

Adaptive nest clustering and density-dependent nest survival in dabbling ducks

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Density-dependent population regulation is observed in many taxa, and understanding the mechanisms that generate density dependence is especially important for the conservation of heavily-managed species. In one such system, North American waterfowl, density dependence is often observed at continental scales, and nest predation has long been implicated as a key factor driving this pattern. However, despite extensive research on this topic, it remains unclear if and how nest density influences predation rates. Part of this confusion may have arisen because previous studies have studied density-dependent predation at relatively large spatial and temporal scales. Because the spatial distribution of nests changes throughout the season, which potentially influences predator behavior, nest survival may vary through time at relatively small spatial scales. As such, density-dependent nest predation might be more detectable at a spatially- and temporally-refined scale and this may provide new insights into nest site selection and predator foraging behavior. Here, we used three years of data on nest survival of two species of waterfowl, mallards and gadwall, to more fully explore the relationship between local nest clustering and nest survival. Throughout the season, we found that the distribution of nests was consistently clustered at small spatial scales (~50–400 m), especially for mallard nests, and that this pattern was robust to yearly variation in nest density and the intensity of predation. We demonstrated further that local nest clustering had positive fitness consequences – nests with closer nearest neighbors were more likely to be successful, a result that is counter to the general assumption that nest predation rates increase with nest density.

Density-dependence typically refers to negative feedback mechanisms that limit populations as they approach carrying capacity. This concept has long been a cornerstone in population biology, and is a central tenet underlying classic ecological paradigms such as resource limitation, competition and predator–prey cycling. Density-dependent population regulation appears to be a pervasive ecological phenomenon (Brook and Bradshaw 2006), and understanding the role of density dependence is especially critical for the conservation of exploited, threatened and heavily-managed species (Hixon and Carr 1997, Williams 2012). When patterns of density dependence are detected in these types of species, researchers seek to understand the negative feedback mechanisms that underlie these patterns so that management actions can be effectively targeted; unfortunately, this can be a daunting task for species with complicated life histories that are entangled in complex food webs.

North American waterfowl populations are intensively managed for sustainable harvest by sport hunters, and can be considered a model system for studying density dependence in complex systems (Gunnarsson et al. 2013). Waterfowl researchers have consistently found evidence for density-dependent population growth at continental scales (Vickery and Nudds 1984, Viljugrein et al. 2005, Sæther

et al. 2008, Murray et al. 2010), although the underlying mechanisms responsible for these patterns remain elusive. In a recent analysis, Murray et al. (2010) suggested that local processes such as density-dependent nest predation could scale up to shape the patterns that are apparent at larger spatial and temporal scales. Indeed, nest predators have long been implicated as potential drivers of density-dependence in waterfowl, because breeding ground productivity limits populations (Hoekman et al. 2002), and nest predation is the primary cause of reproductive failure (Klett et al. 1988, Greenwood et al. 1995).

Nest predation has thus received considerable attention by waterfowl managers, with special emphasis on the functional responses of predators to nest density (Larivière and Messier 1998, 2001a, Gunnarsson and Elmberg 2008). Nevertheless, it is unclear how different types of predators search for nests (Larivière and Messier 2001b, Phillips et al. 2003), and considerable uncertainty remains as to whether nest predation is density-dependent (Major and Kendal 1996, Ackerman et al. 2004). Some studies report strong patterns of density-dependent nest predation (Gunnarsson and Elmberg 2008), while others report weak density dependence (Clark and Wobeser 1997) or density-independent nest predation (Padyakova et al. 2010). These apparent contradictions may

have arisen from differences in the type of nest used (artificial vs natural) (Major and Kendal 1996, Butler and Rotella 1998) and in the predator community (Ringelman et al. unpubl.). However, some of this variation may result simply from differences in the spatial scale at which nest density was defined. With few exceptions (Andrén 1991, Ackerman et al. 2004, Ringelman et al. 2012), nest density is defined typically on the basis of an arbitrary area (number of nests in a study plot or site). Yet, such measures of density may not be ecologically meaningful and predators may not respond to patterns of nest density at these arbitrary scales. Rather, predators may respond to nest densities at smaller spatial scales, such as local clusters of nests. Despite considerable interest in density-dependent nest predation in birds, few studies have examined the spatial scale at which nest clustering naturally emerges, and fewer still have studied the adaptive consequences of this localized nest density.

Any analysis of density-dependent nest predation (on natural nests) must also define a temporal scale over which to measure nest density. Ackerman et al. (2004) and Andrén (1991) used all nests initiated in a season to define nest density (these studies used nearest-neighbor distance), irrespective of whether those nests were simultaneously active. By adopting a season-long temporal window, these studies examined whether predators aggregate in patches of high nest density, either through functional or numerical responses. An alternative approach would be to examine density-dependent predation using a shorter temporal window, which is useful in understanding which nearby nests are available to a predator in a given foraging period. If predator foraging behavior is responsible for density-dependent nest predation (e.g. through area-restricted search after finding a nest, Andrén 1991), then examining only temporally-coincident nests could potentially capture this dynamic. A direct comparison of these methods can be found in Ringelman et al. (2012); they found no evidence for density-dependent predation when analyzing all nests within a season, but were able to detect density-dependence by only considering simultaneously active nests.

In this study, we seek to more fully explore the link between patterns of nest density and predation risk in a well-studied model system of management concern. Using three years of data on waterfowl nesting in California, we examine how nest density changes throughout the season across a continuum of local spatial scales, and then analyze the fitness consequences of those patterns. By studying nest density at the spatial and temporal scales at which it naturally emerges, our analyses provide new insight into how predator foraging behavior influences nest success.

Methods

Our study took place on the Grizzly Island Wildlife Area in the Suisun Marsh of California (38°08'N, 121°59'W), in an 800 ha block of upland nesting fields that is managed by the California Dept of Fish and Wildlife as waterfowl nesting habitat. This section of uplands is further divided into fields (5–30 ha each) by dirt roads, ditches and levees. There are a variety of vegetation types available to nesting waterfowl, including mid-height (<1 m) grasses (*Bromus* spp.,

Lolium spp., *Hordeum* spp.), tall (>1 m) grasses (*Elytrigia* spp., *Phalaris* spp.), herbs (*Atriplex patula*), vetch (*Vicia* spp.), pickleweed *Salicornia virginica*, and thistle (family Asteraceae). The primary predators on Grizzly Island are striped skunks *Mephitis mephitis* and raccoons *Procyon lotor*, although coyotes *Canis latrans* and common ravens *Corvus corax* are transiently present.

We used three years of nesting data in our analyses: 2008, 2010 and 2011. In 2009, a large-scale habitat manipulation was conducted by the California Dept of Fish and Wildlife, California Waterfowl Association, and the US Geological Survey (USGS) to improve nesting habitat for waterfowl (manipulated fields were unavailable for nesting in 2009). Briefly, 11 of the 25 nesting fields were sprayed for weeds, disked and replanted with vegetation (largely novel to Grizzly Island) intended to provide high-quality nesting habitat for waterfowl including triticale (*Triticosecale* spp.), wild oats (*Avena* spp.), and wild radish (*Raphanus* spp.). By analyzing nest data from both before and after the manipulation, we can determine whether patterns of nest clustering and success change when the underlying habitat is dramatically altered.

We conducted nest searches from 1 April through 7 July to ensure that we found both early- and late-nesting ducks (McLandress et al. 1996). Each field was searched at three-week intervals following standard protocols (Klett et al. 1986, Gloutney et al. 1993), slightly modified by McLandress et al. (1996) for this study site. Nests were found on average during the first week of incubation (Supplementary material Appendix A1 Fig. A1). Nest searches were conducted by stringing a 50 m rope between two all-terrain vehicles, and dragging the rope across the top of the vegetation, causing females to flush from the nest. To generate additional noise, tin cans containing rocks were attached every 2 m along the length of the rope. After nests were located, we marked them with a 2 m bamboo stake placed 4 m north of the nest, and a shorter stake placed level with the vegetation height next to the nest bowl. Nest locations were recorded with a GPS receiver, and we revisited nests on foot every seven days until nest termination. We determined the incubation stage of the nest by candling (Weller 1956), and the date of nest initiation by subtracting the nest age when found (number of eggs when found plus the incubation stage) from the date the nest was found. Concordant with previous studies, in our nest fate analyses, we considered a nest to be depredated when ≥ 1 egg was depredated or missing (partial depredations are relatively common at our site) (Ringelman and Stupacuk 2013), and we assumed a depredation occurred on the midpoint between nest checks. For descriptive purposes, we report observed nest density and Mayfield nest success estimates (Mayfield 1975, Johnson 1979) for the different years of our study. On the date the nest was found, we quantified the degree of habitat structure and vegetation density using a Robel pole (Robel et al. 1970). Briefly, we placed a 1.5 m measuring stake at the nest bowl, and recorded the lowest height visible (to the nearest 5 cm) from 4 m distant while viewing the stake from 1 m above the ground. Measurements were taken from each of the four cardinal directions and then averaged. These values are related to the structural complexity and overall biomass of vegetation at the nest site (Robel et al. 1970), and provide a useful measure of visual

and potentially olfactory concealment from terrestrial predators. We did not measure temporal changes in vegetation structure (which could potentially influence nest survival) as the nest aged. However, the vegetation at our site in California is largely full-grown by the start of the breeding season and there is little qualitative change in vegetation structure over the course of a nesting attempt (KMR unpubl.); thus, we feel that our single measurement of vegetation provides a useful index of nest concealment.

There are two closely-related dabbling duck species that nest at our study site: ~70% are mallards *Anas platyrhynchos* and the remaining ~30% are gadwall *Anas strepera* (these two species comprise more than 99% of ducks found at our site). Mallards initiate nests 3–4 weeks earlier than gadwall at our study site in California. There may also be important behavioral differences between species: gadwall are shorter-lived than mallards (Krementz et al. 1997), and tend to exhibit riskier behavior (Ackerman et al. 2006) characteristic of a ‘faster’ life-history strategy (Krementz et al. 1989). Indeed, we generally observed gadwall in shorter, sparser vegetation than mallards, but gadwall tended to hold tighter (flush at shorter human approach distances) to the nest (KMR and JME unpubl.), concordant with these other studies comparing mallard and gadwall risk-taking and life-history strategies.

To understand how waterfowl nests are clustered in both space and time, we divided the nesting season into one-week intervals, and analyzed the local spatial association of active nests for each week. We used the package *Spatstat* (Baddeley and Turner 2005) in R ver. 2.12 to analyze spatial association using Ripley’s *L* function (a variance-stabilized transformation of Ripley’s *K*), with a Ripley’s isotropic boundary correction (which is best-suited for our polygonal study site) applied to the edges of the areas where we searched for duck nests each year. This function compares the level of spatial clustering to complete spatial randomness across a continuum of spatial scales. Clustering was determined to be significant when the *L* estimate exceeded the upper 100% significance band generated by 1000 simulations of a homogenous Poisson point process of equal intensity. Visual examination of Ripley’s *L* plots indicated that clustering was often observed at 400 m, the middle value given the default settings for this analysis. However, we chose to assess clustering at a more conservative value of 200 m because we wanted to examine the distributions of nests at very local spatial scales and ensure that significant ‘clustering’ was not simply a statistical artifact, but rather, a true pattern created by the habitat selection decisions of individual birds. To illustrate how the degree of clustering changed through time at the scale of 200 m, we compared the observed level of clustering (observed *L*-estimate at 200 m) with the maximum value of the 100% upper significance envelope for each week. We present analyses on mallard and gadwall nests separately; when both species were combined, our results closely matched the mallard-only analysis because our sample was so heavily dominated by mallard nests.

To determine whether nest clustering influenced nest survival, we studied the relationship between nest fate and the distance to the nearest neighbor (either species). Similar to Ripley’s *L*, nearest neighbor distances provide a measure of nest dispersion (i.e. local nest clustering) within a field (Clark and Evans 1954). Typically, nearest-neighbor analyses

of waterfowl nests identify nearest-neighboring nests using all nests in a season, regardless of whether the neighboring nests were active simultaneously (Andrén 1991, Ackerman et al. 2004). An alternative method to assess nearest neighbor effects is to restrict the pool of neighbors to only those nests active at the same time as the focal nest (Ringelman et al. 2012). This measure reflects what a predator would encounter if it subsequently searched in a restricted area around the focal nest, or returned to the area in subsequent nights. We adopted such an approach here and used only nests that were simultaneously active to identify the nearest neighbor. Also, any predator functional responses to nest clustering are likely independent of nest species; that is, from a predator’s perspective, there is probably little difference between consuming a mallard versus a gadwall nest. Thus, for each focal nest, we identified the nearest neighbor of either species. For focal nests that were depredated, we assumed that risk to neighbors was greatest near the time of that nest’s depredation event and so we identified the nearest neighbor as the closest active nest on the date when the focal nest was depredated. For successful nests, we determined the nearest active neighbor on the midpoint date between nest initiation and hatching. We omitted nests with nearest ‘neighbors’ more than 500 m away (these were the first nests established, and consequently, nearest-neighbor distances were quite large) because our focus in this analysis was on neighboring nests that a predator might encounter in a local area during a foraging bout; removing these outliers did not change our results. We report means \pm SE unless otherwise noted.

We then used this nearest neighbor distance as a covariate in an analysis of nest survival, conducted using logistic-exposure nest-survival methods (Shaffer 2004) in the R package *nestsurvival*. These methods account for variation in exposure days among nests, and allow the researcher to simultaneously model the effects of several covariates on nest survival. We modeled nest survival as a function of study year, nest initiation date, vegetation density, nest age and nearest neighbor distance. We included squared terms for nest initiation date and nest age (Pieron and Rohwer 2010), and also modeled the interaction between year and nest initiation date. We ranked models based on Akaike’s information criterion (AIC) scores corrected for small sample size (AIC_c) (Burnham and Anderson 2002). We also calculated model-averaged parameter estimates and relative variable weights (for each variable, the sum of AIC weights of the models in which it appears) (Burnham and Anderson 2002).

Results

The three nesting seasons in our study exhibited a wide range of nest densities and predation pressure. In 2008, observed nest density and Mayfield nest success were low: we found 190 mallard nests (0.64 nests ha⁻¹, Mayfield nest success = 22%) and 118 gadwall nests (0.56 nests ha⁻¹, Mayfield nest success = 11%). In contrast, nest density and nest success were both high in 2010, and we found 587 mallard nests (1.51 nests ha⁻¹, Mayfield nest success = 38%) and 316 gadwall nests (0.94 nests ha⁻¹, Mayfield nest success = 36%). In 2011, we again found a large number of

nests (706 mallard = 3.46 nests ha⁻¹, 266 gadwall = 1.50 nests ha⁻¹), but Mayfield nest success was low, at 13% for both species.

Nest clustering

We divided each nesting season into weekly intervals beginning with the first nest initiated, and then used Ripley's *L* to assess the spatial association of nests. Mallard (and to a lesser extent, gadwall) nests were significantly clustered after the first 2–3 weeks of the nesting season at most spatial scales > 50 m (see Fig. 1 for an example). When we assessed the degree of clustering at the scale of 200 m, we found that mallards were strongly clustered throughout the nesting season in all three years of the study (Fig. 2), even after the habitat manipulation in 2009. Across all weeks and years, average mallard nest clustering was 1.2 times more likely than even the maximum amount of clustering expected by

chance alone. However, gadwall showed a more complicated pattern. Gadwall appeared to be clustered during seasonal peaks of nest density in 2008 and 2010, and throughout the entire season in 2011. In general, the tendency for gadwall nests to be clustered was weaker than for mallard (Fig. 2).

Nearest neighbor distance and nest survival

Mallard nearest-neighbor distances (to any species) were large in 2008, averaging 113.9 ± 7.6 m, but were smaller in 2010 (73.3 ± 3.2 m) and 2011 (68.0 ± 2.5 m). Gadwall nearest-neighbor distances to any species were 151.4 ± 18.3 m, 78.0 ± 4.6 m and 90.1 ± 10.1 m in 2008, 2010 and 2011, respectively. The distributions of nearest neighbor distances are presented in the Supplementary material Appendix A1 Fig. A2. Because we examined species-specific nest clustering, we conducted our survival analysis for each species separately to ease interpretation of results. Our logistic exposure analysis of nest survival, including all possible combinations of variables, consisted of 96 models. While this is a large model set, all of the variables under consideration could have plausible biological effects on nest survival, so we are confident our analysis is not 'model dredging' (sensu Burnham and Anderson 2002).

Mallard

Model selection provided substantial support for the top four nest survival models, all of which contained nearest-neighbor distance (Table 1). Based on model-averaged regression coefficients, nests initiated earlier in the season, in dense vegetation, and with closer nearest neighbors were more likely to successfully hatch (Table 2). (Note: coefficients for each individual model were very similar to the model-averaged coefficients). Relative variable weights indicated that nearest-neighbor distance was a much better predictor of nest success than nest vegetation (Table 2). To illustrate the influence of nearest-neighbor distance on daily survival rate we plotted the daily survival rate versus nearest-neighbor distance for each year at the mean values for the other variables, with 85% confidence intervals (Arnold 2010). In all years, nests with closer nearest neighbors were more likely to be successful (Fig. 3a).

Gadwall

For gadwall, nest survival did not depend strongly on any single variable, with estimates for model-averaged regression coefficients overlapping zero (Table 3). Indeed, every variable appeared in at least one model with $\Delta AIC_c < 2$. Still, nearest neighbor distance appeared to be of moderate importance in explaining nest survival (Table 3). Although there was a trend for gadwall nests with closer nearest neighbors to have higher survival (Fig. 3b), the relationship was not nearly as strong as in mallards.

Discussion

Mallard nests were strongly clustered in all three years of our study, a phenomenon that was robust to annual variation in nest density (combined mallard and gadwall: 1.20 to 4.96

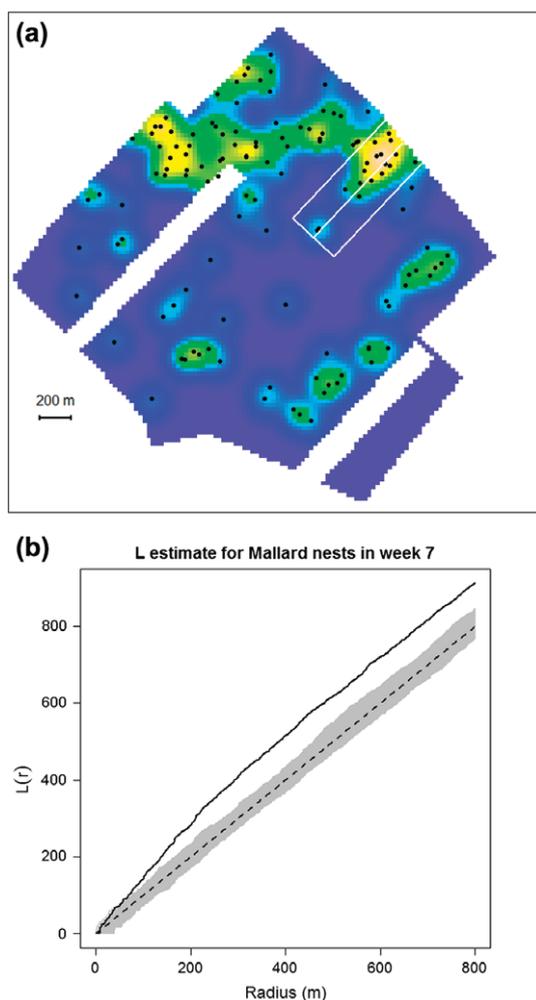


Figure 1. (a) A kernel density plot of active mallard nests in week 7, 2010 (colors range from blue to green to yellow in order of increasing nest density). Areas of high nest density often span anthropogenically-defined field boundaries, as it does in the two fields outlined in white. (b) The corresponding plot of the Ripley's *L* estimate. The observed *L* estimate (solid black line) for the data exceeds the gray band of the simulation envelope (1000 simulations) for complete spatial randomness (shown as a 1-to-1 dashed line) at most spatial scales.

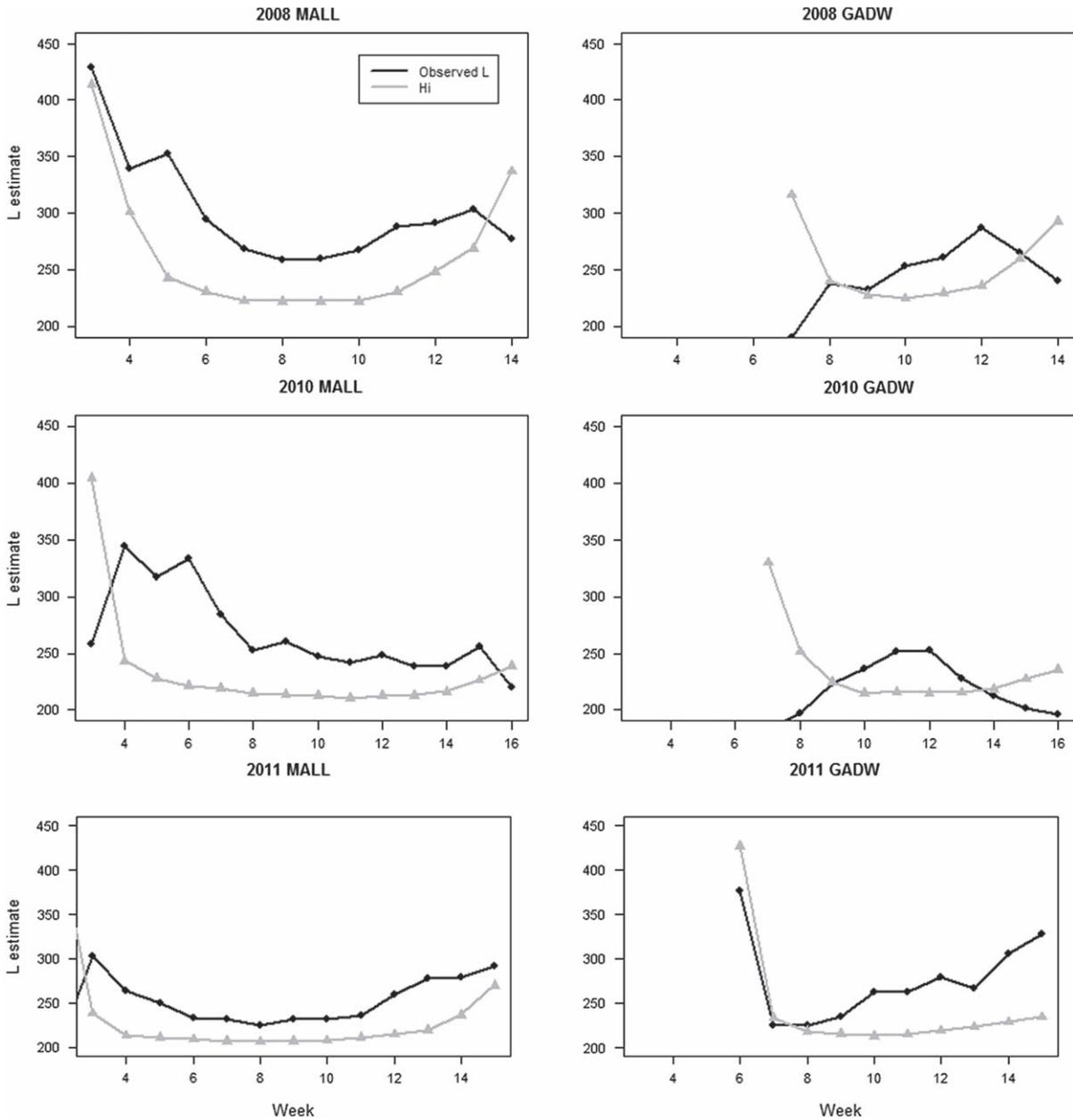


Figure 2. L estimates at 200 m for the observed distribution of duck nests during each week of the nesting season. Also shown is the maximum level of clustering expected under complete spatial randomness at 200 m, represented here as the upper L estimate of the 100% significance envelope generated by 1000 simulations (“Hi”). Duck nests are significantly clustered when the observed L estimate exceeds the high envelope estimate.

nests ha^{-1}) and predation pressure (13% to 37% combined nest survival). Strong nest clustering emerged approximately 2–3 weeks after the start of the nesting season, and was observed at most spatial scales larger than 50 m. In contrast, later-nesting gadwall nests were much less clustered on

average. Whereas there was some indication that the lack of a pattern for gadwall may be due to small sample sizes (in 2008 and 2010 clustering only appeared when nest numbers peaked), this was not supported in 2011 when we did observe clustering even with few gadwall nesting on the landscape.

Table 1. Top four models predicting mallard nest survival.

Rank	Parameters in model	k	AIC _c	Δ AIC _c	Weight
1	year, distance, initiation, initiation ² , age, age ² , year × initiation	9	2499.99	0	0.58
2	year, distance, initiation, initiation ² , vegetation, age, age ² , year × initiation	10	2501.82	1.83	0.23
3	year, distance, initiation, age, age ² , year × initiation	8	2502.91	2.92	0.13
4	year, distance, initiation, vegetation, age, age ² , year × initiation	9	2504.72	4.73	0.05

Table 2. Model-averaged coefficients and parameter likelihoods for mallard nest survival. Nearest neighbor distance is a better predictor of nest success than either nest vegetation or nest age.

Variable	Relative variable weights	Model-averaged coefficient	SE
Year	1.000	-2.3901	0.4102
Initiation date	1.000	-34.1307	6.3645
Year × Initiation date	1.000	0.0170	0.0032
Nearest-neighbor distance	1.000	-0.0033	0.0007
Nest age	0.999	-0.1280	0.0353
Nest age ²	0.999	0.0026	0.0007
Initiation date ²	0.811	0.0002	0.0001
Vegetation density	0.286	0.0029	0.0071

However, the question remains as to whether late-nesting gadwall were joining (spatially-distinct) clusters of mallard nests; that is, whether gadwall were dispersed with respect to conspecifics, but were still clustered with other ducks. A rigorous treatment of this question is beyond the scope of the current manuscript, although our nearest-neighbor analysis of nest fate suggests that gadwall nesting near mallard nests experienced some benefits of clustering.

When we examined the location of nest clusters, we found that they often extended across field boundaries at our study site (Fig. 1a). This is important from a methodological perspective, in that researchers may be imposing an anthropogenic bias when defining nest densities as the number of nests per some arbitrary unit of area, such as a field or management unit. Defining an ecologically relevant measure of density remains a pervasive challenge in ecology,

whether researchers are counting the number of plants per quadrat, starfish per square meter, or duck nests per hectare. Yet, understanding the scale at which heterogeneity in the distribution of organisms emerges naturally is critical to understand how density-dependent processes (e.g. survival, recruitment, predation) operate. In waterfowl, for example, there is little consensus on whether predation is density-dependent and our results suggest that some of the uncertainty may have arisen because of discrepancies in the spatial and temporal scales studied. Using unbiased measures of spatial association (such as Ripley's *L* or neighbor distances) may provide a more ecologically meaningful measure of density.

Indeed, when we use local nest clustering (nearest-neighbor distances) as our metric of nest density, we find that the degree of nest clustering had a strong effect on survival rates of mallard nests. Imperfect detection probability could potentially drive the relationship between nearest-neighbor distance and nest success. Nests in high-risk areas may have large nearest-neighbor distances simply because many of their neighbors are depredated before we find them...and the neighbors that we do find are also likely to be depredated, thus generating a spurious relationship between large nearest-neighbor distances and unsuccessful nests. However, we do not believe this to be true at our site for at least two reasons: 1) in high predation years, we would expect to see many more large nearest-neighbor distances that correspond to unsuccessful nests, but this is not what we observed (Supplementary material Appendix A1 Fig. A2); 2) this artifact should also emerge with artificial nests (where our 'detection' probability is perfect) in high predation fields, but an artificial nest experiment by Ringelman et al. (2012) at our site found no

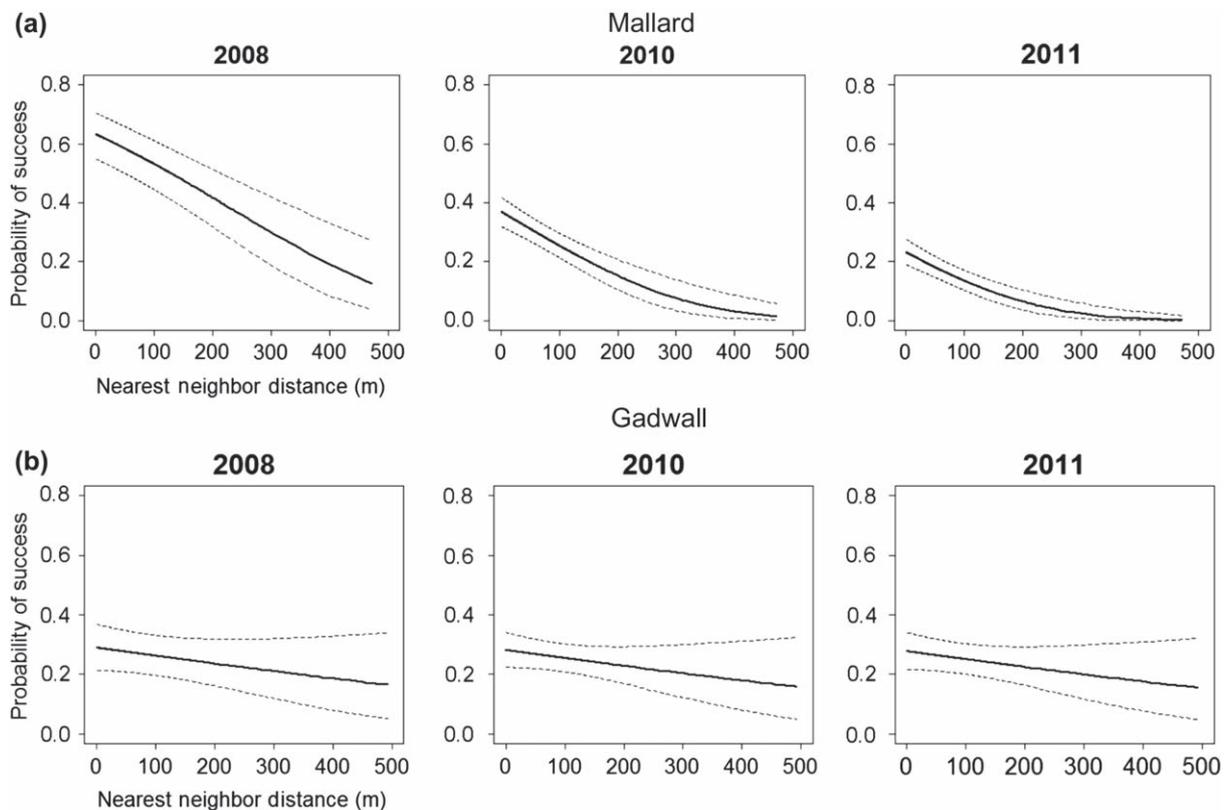


Figure 3. Modeled relationship (\pm 85% CI) between nest fate and nearest neighbor distance, holding all other variables at the mean.

Table 3. Model-averaged coefficients and parameter likelihoods for gadwall nest survival.

Variable	Relative variable weight	Model-averaged coefficient	SE
Initiation date	0.922	-4.4205	6.6296
Nest age	0.843	-0.0585	0.0524
Nest age ²	0.658	0.0012	0.0007
Nearest-neighbor distance	0.617	-0.0008	0.0005
Year	0.493	-0.3018	0.3311
Year × Initiation date	0.302	0.0022	0.0019
Initiation date ²	0.291	0.0000	0.0001
Vegetation density	0.291	0.0041	0.0095

evidence of this. To our knowledge, ours is one of few studies (Ringelman et al. 2012) to use a temporally-refined nearest-neighbor analysis to study density-dependent processes. Using this method, we found that nests with closer nearest neighbors were more likely to survive, a result that is counter to the general prediction that predators respond positively to prey density. The literature on waterfowl generally supports the notion that nest predation is, at least in some cases, positively density-dependent, and so our results challenge that conventional thinking. However, behavioral-ecological theory predicts that there can be many anti-predator benefits to nesting in a group of conspecifics. For example, birds in a group may be more likely to detect predators (reviewed by Lima 2009), and/or successfully deter them (reviewed by Montgomerie and Weatherhead 1988, Caro 2005). Furthermore, because many nest predators would become satiated after (or even before) consuming the large number of eggs (up to nine) in a single mallard nest (Ackerman et al. 2003), the per capita risk of predation may be diluted by nesting near other ducks. In our system, the fitness benefits of nesting in a cluster appear to outweigh the potential risks.

Similarly, gadwall with closer nearest neighbors tended to survive better, though the magnitude of this effect was small. This perhaps is not surprising, given that gadwall do not cluster as strongly as mallards; we would only expect to see a benefit of clustering, if, in fact, gadwall were clustered in the first place. The weak relationship between gadwall nest survival and nearest-neighbor distance was likely driven by gadwall proximity to mallard nests (recall that our nearest-neighbor analysis calculated the distance between a gadwall nest to the nearest nest of either species). When we repeated the logistic exposure analysis using only gadwall-to-gadwall nearest neighbor distances, neighbor distance had no effect on nest fate (there is no benefit for gadwall to cluster with conspecifics). Thus, it would seem that gadwall were gaining some benefit from nesting near mallard nests, as our original analysis shows. One avenue for future research is to examine whether late-nesting gadwall are nesting unusually close to mallard clusters, or alternatively, whether their nesting strategy does not depend on clustering and dilution effects, but rather on widely dispersing their nests and holding tighter when predators approach.

Finally, examination of Fig. 3a suggests density dependence could yet be operating at large spatial and temporal scales; years with higher nest densities are associated with higher overall levels of predation (though Fig. 3a shows modeled, not raw data). Our analysis was designed to pick

out density dependence caused by processes that operate at small spatial and temporal scales, such as predator foraging behavior; however, mechanisms occurring at larger scales (e.g. predator functional or numerical responses) may yet drive inter-annual patterns of density dependence. That is, within a year, clustered nests may survive better (e.g. through dilution effects caused by predator foraging behavior), but predation risk could be higher in years of high nest density (more prey attracts more predators). We are currently using 18 years of nesting data at our site to examine large-scale spatial and temporal variation in density-dependent predation (Ringelman et al. unpubl.).

Our study was conducted on a population of ducks breeding in California, where the primary nest predators – striped skunks and raccoons – are believed to depredate waterfowl nests opportunistically while searching for small mammal prey (Larivière and Messier 2001b, Ackerman 2002). Group nesting by ducks in California could function effectively to dilute predation risk from these types of predators that are “just passing through” (Andrén 1991), and depart after destroying (or partially destroying) a single nest. However, large numbers of North American waterfowl breed on the prairies of the Dakotas and south-central Canada, where the predator community is quite different (Klett et al. 1988, Greenwood et al. 1995). In those regions, red foxes *Vulpes vulpes* are important nest predators and they specifically target duck nests, posing a risk to both eggs in the nest and the incubating female (Klett et al. 1988, Johnson et al. 1989, Pasitschniak-Arts and Messier 1995). After depredating a nest, foxes are likely to employ area-restricted searching to locate additional nests (Seymour et al. 2003, 2004), because foxes do not become “satiated” after depredating a single nest. Instead, foxes are known to cache eggs that they do not immediately consume (Sargeant et al. 1998). Thus, unlike at our site in California, waterfowl breeding in regions where foxes are present may benefit from dispersing their nests across the landscape (Tinbergen et al. 1967). Indeed, the potential cost of clustering when foxes are present is also much higher, because foxes pose a mortal threat to incubating females (Sargeant et al. 1998). Very few studies report on the dispersion of duck nests on the prairies; however, those that do have noted a random nest dispersion, or even higher levels of nest dispersion (nests are unusually far apart) where foxes are present (Duebbert and Lokemoen 1976, Hines and Mitchell 1983). Understanding the foraging methods of predators and the fitness costs and benefits of nest dispersion could not only help us better understand the driving factors that impact nest success for these species of management concern, but could also provide insight and perhaps some explanation for the apparently contradictory patterns of density-dependent nest predation reported among sites.

What habitat selection mechanisms could lead to patterns of nest clustering? The most obvious explanation is that nests may be clustered simply because the underlying, preferred habitat is inherently clustered. If this preferred vegetation conveys protection from predators, then this would also explain why these clusters of nests survive better. However, our analyses showed that nearest-neighbor distance had a much stronger influence on mallard nest fate than nest vegetation. Furthermore, we found that patterns of nest clustering persisted (in 2010 and 2011) after the large-scale

habitat manipulation that produced relatively uniform vegetation, and there was still a benefit to nesting near other birds. This suggests that vegetation alone may not be sufficient to explain the patterns of clustering and nest success that we observed. Given the consistently strong tendency for nests to be clustered at our site, we suggest that social cues may play an important role in habitat selection.

Regardless of the mechanism by which nest sites were selected, at a population level, our results provide strong evidence that mallard nests were clustered at local spatial scales and this clustering had important fitness consequences. To understand the patterns that emerge at a population scale (e.g. nest dispersion) and that affect ecological processes (e.g. density-dependent predation), we need to better understand the behavioral ecological mechanisms (nest site selection cues, conspecific attraction, predator search rules) that most influence the fitness of predators and prey at an ecologically relevant scale. In doing so, we might not only account for the apparently conflicting patterns of density-dependent predation often reported, but we may also be in a better position to manage populations of conservation concern in the face of rapidly changing environmental conditions.

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Supplementary material (available online as Appendix oik-00851 at <www.oikosoffice.lu.se/appendix>). Appendix A1.