

# Predator foraging behavior and patterns of avian nest success: What can we learn from an agent-based model?



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## ABSTRACT

Mammalian predator foraging behavior is an important, but understudied determinant of avian nest success. Predator behavior may also affect the nest-site selection decisions of females: when predators respond strongly to prey density (e.g. through area-restricted search), the optimal strategy may be for birds to disperse their nests widely across the landscape. Conversely, clustered nests may benefit from dilution effects in the presence of incidental nest predators. In dabbling ducks, nest distributions range from clustered to dispersed and there is conflicting evidence about whether clustering enhances or reduces nest success, although presumably this depends on predator behavior. Here, I present results from an agent-based model designed to answer two qualitative questions: are clustered nests more or less successful than dispersed nests, and how does that relative benefit vary depending on predator behavior? I modeled three types of waterfowl nest predators (to emulate the foraging behavior of skunks and foxes) that differ in their degree of spatial memory and their capacity for area-restricted search, foraging on different distributions of nests. As hypothesized, well-dispersed nests survived better with fox-like predators that performed area-restricted searches. On the other hand, clustered nests survived better when incidental skunk-like predators were present, but survival was dramatically reduced in the presence of foxes; thus, small changes in the predator community (e.g. introduction of foxes) without commensurate changes in nest clustering could have important effects on waterfowl populations. On simulated landscapes containing both clustered and dispersed nests and a mixed predator community, average nest success for clustered versus randomly placed nests was the same across possible predator mixes, but the variance in success for clustered nests was much higher; this suggests that there may be risk-reward tradeoffs when nesting near conspecifics. That said, the degree to which ducks can actually assess and respond to the presence of conspecifics is largely unknown, and it is believed that nest sites are selected based on habitat. Results from this model, combined with empirical data suggest that commonly used management strategies that promote nest clustering, such as restoration of small parcels of habitat, can actually create ecological traps for nesting ducks, driven by predator behavior.

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## 1. Introduction

### 1.1. The importance of predator behavior

Predation is the primary cause of reproductive failure in most bird species (Ricklefs, 1969), and while the term “nest predation” implies a role for both the breeding bird and foraging predator, this topic has largely been studied from the perspective of the breeding bird (Lima, 2002). For example, an excellent review of nest predation by Lima (2009) cites 340 studies about avian responses to predation risk, but in contrast, there appears to be relatively

little research on the foraging behavior of nest predators (Chalfoun et al., 2002; Lima, 2002; Schmidt and Whelan, 1999; Thompson, 2007; Weatherhead and Blouin-Demers, 2004). Predator identity and foraging behavior are important because predators vary dramatically in home range size, cognitive ability, lethality, and the degree to which they specifically target nests as prey (Caro, 2005; Lahti, 2001; Lima, 2009; Peluc et al., 2008; Powell and Fransch, 2000; Thompson, 2007). These differences have important conservation implications: incidental nest predation by spatially restricted small mammals may have little aggregate effect on populations, but spatial memory and area-restricted search of a fox could potentially lead to density-dependent nest mortality that scales up to limit populations (Murray et al., 2010; Schmidt and Whelan, 1999). Critically, predator behavior may also affect nest-site selection decisions: in the presence of predators that respond strongly to prey density (e.g. through area-restricted search), the optimal strategy may be for birds to disperse their nests widely across the

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landscape (Page et al., 1983; Tinbergen et al., 1967). Conversely, tightly clustered nests may benefit from dilution effects in the presence of incidental nest predators that are primarily searching for alternate prey (Andr  n, 1991).

### 1.2. North American waterfowl as a model system

Management of North American waterfowl (family Anatidae) is widely recognized as a premier science-based program, one that also provides a model system for studying population dynamics and density dependence (Gunnarsson et al., 2013). Dabbling ducks (subfamily Anatinae) are the best-studied guild in this family, and there has been special emphasis on understanding their breeding biology. In most species of dabbling ducks, males and females pair on the wintering grounds and then migrate north to breed. Females are non-territorial when selecting nest sites and many are philopatric to former breeding areas. Dabbling ducks nest on the ground in upland areas, typically within 3 km of water, which is necessary for rearing broods (though adult foraging requirements are not considered to be an important factor in nest-site selection). Dabbling ducks typically lay 9–13 eggs that are incubated for approximately 25 days before synchronously hatching highly precocial ducklings; nests are especially vulnerable to mammalian mesopredators, and predators typically destroy 80–90% of nests (references for this paragraph in Batt, 1992).

Indeed, predation levels are so extreme that nest success is believed to limit population growth in waterfowl (e.g., Mallard [*Anas platyrhynchos*], Hoekman et al., 2002). In a recent analysis, Murray et al. (2010) suggested that local processes, such as density-dependent nest predation, could scale up to shape the population-level density dependence consistently observed at continental scales (Gunnarsson et al., 2013; Murray et al., 2010; Saether et al., 2008; Vickery and Nudds, 1984; Viljugrein et al., 2005). However, empirical studies of density-dependent nest predation (using artificial and/or natural nests) reveal no consistent pattern (Caro, 2005; Gunnarsson et al., 2013; Major and Kendal, 1996): some studies report that predation risk increases strongly or weakly with density (Clark and Wobeser, 1997; Gunnarsson and Elmsberg, 2008), while others report no correlation (Padyakova et al., 2010), or even an inverse relationship, with high densities of nests having relatively higher survival rates (Ringelman et al., 2012, 2013). Part of this uncertainty may be caused by differences in the types and foraging behaviors of the nest predators present in the various systems studied.

Two primary predators of waterfowl nests are Striped Skunks (*Mephitis mephitis*) and Red Foxes (*Vulpes vulpes*) (Greenwood et al., 1995; Klett et al., 1988), which display different types of foraging behaviors. While we lack high-resolution GPS telemetry on either predator, radio-telemetry and direct observational studies provide some insight into important behavioral differences between these two species. Skunks generally prefer to forage along wetland edges, and are believed to depredate nests incidentally while searching for small mammals or invertebrates, though there is some indication that they may form search images for prey and aggregate in areas of high nest density (Ackerman, 2002; Larivi  re and Messier, 2000, 2001b; Nams, 1997; Phillips et al., 2003, 2004). Skunks become satiated after consuming one, or only part of a clutch of eggs in a nest (Ackerman et al., 2003; Ringelman and Stupaczuk, 2013), and subsequently return to a den or other nearby resting place. Foxes are widely believed to have greater cognitive abilities, and display sophisticated foraging behavior such as area-restricted searching following an encounter with a prey item (Seymour et al., 2003, 2004). Furthermore, foxes cache eggs for later consumption, meaning that they are capable of destroying more than one nest per foraging bout (MacDonald et al., 1994; Sargeant et al., 1998). These different types of predator foraging behaviors could impact the

nest-site selection decisions of females. Waterfowl may benefit from dispersing their nests widely across the landscape in the presence of foxes, but should nest close to conspecifics in the presence of skunks. Few studies report on the degree of nest clustering in waterfowl, but there is some evidence that waterfowl nests are widely dispersed on the prairies where both foxes and skunks are present (Duebber and Lokemoen, 1976; Hines and Mitchell, 1983), while nests are tightly clustered at a site where foxes are absent (Ringelman et al., 2013).

### 1.3. An agent-based approach

In summary, the distribution of waterfowl nests varies from dispersed to clustered, and nest survival may be affected by local nest density. These patterns of nest distribution and survival should in theory depend on the foraging behavior of local predators (as well as on other factors, such as habitat), but we have only qualitative information on predator foraging behavior. While we currently lack the capacity to carry out controlled empirical studies of different types of predators foraging on different distributions of nests, it may be possible to explore these questions using an agent-based model. Indeed, there are already several agent-based models in which a simulated predator “agent” forages for patchily distributed prey according to various behavioral rules (e.g. Fronhofer et al., 2012; Klaassen et al., 2006). More than a decade ago, Carter and Finn (1999) recognized the potential to apply agent-based modeling to study waterfowl nest predators, and they created MOAB, an agent-based model of foxes foraging on waterfowl nests. Their focus was on developing a hierarchy of behavioral rules that would create a model of realistic predator foraging, but MOAB was never extended to explore the interactions between predator behavior, nest clustering, and nest success. Here, I present results from an agent-based model of waterfowl and their nest predators, created using modern, open-source software (Netlogo), and parameterized with empirically derived data from my study site in California. This study builds on the empirical work of Ringelman et al. (2012, 2013), which documented tight clustering of waterfowl nests, and density-dependent nest survival at their site in California. They hypothesized that nest clustering was adaptive in California because the primary (incidental) predators are skunks, and following Duebber and Lokemoen (1976) and Hines and Mitchell (1983), they speculated that nests should be well dispersed in areas where foxes are present. The model I present here was designed to answer two qualitative questions: are clustered nests more or less successful than dispersed nests, and how does that relative benefit vary depending on predator behavior?

## 2. Methods

### 2.1. Model setup

The only factor limiting the complexity of today’s agent-based models is human patience for computation time, and indeed, many models are so complex that they are difficult for the average ecologist/conservation biologist to code and modify themselves (McLane et al., 2011). Furthermore, in some cases, very detailed models require estimation of parameters for which there is little empirical evidence (e.g. Stillman, 2008), which can lead to greater uncertainty about model output. Here, following the general philosophy of pattern-oriented modeling (Grimm and Railsback, 2012; Grimm et al., 2005), I opted to create a simple, empirically based model of a waterfowl-nest predator system using the user-friendly, open-source software Netlogo (version 5.0.1, Wilensky, 1999). In pattern-oriented modeling, the researcher: (1) empirically identifies an ecological pattern (nest distributions, patterns of nest

success), (2) models the hypothesized processes believed to underlie that pattern (different types of predator behavior), and (3) determines which process-based model most closely matches the empirical data.

This model was designed to represent the nesting patterns of dabbling ducks observed at the Grizzly Island Wildlife Area, CA. All empirical values were derived from earlier studies at that site (Ackerman et al., 2004; McLandress et al., 1996; Ringelman et al., 2012, 2013) unless otherwise noted. Below I present a brief summary of model design and implementation; Supplementary Material, Appendix A contains a full ODD protocol (Grimm et al., 2006; Grimm and Railsback, 2012) describing the simulation space, agent states, initialization, and agent scheduling. The full Netlogo program is available online as Supplementary Material (Cluster-Duck-3.2.nlogo).

The simulation space was a discrete 2D square grid of  $240 \times 240$  cells; each cell represented an empirical distance of 5 m, chosen because waterfowl nests are typically not closer than 5 m apart. The grid space equates to an area approximately half the size of the Grizzly Island study area; I modeled only half of the study area both for computational speed, and because the home ranges of individual predators typically do not span the entire site [unpublished data for skunks and raccoons at my site; home ranges are much smaller on Grizzly Island than they are, for example, on the prairies (Phillips et al., 2004)]. In total, 150 nests were placed on the landscape, which approximates the maximum density of simultaneously active nests on the study area. Nests were distributed on this simulation space in two ways: (1) 150 nests were distributed randomly, or (2) five cluster centers were randomly chosen, and 30 nests were then distributed around that center according to a normal distribution, with a standard deviation that could be varied (termed *dispersion*). (Note: because cluster centers were randomly chosen, some simulations contained larger aggregations of nests.) This level of clustering corresponds with the density and distribution of simultaneously active nests observed at my site during the peak of the nesting season, and earlier model exploration confirmed that changing the number of clusters did not qualitatively change results. For simulations including both random and clustered nests, (i.e., 75 random,  $5 \times 15$  clumped), random nests were located at least 10 cells away from the nearest clustered nest, which ensured that random nests were not located in the middle of a group of clustered nests. Each nest was given an energy value of 9, representing the mean clutch size of a Mallard (the most common duck at my study site), energy which was transferred to the predator when the clutch was eaten.

## 2.2. Predator agents

Predator agents moved forward one grid cell per time step. Because mesopredators such as skunks and foxes often move ~2 km per foraging bout (Phillips et al., 2004), I defined one day as 400 time steps on the 5 m-cell grid space, and ran simulations for 14,000 time steps, representative of a 35-day nest cycle of a Mallard (i.e., 1 egg laid daily for 9 days followed by 26 days of incubation). As a baseline, I assumed predators would be satiated for the day after consuming a typical Mallard nest of nine eggs; thus, predator metabolism (energy decrease per time step) was set to  $9/\text{satiating.time}$ , with a starting value of  $\text{satiating.time} = 400$  time steps. Predators were “hungry” (eligible to consume nests) when their energy reserves fell below zero. There was no lower bound to predator energy reserves and predators never starved; predator energy reserves were set to 9 upon consuming a clutch of eggs regardless of how negative their energy reserves were. In a biological sense, I am implicitly assuming that predators are capable of surviving on alternative prey, but consuming a full clutch leaves them fully satiated – this is well-supported in the literature (e.g. Ackerman, 2002;

Crabtree and Wolfe, 1988). Predators consumed a clutch if their energy reserves were negative, and they occupied a cell where an active (non-depredated) nest was present. This is equal to a detection range of approximately 7 m, which is a reasonable value for predators such as foxes or skunks (Seymour et al., 2004; Österholm, 1964).

After preliminary model exploration, I chose to simulate 8 predators, which yielded nest successes within observed ranges (10–40%), and is probably a reasonable estimate for predator densities at my site (based on >1200 trap-nights, unpub. data). There were three types of predators in the model, *skunks*, *smart-skunks*, and *foxes*, which represent different foraging behaviors. *Skunks* represented incidental nest predators moving in a correlated random walk; movement direction was drawn from a normal distribution with mean =  $0^\circ$ , and standard deviation that could be varied (*turning.skunk*). *Smart-skunks* and *foxes* represent two points on a continuum of foraging behavior that is characterized by some degree of spatial memory and area-restricted search (ARS). After a *smart-skunk* consumes a nest, it moves off in a random direction for some distance (*spatial.error*), “sleeps” until its energy drops below zero, then conducts a tortuous area-restricted search (mean heading  $0^\circ$ , SD = *turning.ARS*) for some time (*duration.ARS*) before resuming standard movement. This approximates the behavior of some skunks, especially males, which do not return to specific dens every day – rather, they sleep under whatever bush is convenient after they are satiated (pers. obs.). Alternatively, this behavior can be thought of as a predator that does retire to a den every day, but returns to the previous foraging area with some spatial error on the subsequent night. A *fox* predator moves like a *smart-skunk*, but searches around the exact area where it found a nest (*spatial.error* = 0), and can destroy more than one nest per day (*satiating.time* = 200). Both area-restricted search strategies are qualitatively similar to Lévy flight behavior, characterized by clusters of short, tortuous movements interspersed with longer, straighter movements. Many animals, including foxes (Phillips et al., 2004), are thought to forage in a pattern resembling a Lévy flight, though the actual mathematics of the movement paths are debatable (Edwards, 2011). Fig. 1 shows movement paths of *skunks* and *foxes* foraging on randomly placed nests.

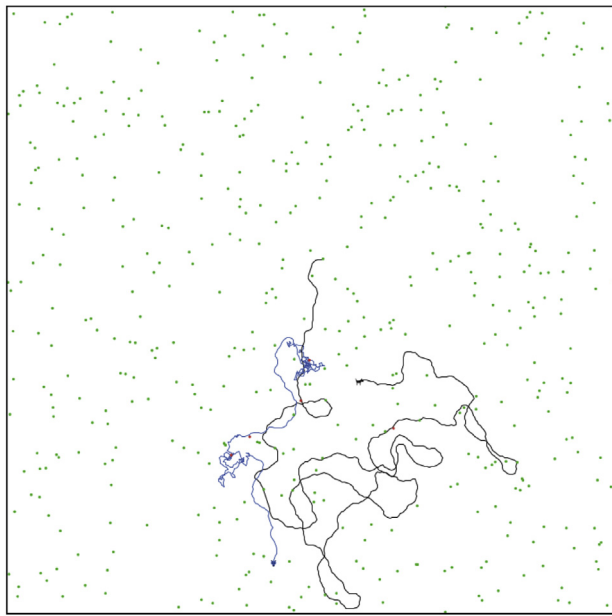
## 2.3. Simulation runs

The results I present here are largely qualitative, commensurate with the original goals of the model. The sole output variable was average nest success from 100 simulations (unless otherwise noted); in some cases, I compare survival of clumped vs. randomly spaced nests. In the first set of simulations, I systematically explored the parameter space of predator behavior to determine if there are “optimal” foraging strategies for *skunks*, *smart-skunks*, and *foxes*, and then examined if these strategies were more or less successful depending on the distribution of nests. I then simulated different predator communities foraging on a realistic landscape with both clustered and randomly distributed nests, to diagnose how the relative benefits of clustering vary with the composition of the predator community.

## 3. Results

### 3.1. Efficient skunk foraging behavior

In the first set of simulations I modeled the effects of movement straightness by a *skunk* predator on the survival of randomly placed nests. I systematically varied *turning.skunk*, and found that when *skunks* foraged along straighter paths, predators were more successful and nest survival was lower, although this appeared to

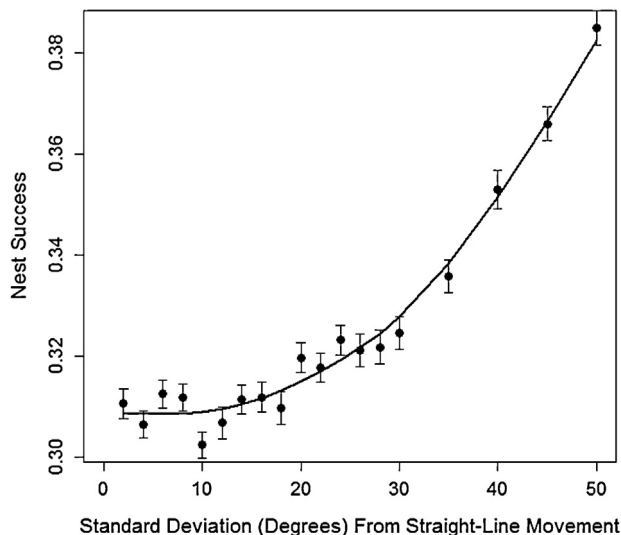


**Fig. 1.** Example of movement paths for skunks and foxes. Model visualization example showing one skunk (black path) and one fox (blue path) foraging on 500 randomly spaced nests (density was increased for demonstration of movement paths). The movement path of the fox shows area-restricted searching after locating a nest. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

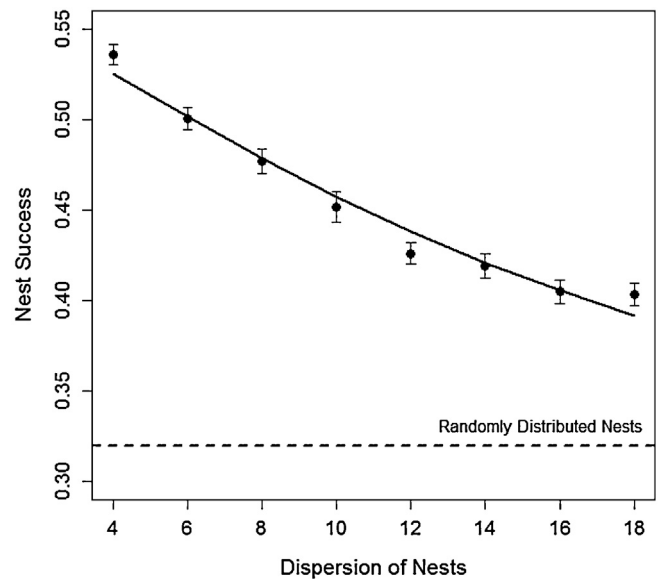
reach a minimum value at  $\text{turning.skunk} \leq 20^\circ$  (Fig. 2). When I simulated efficiently moving skunks ( $\text{turning.skunk} = 20^\circ$ ) foraging on a landscape of clustered nests, there was substantial dilution of predation risk; nests that were more tightly clustered tended to survive better (Fig. 3).

### 3.2. Efficient foraging behavior for smart-skunks

In the second set of simulations, I explored the behavior space for smart-skunks, which included parameters for the spatial memory of the predator (*spatial.error*), how long it spends performing area-restricted search (*duration.ARS*), and how tortuous the area-restricted movements are (*turning.ARS*). With three parameters

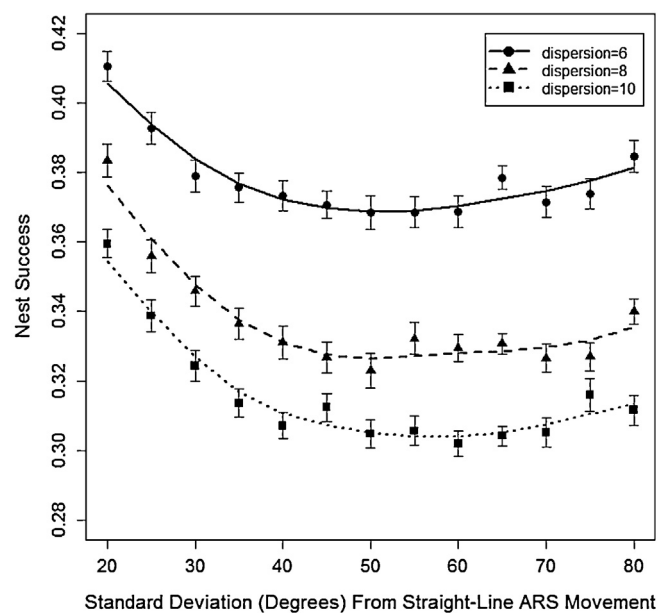


**Fig. 2.** Straightness of skunk movement vs. nest success. Simulation results showing the relationship between nest success (mean  $\pm$  SE) and the tortuosity of predator movement.



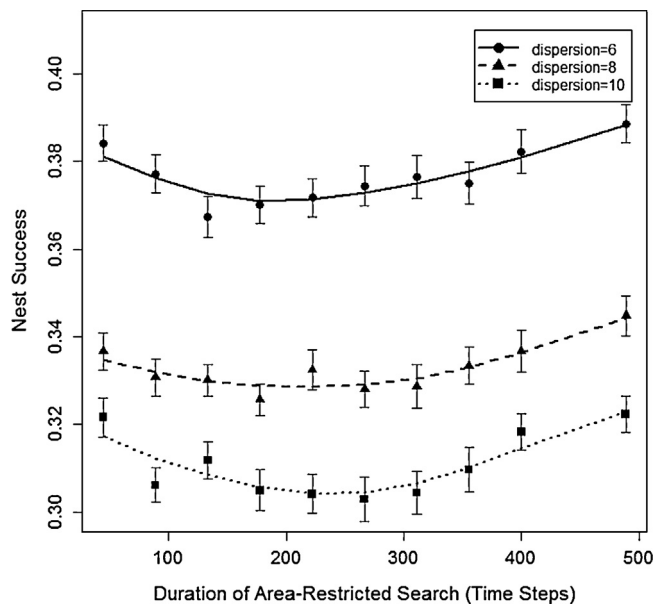
**Fig. 3.** Dispersion vs. nest success for an efficient skunk. Simulation results showing how the dispersion of nests (lower values correspond with high levels of clustering) affects nest success (mean  $\pm$  SE) in the presence of a skunk foraging in a correlated random walk ( $\text{turning.skunk} = 20^\circ$ ).

that can vary and interact with nest *dispersion*, I first attempted to find an efficient *turning.ARS*, and fixed *spatial.error* ( $\approx 20$  cells) and *duration.ARS* (133 time steps = 1/3 day) at reasonable values. From the predator's perspective, the optimal *turning.ARS* was  $\sim 50^\circ$ , and did not depend on the tightness of nest clustering (Fig. 4). Fixing *turning.ARS* at  $50^\circ$ , I next determined the most favorable duration of area-restricted searching after finding a nest before resuming a straighter correlated random walk. The best *duration.ARS* was less obvious (and increasing the number of simulations did not reduce the noise), with the most efficient predators spending between 200 and 300 time steps searching an area before resuming normal movement (Fig. 5). Later model exploration also showed that the most efficient *duration.ARS* did not change when I reduced the



**Fig. 4.** Tortuosity of area-restricted search vs. nest success. Simulation results showing the relationship between tortuosity of area-restricted foraging movements for smart-skunks and nest success (mean  $\pm$  SE) at three levels of nest *dispersion*.

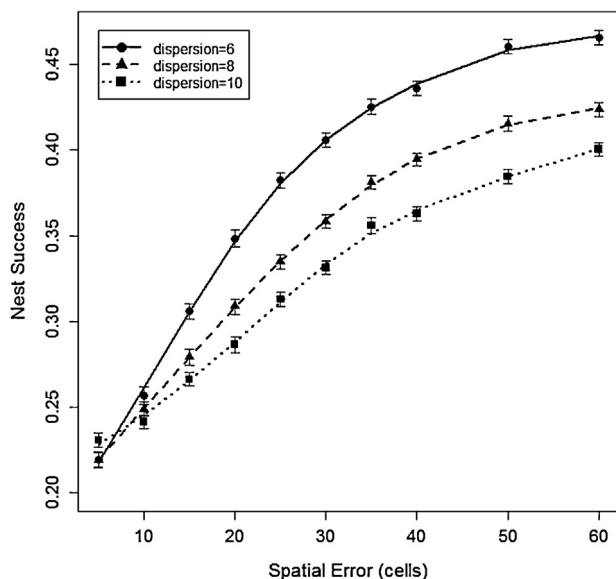




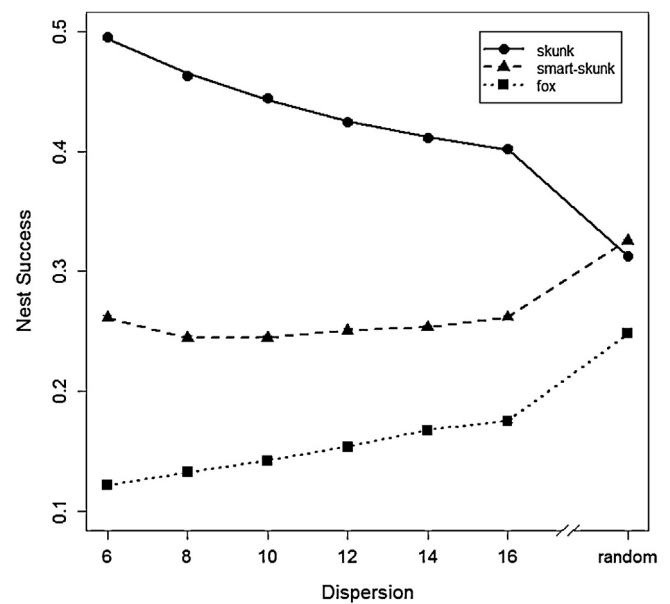
**Fig. 5.** Duration of area-restricted search vs. nest success. Results showing how nest success (mean  $\pm$  SE) varies as a function of how long a *smart-skunk* performs an area-restricted search before resuming standard movement. The three lines show different levels of nest dispersion.

number of nests per cluster from 30 to 15. Finally, I fixed *turning.ARS* at 50° and *duration.ARS* at 250 time steps and explored the relationship between nest dispersion and *spatial.error*. Here, the effects were very strong; predators traveling too far outside the cluster did not benefit from area-restricted searching (Fig. 6).

To summarize my exploration of the behavior space of *smart-skunks*, I conducted a sensitivity analysis, where I systematically varied dispersion, *turning.ARS*, *duration.ARS*, and *spatial.error*. I included these parameters and all two-way interactions in a generalized linear model with nest success as the response variable. Standardized  $\beta$  coefficients indicated that *spatial.error* had



**Fig. 6.** Spatial error vs. nest success. Simulation results showing that nest success (mean  $\pm$  SE) is strongly affected by the distance a predator travels away from the first prey item (*spatial.error*) before performing an area-restricted search. Each cell represents 5 empirical meters, and for reference, the average nest cluster radius for dispersion=8 scales roughly to 75 empirical meters. For comparison, two other levels of nest dispersion are shown.



**Fig. 7.** Comparison of search strategies on different landscapes. Shown are simulation results of three different types of predators foraging on different distributions of nests. Error bars are too small to appear on this graph.

a strongly positive effect on nest success, though there was a negative interaction with dispersion; so while nests were more successful when predators had a poorer spatial memory, this benefit depended on how tightly nests were clustered (Table 1). Finally, *turning.ARS* had a strong effect on nest survival, with highly concentrated searches leading to lower nest success (Table 1).

### 3.3. Effects of different types of predators on nest success

Having created efficient *skunks* (*turning.skunk*=20°) and efficient *smart-skunks* (*turning.ARS*=50°, *duration.ARS*=250 steps, *spatial.error*  $\approx$  10 cells), I directly compared how different types of predators would affect the survival of different distributions of nests (500 simulations). I also included a *fox* that forages like a *smart-skunk*, but with perfect spatial memory (*spatial.error*=0 m) and the capacity to depredate two nests per day (*satiation.time*=200). Generally, a *skunk* moving in a correlated random walk destroys fewer nests than *smart-skunks* or *foxes* that perform an area-restricted search after finding a nest; this is especially true when nests are tightly clustered (Fig. 7). However, when nests are distributed randomly, *smart-skunks* predators depredate fewer nests than predators moving along relatively straight paths (Fig. 7).

### 3.4. When is better to be clustered versus random?

In a final set of simulations, I modeled a realistic landscape of 75 clumped nests, (dispersion=8) and 75 randomly distributed nests, which translates to an average nearest-neighbor distance of 40–45 m, commensurate with empirical data, and examined how different predator communities would affect the nest survival of clustered vs. random nests. I modeled three types of smart predators that varied in their degree of spatial memory (*smart-skunks* with a *spatial.error* of either 10 or 20 cells, and *foxes*), coexisting with *skunks* in different ratios, though the absolute number of predators was held constant at 8. Overall average nest success declined as the number of smart predators increased from 0 to 8, though the effect was much stronger for *foxes* (14% decline) than for *smart-skunks* (3% decline). As the number of smart predators increased (and the number of *skunks* decreased), nest survival declined much

**Table 1**Sensitivity analysis for *smart-skunk* movement parameters, showing each variable's relative effect on nest success. Significant terms are shown in bold.

Parameter	Standardized coefficient ( $\beta$ )	Estimate	Std. error	t value	p-Value
<i>dispersion</i>	−0.00024	$-7.222 \times 10^{-6}$	$5.969 \times 10^{-4}$	−0.01	0.99
<i>turning.ARS</i>	<b>−0.51081</b>	<b><math>-1.542 \times 10^{-3}</math></b>	<b><math>7.688 \times 10^{-5}</math></b>	<b>−20.06</b>	<b>&lt;0.0001</b>
<i>duration.ARS</i>	−0.03094	$-2.101 \times 10^{-5}$	$1.730 \times 10^{-5}$	−1.22	0.22
<i>spatial.error</i>	<b>0.57816</b>	<b><math>3.584 \times 10^{-3}</math></b>	<b><math>1.551 \times 10^{-4}</math></b>	<b>23.11</b>	<b>&lt;0.0001</b>
<i>dispersion × turning.ARS</i>	<b>−0.00540</b>	<b><math>-3.350 \times 10^{-5}</math></b>	<b><math>6.474 \times 10^{-6}</math></b>	<b>−5.17</b>	<b>&lt;0.0001</b>
<i>dispersion × duration.ARS</i>	<b>−0.00220</b>	<b><math>-6.631 \times 10^{-6}</math></b>	<b><math>1.457 \times 10^{-6}</math></b>	<b>−4.55</b>	<b>&lt;0.0001</b>
<i>dispersion × spatial.error</i>	<b>−0.46719</b>	<b><math>-3.173 \times 10^{-4}</math></b>	<b><math>1.330 \times 10^{-5}</math></b>	<b>23.86</b>	<b>&lt;0.0001</b>
<i>turning.ARS × duration.ARS</i>	<b>0.00018</b>	<b><math>5.491 \times 10^{-7}</math></b>	<b><math>1.457 \times 10^{-7}</math></b>	<b>3.77</b>	<b>&lt;0.001</b>
<i>turning.ARS × spatial.error</i>	<b>0.06733</b>	<b><math>4.573 \times 10^{-5}</math></b>	<b><math>1.330 \times 10^{-6}</math></b>	<b>34.39</b>	<b>&lt;0.0001</b>
<i>duration.ARS × spatial.error</i>	<b>0.00008</b>	<b><math>2.665 \times 10^{-6}</math></b>	<b><math>2.992 \times 10^{-7}</math></b>	<b>8.91</b>	<b>&lt;0.0001</b>

more rapidly for clustered nests (Fig. 8) than for randomly distributed nests. In fact, the survival of randomly distributed nests actually increased when the predator community was dominated by *smart-skunks*.

#### 4. Discussion

##### 4.1. Dilution effects

Empirically, the distribution of waterfowl nests varies from tightly clustered to widely dispersed, but the relationship between predator foraging behavior and patterns of nest success is less well-known. Ringelman et al. (2013) hypothesized that nest clustering is adaptive when the primary (incidental) predators are skunks, but that nests should be well dispersed in areas where foxes are present. This agent-based model allowed me to explicitly test these hypotheses about the relationship between nest dispersion, predator foraging behavior, and nest success. I modeled three types of predator foraging behavior, designed to approximate an incidental nest predator (such as a skunk primarily foraging on alternate prey), and two types of smart nest predators, with some capacity for spatial memory and area-restricted search. Undoubtedly, the behavior of individual predators is not so discretized, but falls somewhere along this continuum, and indeed, probably also depends strongly on environmental variables not considered in this model (den locations, territories, impermeable barriers, travel corridors, vegetation types, etc.). Nevertheless, there are several insights to be gained from this simple model of nest predation.

First, results show that foraging behavior dictated by a relatively straight correlated random walk is reasonably efficient when searching for randomly distributed prey, though further refinements not considered here (e.g. very straight movements through areas already searched) may improve this strategy even further (Bovet and Benhamou, 1991). However, this strategy does not perform well when nests are clustered together, and nest survival increases as the tightness of the group increases (Fig. 3). While this dilution effect seems intuitively obvious and has been hypothesized to operate in empirical nest/predator systems (Andr n, 1991), dilution effects in waterfowl have only recently been rigorously documented (Ringelman et al., 2012, 2013). Qualitatively, the patterns of nest success observed at my site (which is dominated by incidental nest predators) appear similar to simulations of incidental nest predators foraging on moderately clustered nests. The agent-based model presented here provides evidence supporting the idea that ducks should nest near conspecifics in the presence of incidental nest predators. This is a critical point: while it is often believed that waterfowl nests are clustered simply because the underlying (high-quality) habitat is inherently clustered, this model shows that clustering *in and of itself* may be adaptive, irrespective of habitat.

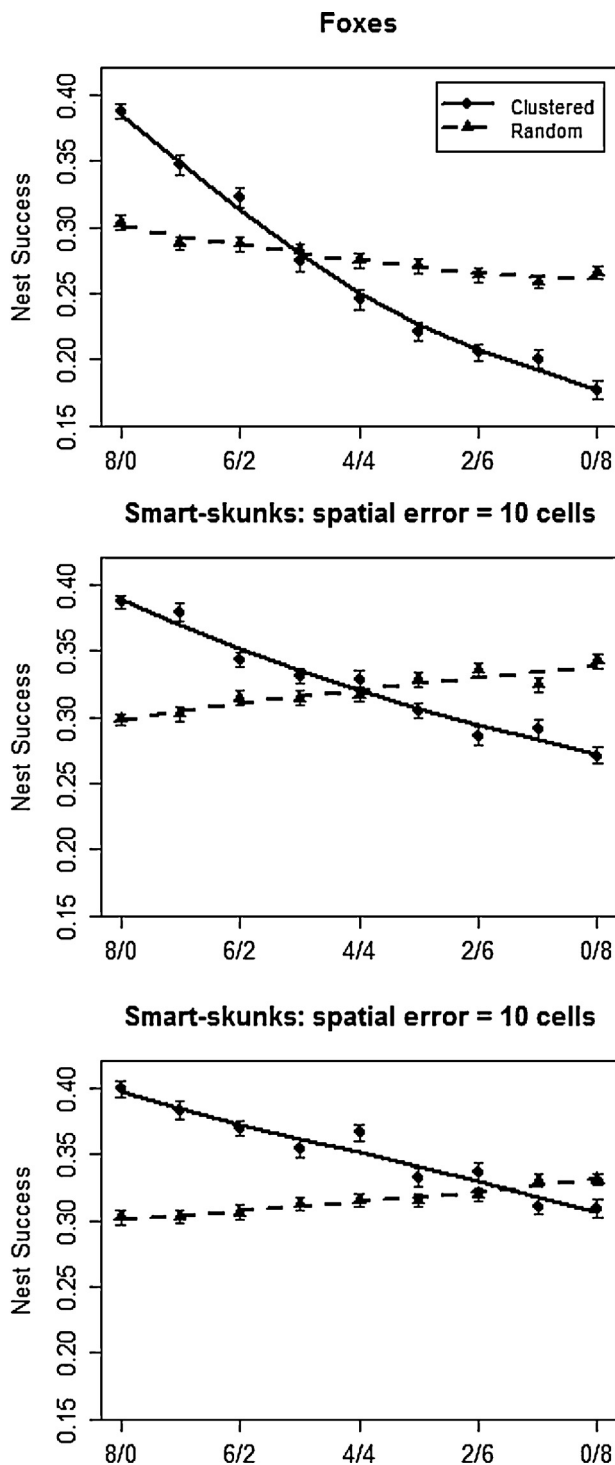
##### 4.2. The costs of clustering

The benefit of clustering likely depends on the search strategy of the predator, but the magnitude of this effect is relatively unknown, and is of great interest to waterfowl managers. This model demonstrates that predators with some spatial memory and capacity for area-restricted search can dramatically reduce the benefits of clustering: nest success for clustered nests was reduced by 15–25% when smart skunks were present (relative to incidental predators foraging on the same distribution of nests). The effects of foxes were even more severe (Fig. 7), largely because this type of predator is capable of depredating more than one nest per day; empirically, foxes can cache eggs from multiple nests per day (Sargeant et al., 1998), and some foxes have larger home ranges than modeled here (Phillips et al., 2004), so these results are likely an underestimate of fox lethality. While it is not surprising that the survival of clustered nests depends on the foraging behavior of the predator, the magnitude of this effect is striking. Waterfowl researchers often observe nest success levels between 10% and 30%, and it is believed that nest success must be greater than 15% to maintain Mallard populations (Hoekman et al., 2002); thus, small changes in the composition of the predator community, such as introduction of foxes, without commensurate changes in how waterfowl distribute themselves could have important effects on the health and stability of populations. The ability (or lack thereof) of birds to respond to novel predators is an important topic in invasion ecology and conservation biology (e.g. Blackburn et al., 2004), and remains an area of active research (Bonnaud et al., 2012; Vanderweft, 2012; Sih, 2013). The agent-based model presented here can be used to understand the effects of a potentially novel waterfowl nest predator before an invasion occurs.

While the optimal strategy for ducks nesting in the presence of incidental nest predators is to be tightly clustered, this is the worst possible strategy when predators remember that location and perform area-restricted searching. The accuracy of predator spatial memory and its interaction with the tightness of nest clustering are the most important determinants of nest success in this model (Table 1), and yet there are few studies on predator spatial memory. Real foxes likely have excellent spatial memories because they routinely cache eggs and relocate them for later consumption (MacDonald et al., 1994; Sargeant et al., 1998). Furthermore, coarse-scale telemetry studies also suggest that both foxes and skunks return to the same general foraging areas where food is abundant (Larivi re and Messier, 2001a,b; Phillips et al., 2004). The results from this model highlight the critical need for detailed studies on the accuracy of predator spatial memory.

##### 4.3. Waterfowl nesting in an uncertain world

Waterfowl managers are primarily concerned with average nest success, which declines when the predator community is



**Fig. 8.** Clustering and the predator community. Simulation results showing the relationship between nest success (mean  $\pm$  SE) for random-placed (dashed lines) and clustered (solid lines) nests and the mix of predators in the community. Moving from left to right on the x-axis corresponds to a greater number of smart predators (either *smart-skunks* or *foxes*). Three different types of smart predators are shown.

dominated by predators with spatial memory employing area-restricted searching; however, Fig. 8 shows that clumped and randomly dispersed nests are differentially affected depending on the mix of predators in the area. From a behavioral-ecological perspective, this means that the optimal nest-site selection choice (to nest near or far from conspecifics) depends on the composition of the predator community, and yet, the types and densities of

nest predators in an area are difficult for birds to assess (Dassow et al., 2012; Lima, 2009). Fig. 8 shows that while there seems to be a consistent benefit to clustering when predators have a relatively poor spatial memory (*smart-skunks*, *spatial.error* = 20 cells), there is a strong risk/reward tradeoff when predators have a better spatial memory. That is, across all potential predator communities, the average nest success for random and clustered nests is nearly the same (*foxes*: random = 0.265, clustered = 0.277, *smart-skunks* (10 cell): random = 0.325, clustered = 0.320), but variance is much higher for clustered nests than for random nests. Randomly dispersed nests always have approximately the same expected survival, regardless of the predator community, but the survival of clustered nests depends very strongly on the types of predators that are present. There are several insights to be gained from this result: (1) any information females are able to acquire about the predator community (through prior experience, prospecting, etc.) could strongly influence the final distribution of nests. (2) In the absence of good information about current predator composition, the average predator community composition (across years) may be more important in determining patterns of nest density. (3) Species with different life histories (life span, re-nesting propensity, risk prone vs. risk averse, etc.) (Ackerman et al., 2006; Kremenetz et al., 1989) may be distributed differently. For example, long-lived, risk-averse species such as Northern Pintail (*Anas acuta*) may be more dispersed to achieve consistent levels of reproductive success across changing predator communities.

#### 4.4. Ecological traps

There is little evidence to date that birds can gather reliable information about predators, and even less evidence that they then distribute themselves accordingly with respect to conspecifics (Lima, 2009). In waterfowl, vegetation is an important nest-site selection cue (e.g. Clark and Shutler, 1999; Crabtree et al., 1989), and so heterogeneity in the habitat is likely to be driving patterns of nest density. When humans increase heterogeneity in the environment by fragmenting grasslands with agricultural fields, grazed pasture, and urban areas, duck nests become concentrated in the remaining nesting habitat. Furthermore, one of the most common waterfowl management strategies is to create patches of dense nesting cover (DNC) to attract breeding ducks (Klett et al., 1988), which also imposes a clustered distribution of waterfowl nests. Results from my model suggest that by forcing ducks to cluster in certain habitat patches, predation rates might be elevated in those areas (depending on the predator community), or between-year variation in nest success could increase because the predator community changes over time. This is, in fact, exactly what has been reported for patches of DNC on the prairies. Nest success in DNC has been shown to vary strongly among study plots and years (Arnold et al., 2007; Klett et al., 1988); one study reported nest successes that ranged from 2.7% to 39.4% (McKinnon and Duncan, 1999). The high concentration of nests in DNC may also promote spatial memory in predators: nest success decreases throughout the season in patches of DNC, but increases in unmanaged cover types with lower densities of duck nests (Emery et al., 2005). These observational studies, combined with results from the agent-based model presented here suggest that waterfowl management strategies that fail to account for predator foraging behavior may actually create ecological traps for nesting waterfowl by forcing ducks to cluster in specific habitats.

This agent-based model highlights the complex interaction between local nest density, predator foraging behavior, and nest success. Future versions of the model could incorporate different types of habitat that vary in attractiveness to ducks and predators and that convey more or less protection from predation. This model could also be extended to explore inter-annual population dynamics and behavioral dynamics (such as win-stay, lose-shift) of



predators and prey. The results presented here underscore need for a greater understanding of predator movement strategies and spatial memory, and experiments to determine if and how waterfowl select nest sites differently when presented with different suites of predators.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolmodel.2013.09.028>.

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