switching in colonial birds. In one scenario, a disturbance (often unobserved) to a site is assumed to have occurred, causing individuals to avoid that site en masse. Examples relevant to NYNJH include the introduction of a new nest predator (e.g., rats, racoons), or human activity. [Discussions about the state of the NYNJH colonies among stakeholders often include much speculation about disturbance (Russell, pers. obs.).] The other common explanation involves a negative association between site occupancy and quality. Substantial densities of individuals are assumed to gradually cause a decline in site quality, for example, by degradation of vegetation, or an increase in densities of predators or parasites. Large-scale switching might be a direct response to these environmental changes, or a more "programmed" response ("leave after x years") that has evolved due to fitness benefits (Lemmon et al. 1994; Ganter and Cooke 1998; Ellis 2005). Either way, evidence for this phenomenon is scarce and restricted to certain species known to have major impacts on the local environment.

In this paper, we demonstrate that neither explanation is *necessary*. We present a general stochastic model for a colonially breeding species, assuming only

that individuals have an imperfect 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. Our model does not invoke fitness, or incorporate evolution directly, assuming only that a tendency to breed colonially has evolved. The exact mechanism (e.g., predator avoidance) does not matter for our purposes: by avoiding an *additional* fitness-based mechanism for site switching, we seek to apply Occam's razor and make the simplest model that will explain the observations. This also makes our model more general, being potentially applicable wherever colonial behavior has arisen (and for whatever reason). This does not, of course, mean that there is *not* a fitness component to inter-colony movements in specific systems.

Material and methods

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 straight-forward 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 (Fig. 2).

Our model shares a number of similarities with the 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 our model actually reproduces their data better than their own model does (see "Discussion").

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."

Fig. 2 Components of the model
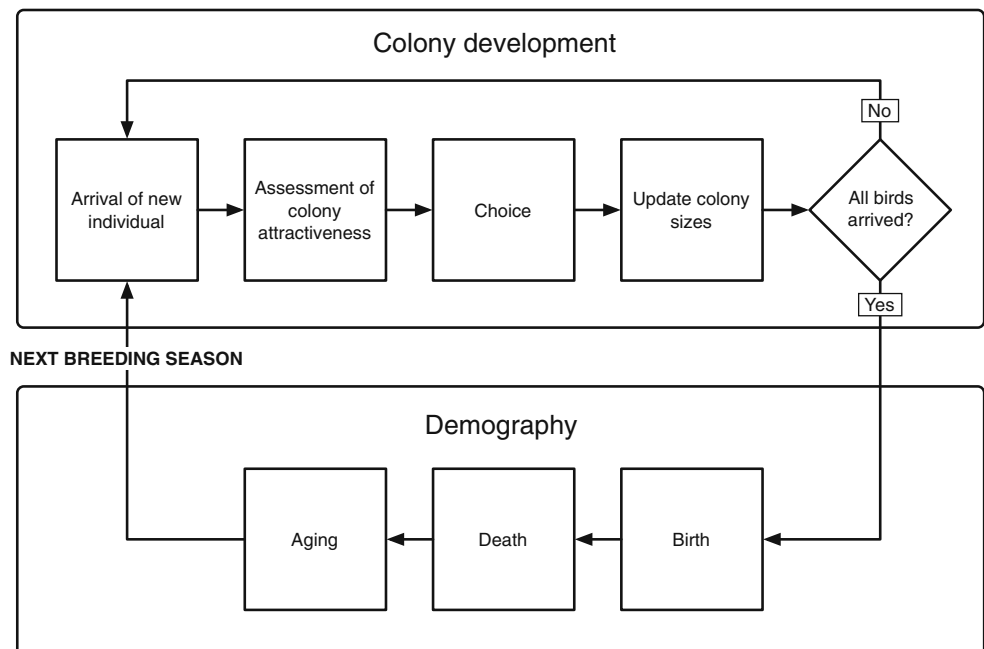
Colony development

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 $N_1, N_2, \ldots, N_P$ by one. The order in which individuals arrive is random, and this represents one of two sources of stochasticity in our model. 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:

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

The "no 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 $\theta_C = 2.2$ 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 (Fig. 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 is 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 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 $s \to \infty$ (in practice, $s > \sim 8$), the individual tends to always pick the best location. Thus, s scales the key behavioral trait
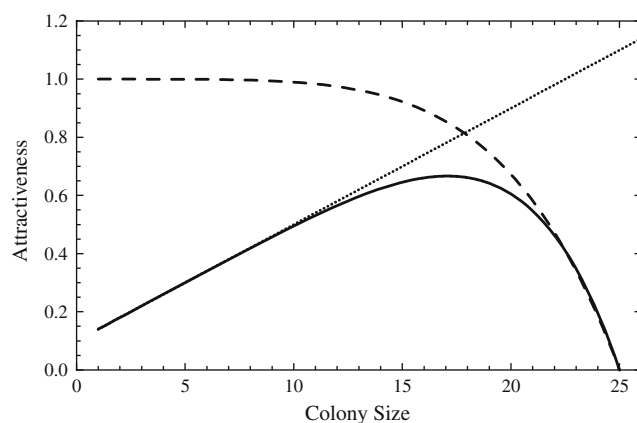
Fig. 3 The attractiveness of a location ($d(N_i)$, *black line*) to an arriving individual as a function of the current colony size at that location. It is the product of the attractiveness based on colonial attraction ($c(N_i)$, *dotted line*) and the attractiveness based on space availability ($l(N_i)$, *dashed line*)

of these species: the ability to evaluate and select a nesting site.

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 (Newman et al. 2004, 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. λ, 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 $d = 0.1$, except those that have reached the age of 15, which always die. Finally, individuals are "aged" 1 year.

Model exploration

We ran our model simulations from 20 to 1,000 breeding seasons, and with three to 1,000 replicates, depending on the kind of data required. Each simulation was initialized with the same, plausible age distribution (an exponential decay across age classes 0–15) and either an even distribution across sites, or a distribution based upon the observed data. Model behavior was insensitive to these starting conditions and settled down into self-consistent long-term behavior after just a few

seasons. We ran six variations on the basic model. The first two variants had five locations with identical per-site nesting capacities K_i of 50 (set 1) or 200 (set 2) and proportional global carrying capacities of $K_G = 140$ and 560, respectively. The third variant also had five locations, but with different per-site capacities of 10, 20, 40, 70, and 110 nests (mean = 50). These first three variants were used to explore how the model's dynamics are affected by overall system size, system heterogeneity, and by the ability to choose (s). The fourth set of simulations used the $K_i = 50$ set-up but varied K_G in small increments to examine its effect independent of the K_i.

The fifth and sixth variants had a number of parameters based on the data and were used to examine how closely the model's dynamics can resemble those of the real colonies. Because the model is stochastic, we cannot fit it directly to the observed abundances on each island. An alternative would be to attempt to match a macroscopic property of the data, such as the frequency of large-scale cascades, but alas the 21-year data record means that estimates of this frequency (on the order of one cascade per colony per decade) can only be approximate. Instead, we estimated some parameters based on observable properties of the data and chose arbitrary but plausible values for others, as described below.

For each species, we assigned our local K_i as the observed site maxima multiplied by 1.2, because the optimal attractiveness for a colony is somewhat below its theoretical capacity, as shown in Fig. 3 and borne out by the simulations. We chose the global carrying capacity as the maximum observed number of nests summed across all colonies. For the maximum population birth rate r, we used the intercept of a linear fit of $1 - N_{t+1}/N_t$ against "time since 1982," adding 0.1 to compensate for the death rate of 0.1. (For example, this produced estimates of $r = 0.66$ for Great Egret and $r = 0.43$ for Black-crowned Night Heron.) Finally we chose $s = 2.5$ for both species as being an intermediate value of the ability to choose (based on the earlier simulations—see Fig. 5). We initialized each model with the same initial population distribution across islands as seen in the data.

The fifth set of simulations was as described above, with just arrival order and decision-making stochasticity, and the sixth set added environmental stochasticity: each site's nesting capacity K_i varied from year to year as a random normal deviate with the same mean as the "site maximum $\times 1.2$" value used in the other simulations and a standard deviation set to be 30% of the mean. (This degree of stochasticity was determined by examining the size fluctuations of those colonies that

reached significant size and maintained it for several years, within the observed data.)

We ran the "data-based" simulations for all species, but for concision, we present results for just two—Great Egret and Black-crowned Night Heron (BCNH)—plotting the same span of time for the model and the data (21 years, corresponding to 1985–2005).

Results

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 time series of population densities for each site therefore resembles white noise, no matter what the capacities of the sites. Also, because the global carrying capacity is always substantially less than the total nest capacity, the sites in the "varying K_i" simulations host similar populations.

As s increases, the amplitude of the dynamics also increases, and structure begins to emerge. At $s = 4$ (for $K_i = 50$) and $s = 2$ (for $K_i = 200$), 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). We note that in the larger system, such instability appears with a lower degree of choosing ability. Finally, when s becomes large, the rate of switching cascades decreases, with a subset of sites remaining dominant for many years at a time.

The simulations with unequal site capacities are similar, but unsurprisingly, the largest couple of sites are consistently the ones that dominate the system, and switching cascades are between these. Almost complete domination by the largest site occurs with a relatively low choosing ability. Thus, variation in local site capacity seems to stabilize the system.

To explore the interaction of individual movements and site dynamics, we ran a series of ten 1,000-year simulations using the two "equal K_i" variants, 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
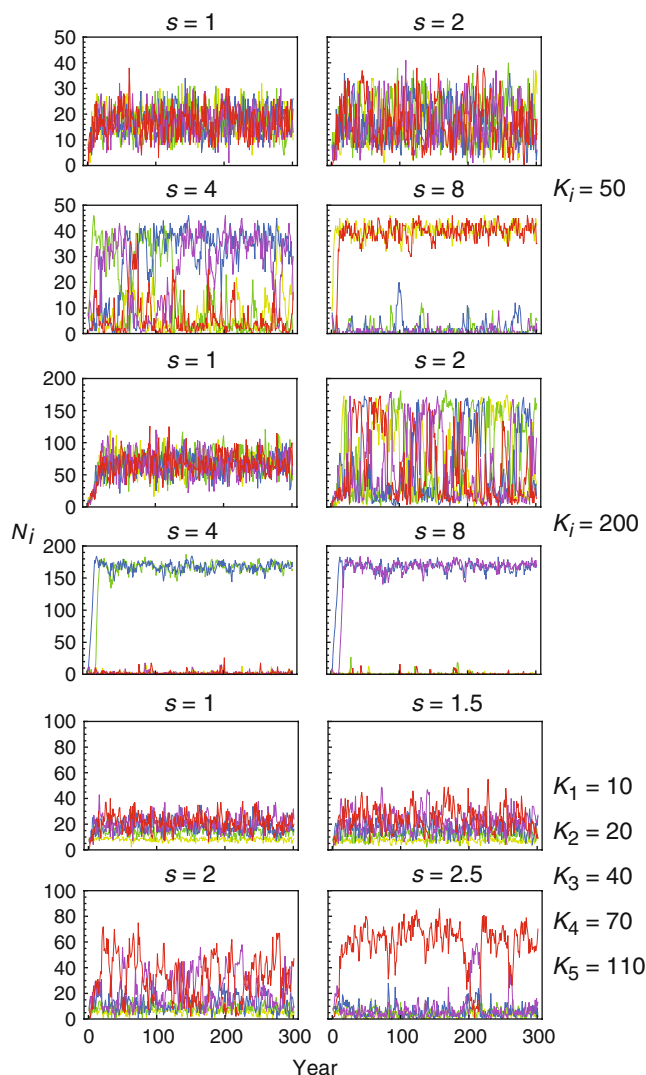
Fig. 4 Varying s, the ability to choose, produces a variety of dynamics from white noise through complex dominance switching to complete dominance by a subset of locations. *Colors* represent different model patches. The first two groupings represent systems with equal patch size K_i. In grouping 1 ($K_i = 50$, $K_G = 140$), the greatest frequency of switching cascades is seen at approximately $s = 4$, whereas when the size of each patch is increased to $K_i = 200$, even with a proportional increase in the global carrying capacity to $K_G = 560$ (grouping 2), switching cascades occur at a lower value of s, meaning that a lesser degree of active choice is required to produce the same complex dynamics. In the third grouping, patch sizes are unequal but with a mean of 50 nests. Here, switching cascades occur at a relatively low value of s, but mainly between the largest two sites
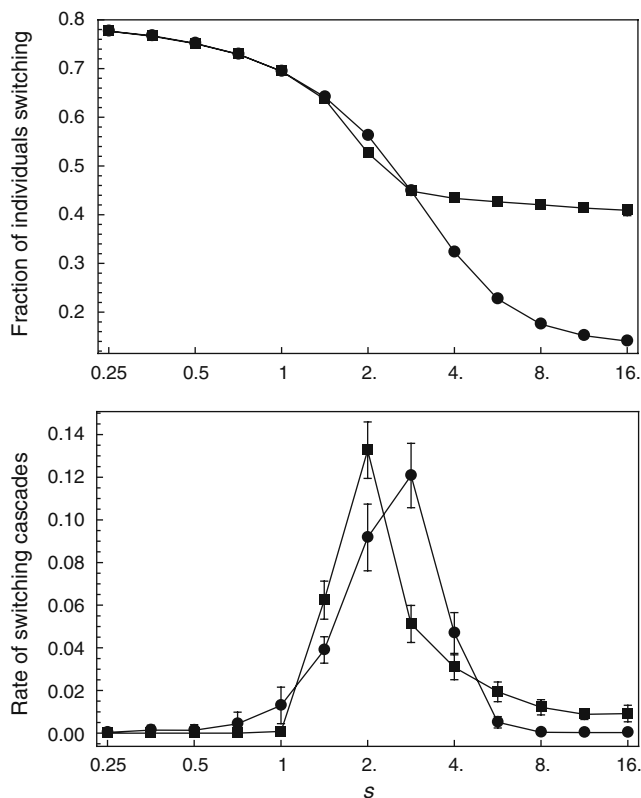
Fig. 5 In a system with equal site capacities, increased choosing ability s reduces the rate of site switching by individuals (*top*), but intermediate levels of choosing ability cause the maximum rate of large-scale switching cascades that alter the set of "dominant" patches (*bottom*). *Circles* and *squares* represent $K_i = 50$ ($K_G = 140$) and $K_i = 200$ ($K_G = 560$), respectively. *Each point* is the mean of ten simulations of 1,000 seasons; *error bars* indicate 95% bounds

"switch".) We calculated 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 (Fig. 5, upper plot). In the lower limit of s, with five sites chosen at random, birds will switch in four out of every 5 years on average. This fraction decreases sigmoidally as choosing ability increases, to a minimum value close to 0.1 (for $K_i = 50$) or 0.4 ($K_i = 200$). Even for large s, 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 $s = 3$ (for $K_i = 50$) or $s = 2$ (for $K_i = 200$; Fig. 5, lower plot). 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.

The effect of the global carrying capacity

An intermediate level of choosing ability appears necessary for complex dynamics with frequent switching cascades, but is it sufficient? For the model with equal site carrying capacities, the dynamics also depend crucially on the global carrying capacity. Figure 6 shows that both the rate of individual switching and the rate of switching cascades is periodic with respect to K_G. For
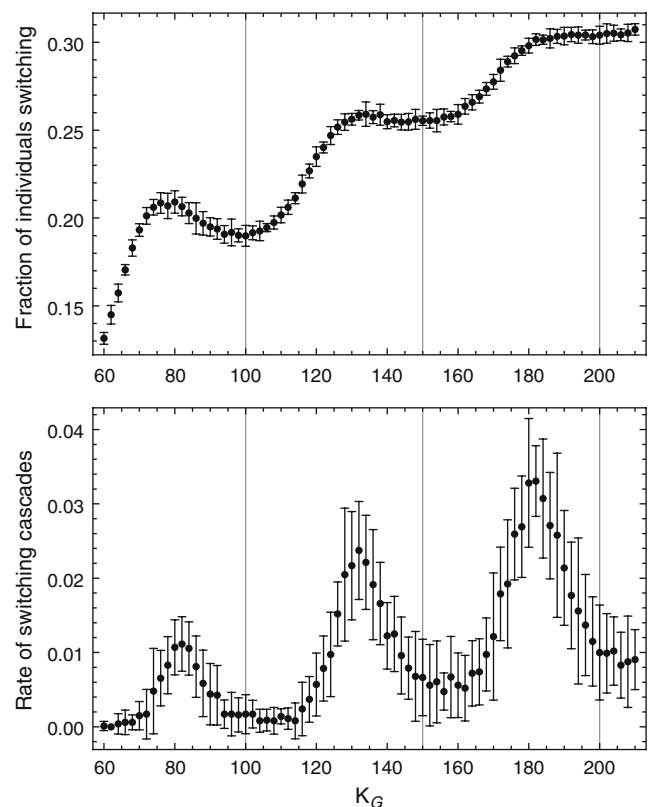
Fig. 6 The rate of both individual switching (*top*) and switching cascades (*bottom*) is periodic with respect to the global carrying capacity K_G. *Vertical lines* indicate integer multiples of the site capacity ($K_i = 50$ for all i). *Each point* is the mean of ten simulations of 1,000 seasons; *error bars* indicate 95% bounds
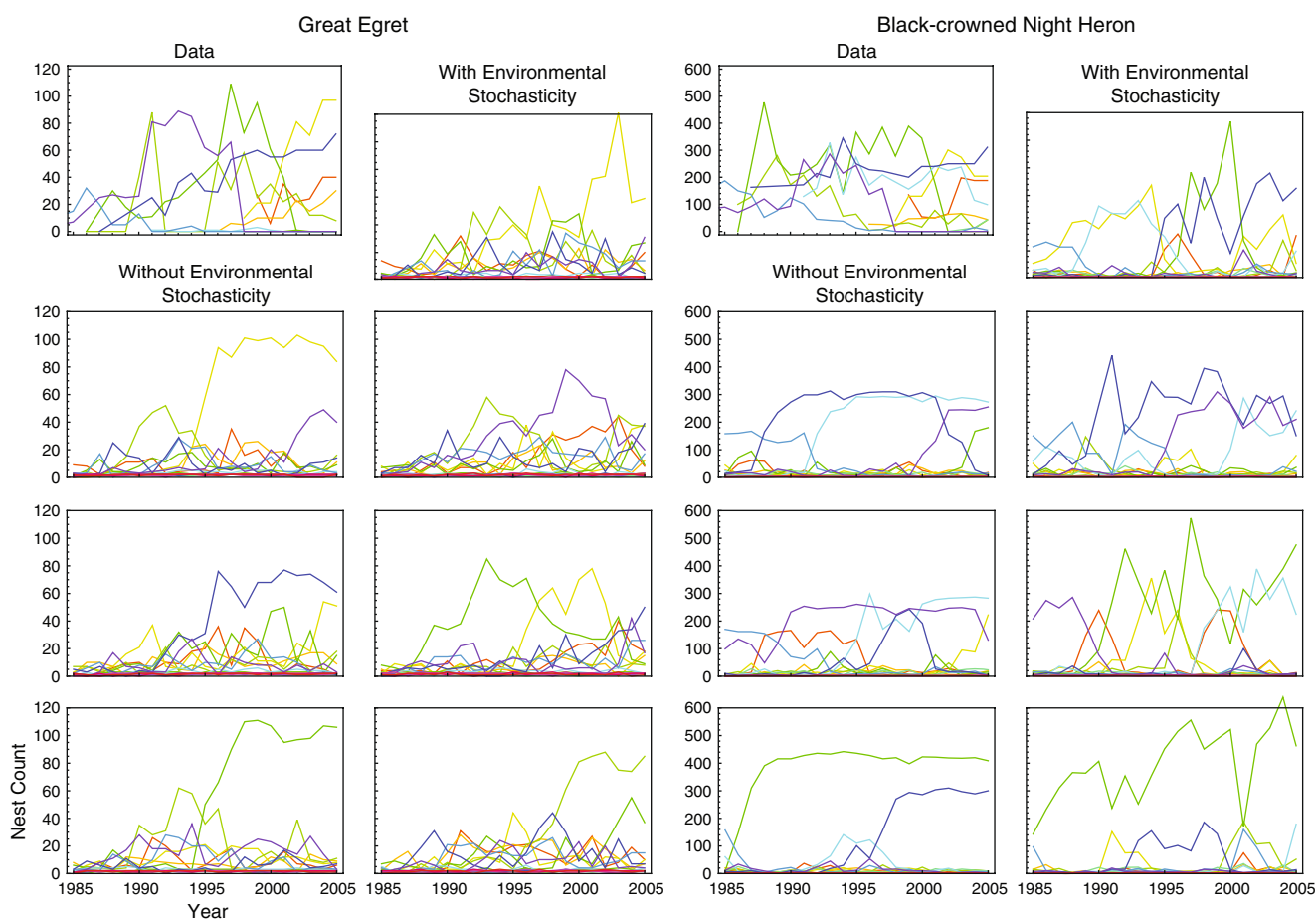
Fig. 7 A comparison of the observed nesting populations of Great Egrets and Black-crowned Night Herons with runs of our stochastic simulation model with global and nesting capacities estimated from the data, and with and without additional environmental stochasticity. *Colors* indicate corresponding locations between the simulations and the data (some locations with zero population size are not shown in the data plot). For both species, the simulations with environmental stochasticity closely resemble the data in terms of both year-to-year variability and the frequency of switching cascades

clarity, only results for $K_i = 50$ are shown, but no matter what the value of K_i, the rate of switching cascades is maximized when $K_G \approx n.7 \times K_i$, where $n = 1, 2, \ldots$ 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.

Matching the data

The observed data for both species show frequent, large-scale site switching (Fig. 7).

The simulations without environmental stochasticity also show some switching, but for both species, they were characterized by the rise to dominance of a single site, which often maintains that position for many years with relatively little fluctuation (particularly in the BCNH simulations). This does not match the data, in which even dominant sites show significant year-to-year variability in numbers and relatively short persistence times. Adding environmental stochasticity to the model produces model runs that match the data much more closely, not just by adding fluctuations (which are, after all, built directly into the model), but by consequently shortening dominance times and increasing the overall rate of site switching.

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 multi-site dispersal model by amplifying minor stochastic variation into large-scale population instability. They also show that such behavior, when combined with moderate environmental variability, could potentially explain the macroscopic 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 spatio–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.

Johst and Brandl (1997) created a similar model, inspired by the dynamics of Black-headed Gulls (*L. ridibundus*). Inter-colony movements of gulls and terns (Laridae) have traditionally been attributed to disturbance (McNicholl 1975), and like us, Johst and Brandl (1997) concluded that density-dependent dispersal can play an important role in amplifying minor stimuli into large-scale dispersal events. Our model, which assigns individuals one at a time, is somewhat simpler than theirs, which distributes all individuals among sites in one step (and therefore requires some adjustment to totals). Perhaps more relevant, when run with sites of varying carrying capacity, their model shows fluctuations only among the larger sites under almost all circumstances, and these fluctuations never involved crashes to local extinction. Our model does exhibit such crashes, and in fact, the kinds of dynamics shown in Fig. 7 resemble their data from real colonies of *L. ridibundus* more closely than their own model's output.

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 and Wright 1994) have been empty for one or more years. A number of concerned organizations 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 the 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. [At least one other field study supports this idea: Fasola et al. 2002 found no environment "triggers" for dispersal of Little Egrets (*Egretta garzetta*) in France.] 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, in the absence of remediation, the location may be "written off" as unsalvageable, and genuine disturbances (such as development) allowed. Our model implies that short-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*) 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 and Wright 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 0.5-km radius around the infestation site—a loss of approximately 3,000 trees on the island itself and 8,000 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 the Beetle 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 *existing* colonies. Our model shows that important sites may not be restricted to those currently occupied by birds.

Key aspects of the model remain untested against the real world. Although there is no plausible alternative, we cannot currently *prove* that individuals are switching sites in large numbers. We also do not know if it is reasonable to treat individuals as arriving in random order or not (the important question concerns the ordering of the first few individuals, as their choices set the template for colony growth), or the relative importance of site fidelity vs. colony size. If we could track the movements of a substantial sample of individual birds over a number of years, we could test all these model components. The data would provide 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 made mostly by young birds (as seen by Ganter and Cooke 1998 and Fasola et al. 2002). A good match between model and data would support the behavioral hypothesis and justify further development of the model for this particular system. Finally, as discussed earlier, we should investigate the possibility of a programmed (evolved) movement strategy based on the fitness consequences of remaining at a colony for many years. A first step would be to test whether there is a reduction in per-capita nesting success in successive years from the time when a colony first approaches its maximum size.

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