

# Spatiotemporal patterns of duck nest density and predation risk: a multi-scale analysis of 18 years and more than 10 000 nests

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Many avian species are behaviorally-plastic in selecting nest sites, and may shift to new locations or habitats following an unsuccessful breeding attempt. If there is predictable spatial variation in predation risk, the process of many individuals using prior experience to adaptively change nest sites may scale up to create shifting patterns of nest density at a population level. We used 18 years of waterfowl nesting data to assess whether there were areas of consistently high or low predation risk, and whether low-risk areas increased, and high-risk areas decreased in nest density the following year. We created kernel density maps of successful and unsuccessful nests in consecutive years and found no correlation in predation risk and no evidence for adaptive shifts, although nest density was correlated between years. We also examined between-year correlations in nest density and nest success at three smaller spatial scales: individual nesting fields (10–28 ha), 16-ha grid cells and 4-ha grid cells. Here, results were similar across all scales: we found no evidence for year-to-year correlation in nest success but found strong evidence that nest density was correlated between years, and areas of high nest success increased in nest density the following year. Prior research in this system has demonstrated that areas of high nest density have higher nest success, and taken together, our results suggest that ducks may adaptively select nest sites based on the local density of conspecifics, rather than the physical location of last year's nest. In unpredictable environments, current cues, such as the presence of active conspecific nests, may be especially useful in selecting nest sites. The cues birds use to select breeding locations and successfully avoid predators deserve continued attention, especially in systems of conservation concern.

A primary concern for avian conservation biologists is providing attractive and high quality nesting habitat for breeding birds. To do so requires a thorough understanding of how birds identify and select nest sites. Habitat quality inevitably changes over time; the degree and speed of environmental change, and the ability of birds to successfully track those changes is a key issue in conservation biology (Lebbin et al. 2010). In particular, human-induced rapid environmental change can lead to the decoupling of habitat quality and habitat selection cues, creating ecological traps (Schlaepfer et al. 2002, Robertson and Hutto 2006, Robertson et al. 2013). Birds relying on environmental cues that no longer reliably indicate high-quality nesting sites may suffer population declines, whereas species that exhibit plastic, adaptive habitat choice should be able to better cope with changing conditions (Møller et al. 2010, Sih 2013).

One form of behavioral plasticity in nest site selection is based on prior breeding experience: birds return to previously successful areas, but avoid areas where they were

unsuccessful (“win-stay, lose-shift”, Shields et al. 1988). This win-stay, lose-shift behavior has been documented in dozens of avian species over the last 35 years in both observational and experimental studies (Hoover 2003, Lima 2009, Chalfoun and Martin 2010, Kearns and Rodewald 2013). However, the relative benefit of this strategy depends on the temporal correlation in predation risk among habitat types and locations; there is no benefit to shifting nest sites if predation risk is unpredictable from one time period to the next (Doligez et al. 2003, Schmidt 2004).

The win-stay, lose-shift strategy is an individual-level behavior based on prior nesting experience. However, if there is predictable spatial variation in predation risk, the process of many individuals adaptively changing nest sites may scale up to create shifting patterns of nest density at a population level. In environments with strong temporal correlation in predation risk, birds should tend to vacate areas of high nest predation risk and cluster in safer areas over time (Hoover 2003). Adaptive aggregation may even

be enhanced in species that use population-level metrics of patch quality – such as the prior success of conspecifics – as a cue for selecting future nest sites (Doligez et al. 1999, 2003, 2004, Danchin et al. 2004, Valone 2007, Mihoub et al. 2009, Hoi et al. 2012).

Population-level shifts in response to predation are more likely to be detected in species that are both philopatric to an area, and are not limited by the availability of nest sites through intense territoriality. In one such group, ground-nesting dabbling ducks *Anas* spp., individuals have been shown to disperse farther (select new breeding home ranges) in the subsequent season following nest failure (Lokemoen et al. 1990, Lindberg and Sedinger 1997, Clark and Shutler 1999, Blums et al. 2002). In cavity-nesting waterfowl, individuals select specific nest locations following win-stay, lose-shift rules (Doty and Lee 1974, Majewski and Beszterda 1990, Hepp and Kennamer 1992), and so it is reasonable to expect ground-nesting species may follow a similar strategy. While spatially-explicit mark–recapture data on ground-nesting individuals is lacking, a population-level analysis of nesting patterns may provide new insight on adaptive shifts in these ducks.

Here, we used data from more than 10 000 waterfowl nests collected over 18 years in the Suisun Marsh of California to assess the between-year correlations in patterns of nest density and predation risk. This is one of the largest data sets of ground-nesting ducks collected from a single study site, and offers a unique opportunity to explore spatial and temporal trends in nest density and nest success. Each year we mapped ambient levels of predation risk onto the study area and then assessed: 1) whether there were areas of consistently high or low predation risk (temporal correlation in habitat quality), and 2) whether spatial patterns in nest density were related to habitat quality in the previous year.

## Methods

### Study area

Our study took place in the Suisun Marsh of California on the Grizzly Island Wildlife Area (38°08'N, 121°59'W) in a large (~800 ha) section of upland nesting habitat managed specifically for nesting ducks by the California Dept of Fish and Wildlife. This section of uplands is divided into fields (10–25 ha each) by unmaintained roads, levees and ditches. Vegetation at this site is heterogeneous, and includes grasses, forbs, cereal grains and leafy weeds (see Ringelman et al. 2014 for a complete description). There are several closely-related dabbling duck species that nest on Grizzly Island: currently, 60–70% are mallards *Anas platyrhynchos*; MALL and 30–40% are gadwall *Anas strepera*; GADW, although northern pintail *Anas acuta* were more common in earlier years (~3%); cinnamon teal *Anas cyanoptera* and northern shovelers *Anas clypeata* have always nested in low densities (Ackerman 2002). Unless otherwise noted, we only considered mallard and gadwall nests and ran analyses separately for each species. The nest predator community has fluctuated over time, but has primarily consisted of striped skunks *Mephitis mephitis* and raccoons *Procyon lotor*, although coyotes *Canis latrans*, common ravens *Corvus corax* and gopher

snakes *Pituophis catenifer* have been present in some years (Ackerman 2002).

Duck nesting data have been collected at Grizzly Island Wildlife Area since 1985. Between 1990 and 2011, annual observed nest densities averaged 2.78 nests ha<sup>-1</sup> (range 0.91–6.98 nest ha<sup>-1</sup>) and Mayfield nest success (Mayfield 1975) averaged 23.4% (range 3.8%–47.3%). We included 18 years of data in our analysis (1990–1992, 1994–2004, 2008–2011) totaling 10 706 nests. Nest searches were not conducted from 2005–2007 and precise nest site locations were not available for 1993 or prior to 1990. Nests that were abandoned after researcher disturbance (female did not return after we first found the nest, or abandoned after capture or accidental nest damage) were censored from our analyses (1441 nests excluded). Because our goal was to explore the spatial overlap in nest density between consecutive years, our analyses considered 15 year-pairs. Within each year-pair, we included only those fields that were searched in both years (Supplementary material Appendix 1 Table A1), except we excluded the 1998–1999 year-pair due to low sample size ( $n < 70$  nests in each year) for the kernel density analysis.

In each year, nest searches were conducted between April and July and fields were searched at three-week intervals using standard protocols (Klett et al. 1986, Gloutney et al. 1993, McLandress et al. 1996). Searches were conducted by attaching 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 increase the probability of flushing a hen, tin cans filled with rocks were attached to the rope every 1 m. When a nest (a scrape or bowl containing at least one egg) was found, we marked it with a 2 m stake placed 4 m north of the nest bowl (Hein and Hein 1996), and a shorter stake placed at the nest bowl, level with the vegetation height to facilitate capture of hens on the nest. Nests were revisited every seven days on foot and we considered a nest to be successful if  $\geq 1$  egg hatched (Klett et al. 1986a), and unsuccessful if the nest was depredated or abandoned by the female due to natural causes.

From 2000–2011, we marked nest locations with a handheld GPS device; in earlier years (prior to the public availability of GPS), researchers measured the distance in meters from each nest to at least two field boundaries, and then marked the nest location on hand-drawn maps. For these earlier years, we used Google Earth (ver. 7.1.2.2041) to calculate the angles of the field boundaries relative to north, and then used trigonometry to calculate the approximate UTM coordinates for each of the nests for which we had measurements. We acknowledge some imprecision in this method, but it is probably on the scale of the 5–10 m accuracy of a handheld GPS.

### Kernel density analysis

In our first analysis, for each year, we divided the data into successful and unsuccessful nesting attempts and created nest density maps of the study area using kernel smoothing methods in the *adehabitat* package (Calenge 2013) in R ver. 2.14.2 (<www.r-project.org>). We used a fixed bivariate-normal kernel estimator and selected our bandwidth by least squares cross-validation, which resulted in a peaky density

map that was well suited for identifying local areas of high nest density (Seaman and Powell 1996, Gitzen et al. 2006). For each species and year, we created three maps: 1) a density map of all nests, 2) a density map of successful nests, and 3) a density map of unsuccessful nests. We then compared the overlap of the three-dimensional probability density functions, the volume of intersection (hereafter VI, which ranged from 0 to 1), for all map pairs to examine patterns of spatial overlap between years (Fig. 1 shows maps from two representative years).

We were particularly interested in whether some areas were consistently safe or risky. If so, we would expect the spatial overlap (VI) of successful nests in year  $t$  and successful nests in year  $t + 1$  (S-S) and the VI of unsuccessful-unsuccessful (U-U) year-pairs to be greater than the VI of successful-unsuccessful (S-U) and unsuccessful-successful (U-S) year-pairs (i.e. consistency in risk means that the VI of S-S and U-U > S-U and U-S pairs). If ducks adaptively shift nest sites to safer areas, we would expect the VI of successful nests in year  $t$  and overall nest density in year  $t + 1$  would be higher than the VI of unsuccessful nests in year  $t$  and overall nest density in year  $t + 1$  (S-all > U-all).

Finally, we examined whether there was persistent spatial overlap in nest density. To accomplish this, we calculated the mean  $\pm$  SE VI of map pairs (all nests) in consecutive years ( $t$  and  $t + 1$ ), and in pairs with longer lag times ( $t$  and  $t + 2$ ,  $t + 3$ ,  $t + 4$ ,  $t + 5$ ). This analysis becomes increasingly sparse at longer lag times, because fewer appropriate map pairs exist; hence, we restricted any quantitative comparisons to lags  $\leq 3$  years. We repeated this lag analysis using map pairs of successful nests to diagnose spatiotemporal consistency in nest success.

Throughout the kernel analysis, we used the density of unsuccessful nests as our measure of predation risk. We

created our density maps using only nests that were actually found; however, some duck nests are depredated before they are located. This likely means that our density map of unsuccessful nests is over-smoothed: areas with many unsuccessful nests probably also contained even more unsuccessful nests that were never found. This is a conservative bias in our analysis, because birds should avoid risky areas even more strongly than our unsuccessful nest map predicts because those areas are more dangerous than we have estimated. Furthermore, our kernel overlap results suggest broadly similar patterns to the bias-corrected nest success analyses described below.

## Field-level analyses

The density of unsuccessful nests in an area provides a metric of ambient predation risk; an alternative measure of predation risk considers the percent of nests that are successful in a given area. To account for those nests that were depredated but not found, researchers calculate daily survival rates (DSR) for nests with known exposure periods (Mayfield 1961, 1975, Johnson 1979). Accordingly, we used the following equations to estimate percent nest success for mallards and gadwall, with nests hatching at approximately 35 days of age (Klett et al. 1986):

$$DSR = 1 - \left( \frac{\text{no. failed nests}}{\text{no. exposure days}} \right) \quad \% \text{ Success} = DSR^{35}$$

To reliably estimate the numbers of unobserved nests, Mayfield methods require large sample sizes of observed nests, where the total number of exposure days is greater than 750 (Klett et al. 1986). In any given year, most fields in our dataset fail to meet this expectation, so we used an

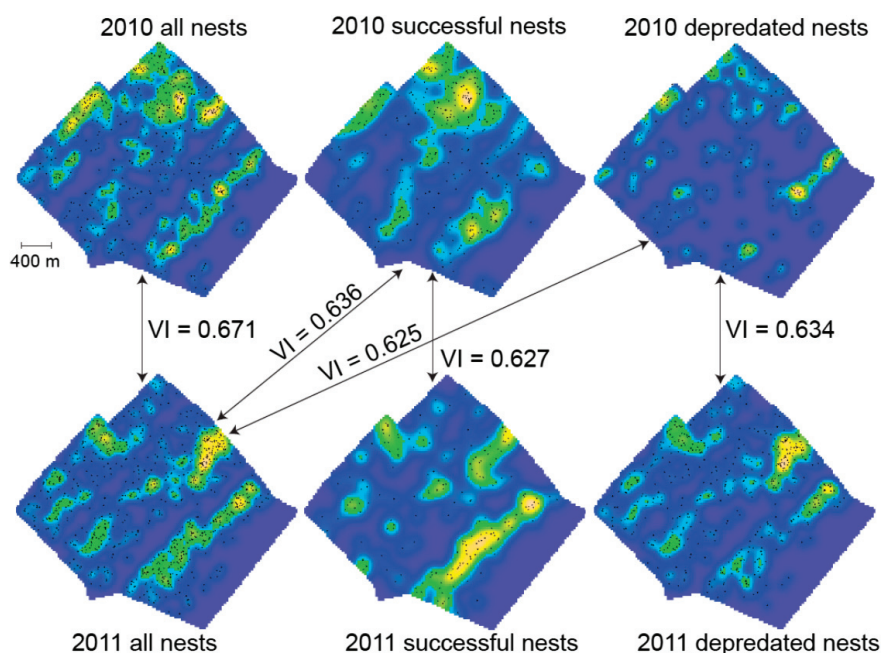


Figure 1. An example of kernel density plots for all nests, depredated nests, and successful nests in 2010 and 2011 (mallard *Anas platyrhynchos* and gadwall *Anas strepera* are combined here) at Suisun Marsh, CA, USA. Warmer colors represent higher nest densities. Also shown are the volumes of intersection (VI) for pairs of maps.

alternative formulation proposed by (Arnold et al. 2007) for estimating the number of unobserved nests (and thereby nest density) in each field:

$$\text{no. estimated nests} = \frac{\text{no. nests found}}{\text{DSR}^{\text{Average age when found}}}$$

Because years vary dramatically in estimated nest density and success, we standardized these metrics for each year using z-scores (i.e. percent success in a field minus the average percent success across all fields in that year, divided by the standard deviation in percent success). For each field, we then examined the between-year correlations among these metrics, specifically: 1) the correlation in nest success between years, 2) the correlation between nest success in year  $t$  and the change in nest density between year  $t$  and year  $t + 1$ , and 3) the correlation between nest densities in consecutive years. If ducks shift nest sites to safer areas, we expect previously successful areas to support higher densities the following year.

### Grid cell analyses

Previous studies at our site have shown that using field boundaries may not be an ecologically relevant way to measure nest density and success (Ringelman et al. 2012, 2014); we thus repeated our analyses at two smaller spatial scales. We overlaid a square 16 ha and 4 ha grid on a map of our site (Ringelman et al. (2014) showed that nests are often clustered at these small scales), and calculated the z-scores of apparent nest density and apparent nest success in each cell. This resulted in a total of 445 cell-year-pairs on the 16 ha grid and 894 cell-year-pairs on the 4 ha grid (cells that were empty in both years were removed from analysis). In this analysis, we combined mallard and gadwall nests to increase our statistical power. Nevertheless, in some cells, small sample sizes and low estimates of DSR caused the estimated number (see equation above) of nests to be  $> 5$  times the number of observed nests. Based on our knowledge of methodology and duck nesting ecology, we judged these outliers to be unrealistic and removed these cells from the analysis. Similar to the field-level analysis, we then calculated the correlations among density and success metrics to assess the degree of correlation between cell-year-pairs.

### Individual-level analyses

Our last set of analyses examined 1807 hens that were captured (using handheld dip-nets) on their nests and banded between 1990 and 2011. We recaptured hens 352 times, and of these, 86 individuals (66 mallard, 15 gadwall, 5 northern pintail) were recaptured in consecutive years. Using the recapture histories for these 86 birds, we used a t-test (Zar 2009) to compare the dispersal distance of successful and unsuccessful birds the following year. All analyses were conducted in R ver. 2.14.2. We report means  $\pm$  SE unless otherwise noted.

### Data deposition

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.m5r3n>> (Ringelman et al. 2016).

## Results

### Kernel density maps

The kernel density analysis considered the spatial overlap of nests across 14 year-pairs ( $n = 9265$  nests). Two representative years are shown in Fig. 1, with the volumes of intersection calculated for each pair of maps. For example, Fig. 1 shows that 1) the distribution of all nests was similar between years, with some differences in nest density in the northern corner; 2) the between-year overlap of safe and risky areas was not substantially greater than the overlap between successful-unsuccessful and unsuccessful-successful map pairs, indicating that there was little temporal consistency in the spatial distribution of risk; and 3) previously successful areas were used about as often as previously risky areas. In analyzing all years, we found no evidence for consistently safe or risky areas: although we predicted that S-S and U-U map pairs would have a greater VI than S-U and U-S pairs, there were no differences in VIs among any pairings for either mallards (all  $p > 0.45$  for each pairwise t-test) or gadwall (all  $p > 0.16$  for each pairwise t-test) (Fig. 2). When we compared the intersection of successful nests in year  $t$  and all nests in year  $t + 1$  (S-all) to the intersection of unsuccessful nests and all nests (U-all), we found no evidence for adaptive shifts in nest density in either mallards ( $t = -0.677$ ,  $p = 0.51$ ) or gadwall ( $t = -0.967$ ,  $p = 0.34$ ).

The previous analysis suggested inconsistency in predation risk between years; this was further corroborated when we examined the potential for lag effects in patterns of nest success, and found moderate year-to-year variation, especially for Gadwall (Fig. 3). However, we found some evidence for temporal consistency in patterns of nest density that may persist for up to three years at our site (Fig. 4), though pairwise statistical tests were mostly non-significant for gadwall and only marginally significant for mallards (Table 1).

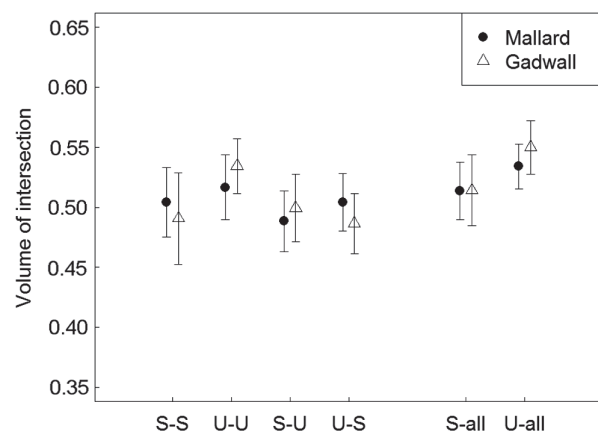


Figure 2. Volumes of intersection for each consecutive map-pair for mallard *Anas platyrhynchos* and gadwall *Anas strepera* nests at Suisun Marsh, CA, USA. Volumes of intersection for successful (S-S) and unsuccessful (U-U) map pairs, and their cross-comparisons (S-U and U-S) suggest no temporal correlation in predation risk. There is also no evidence for adaptive shifts to previously successful areas (S-all  $\approx$  U-all).



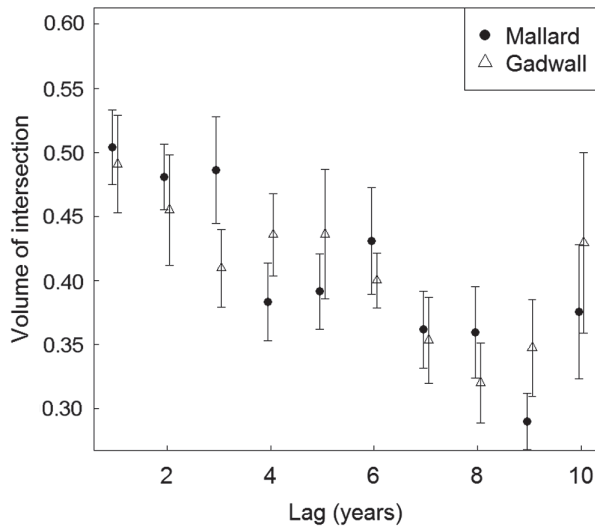


Figure 3. Temporal inertia in patterns of nest success for mallard *Anas platyrhynchos* and gadwall *Anas strepera* nests at Suisun Marsh, CA, USA. Higher volumes of intersection indicate a greater degree of spatial overlap.

### Field-level analyses

In this analysis, we examined between-year correlations of nest density and success in fields that averaged  $18.59 \pm 1.15$  ha in size ( $n = 136$  field-year-pairs). Nest success was not correlated within the same field between years  $t$  and  $t + 1$  for mallards ( $r = 0.093$ ,  $p = 0.26$ ) or gadwall ( $r = 0.118$ ,  $p = 0.24$ ). However, nest density was strongly correlated between years for both species (mallard:  $r = 0.483$ ,  $p < 0.0001$ ; gadwall:  $r = 0.394$ ,  $p < 0.0001$ ), corroborating the trend revealed in the kernel density analysis. We also found that more successful fields tended to show an increase in nest density the following year (mallard:  $r = 0.332$ ,  $p < 0.0001$ ; gadwall:  $r = 0.266$ ,  $p < 0.01$ ; combined:  $r = 0.304$ ,  $p < 0.001$ , Fig. 5).

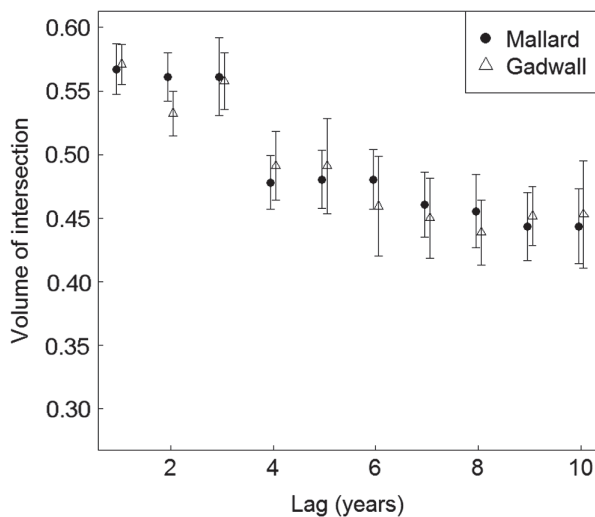


Figure 4. Temporal inertia in patterns of nest density for mallard *Anas platyrhynchos* and gadwall *Anas strepera* nests at Suisun Marsh, CA, USA. Higher volumes of intersection indicate a greater degree of spatial overlap.

Table 1. Pairwise tests of spatial consistency (kernel volume of intersection; VI) in nest density for mallard *Anas platyrhynchos* and gadwall *Anas strepera* at Suisun Marsh, CA, USA (Fig. 4). Shown are p-values of pairwise comparisons of lags ranging from 1–4 years from an ANOVA with Holm correction factors for independent contrasts.

MALL	VI <sub>1</sub>	VI <sub>2</sub>	VI <sub>3</sub>	GADW	VI <sub>1</sub>	VI <sub>2</sub>	VI <sub>3</sub>
VI <sub>2</sub>	1.000	–	–	VI <sub>2</sub>	0.575	–	–
VI <sub>3</sub>	1.000	1.000	–	VI <sub>3</sub>	0.775	0.775	–
VI <sub>4</sub>	0.043	0.075	0.078	VI <sub>4</sub>	0.043	0.575	0.191

### Grid cell analyses

Results from the field-level analysis were similar between mallards and gadwall, so we combined species in our grid cell analysis to increase statistical power. Similar to the field-level analysis, we found no temporal correlation in nest success at the 16 ha ( $r = 0.161$ ,  $p = 0.85$ ) or 4 ha scale ( $r = 0.029$ ,  $p = 0.45$ ). Nest density, on the other hand, was correlated among years at both spatial scales (16 ha:  $r = 0.518$ ,  $p < 0.0001$ ; 4 ha:  $r = 0.361$ ,  $p < 0.0001$ ). Additionally, we found evidence that cells with higher levels of nest success increased in nest density the following year at both the 16 ha ( $r = 0.161$ ,  $p < 0.01$ ) and 4 ha scales ( $r = 0.255$ ,  $p < 0.0001$ ).

### Individual-level analyses

Successful birds ( $n = 72$ ) moved an average of  $272 \pm 42$  m, whereas unsuccessful birds ( $n = 14$ ) moved  $365 \pm 103$  m in the following breeding year. Although unsuccessful birds had a tendency to move farther than successful birds on average, nest fate was not a statistically significant predictor of distance moved ( $t = -0.888$ ,  $p = 0.37$ ). In post hoc analyses, we also found that the average change in Robel vegetation measurements (in dm; [(Robel et al. 1970) at the nest was similar for unsuccessful ( $2.00 \pm 0.44$ ) and successful birds ( $2.38 \pm 0.22$ )]).

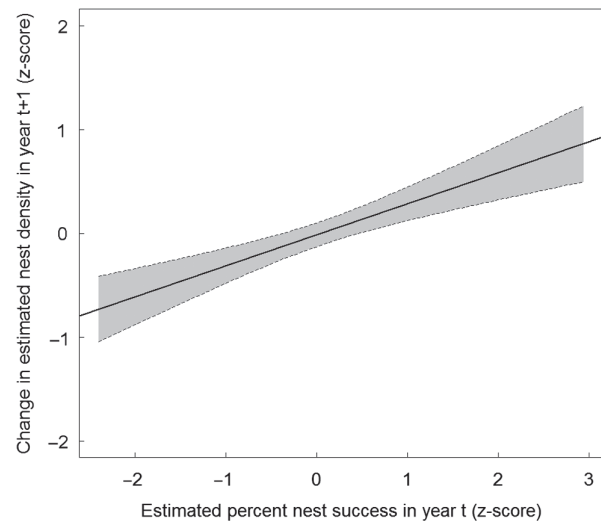


Figure 5. Relationship between nest success and the change in nest density the following year for mallard *Anas platyrhynchos* and gadwall *Anas strepera* (combined) nests found in the Suisun Marsh, CA, USA.

## Discussion

Previous breeding success or failure determines the strength of fine-scale philopatry in many bird species, but it is unclear if and how this individual win-stay, lose-shift strategy manifests at the population level. Using long-term duck nesting data, we documented (at most spatial scales) that the population tends to increase in areas that were previously successful, and areas of high nest density persist in consecutive years. In our first analysis, we used kernel estimators to interpolate nest density across a continuum of spatial scales, and found that density maps remained similar for up to three consecutive years. However, we were unable to detect adaptive shifts in nest density at this largest spatial scale: maps of previously successful nests and maps of previously unsuccessful nests had similar degrees of overlap with nest density the following year.

We also used bias-corrected estimates of nest density and nest success calculated at three smaller spatial scales to evaluate how patterns of nest density correlate with prior predation risk. Across species and all spatial scales, our results point to the same spatial correlations between years: 1) nest success is not correlated, 2) nest density is correlated, and 3) successful areas increase in nest density from one year to the next. These results suggest an interesting and multilayered interpretation. Because nest success is not spatially correlated among years, there should be no fitness benefit for ducks that use a location-based win-stay, lose-shift strategy (Doligez et al. 2003, Schmidt 2004). Furthermore, because habitat is relatively static between consecutive years at our site, but nest success is spatially variable, this suggests that habitat is not a sole driver of nest success. The limited importance of habitat is supported by recent empirical and model-based evidence; for example, at small spatial and temporal scales, clusters of high nest density survive better in Suisun Marsh, regardless of the habitat in which they are located (Ackerman et al. 2004, Ringelman et al. 2012, 2014, Ringelman 2014). This is in contrast to many waterfowl studies that have demonstrated density-independent nest predation at larger spatial scales (reviewed by Ackerman et al. 2004). Unlike nest success, nest density at our study site was positively correlated between years. This may suggest that static variables such as habitat are driving nest site choice (Crabtree et al. 1989, Clark and Shutler 1999). However, choosing a nest site based on habitat cues alone would be a poor strategy at our site, if nest density per se is a more important determinant of nest success. The critical question is this: if nest density is correlated between years, and clustering of nests at small spatial scales drives nest success, why then is nest success not also correlated between years?

We found that areas of higher nest success increased in nest density the following year. At an individual level, this could mean that successful breeders are returning to high density safe areas, and failed breeders could be shifting out of low density risky areas and (potentially) into safer high-density areas. Nest density remains correlated because high density areas remain high, and most low density areas remain low. But, nest success remains unpredictable because: 1) many failed breeders (and first-year breeders) will fail again in new, different, low density locations and 2) failed breeders (and first-year breeders) that accidentally form or adaptively select new high-density clusters could be successful.

When predation risk is spatially unpredictable between years, but the density of conspecific nests is reliably and positively related to nest success (Ringelman et al. 2012, 2014, Ringelman 2014), we hypothesize that ducks may use conspecific cues to select nest sites. The presence of currently active conspecific nests may be a valuable nest-site selection cue, not only because areas of high nest density may be inherently safer in this system, but because the presence of active conspecific nests integrates current information such as lack of predators and disturbance, safety conferred by nesting vegetation, or presence of alternate prey (Ackerman 2002). Aggregation of ducks into high-density safer areas may be enhanced if ducks can identify high-quality locations by assessing the previous success of conspecifics, and then use that information to select nest sites the following year ("patch success" models; Danchin et al. 1998, Doligez et al. 2003, 2004). That said, precocial ground-nesting dabbling ducks provide relatively little public information on patch quality for prospecting individuals.

There are other potential explanations for the patterns we observed. For example, strong natal philopatry of recruits from productive, high-density areas may cause increases in local nest density. However, most nests are initiated by after hatch-year females, not first-year breeders (Ringelman et al. unpubl.). Furthermore, those few ducklings that survive to hatch quickly leave the nest, and at our site, are raised outside of the complex of upland nesting fields we studied. Taken in combination with the fact that philopatry to breeding home ranges (hundreds of hectares) varies from 5–28% in mallards and gadwall (Anderson et al. 1992), it seems unlikely that local recruitment can explain the small-scale patterns we observed in this study.

Our results suggest that ducks use a variety of cues to track environmental variation in risk. At our site, a lack of year-to-year spatial consistency in predation risk reaffirms that (relatively static) habitat variables are not reliable cues for selecting safe nest sites. In concordance with the literature, in our banding data we found some indication that successful breeders were more likely to stay in the same location, which suggests a role for prior experience. This manifests in the population data as year-to-year consistency in nest density, and previous research indicates that high density areas tend to be more successful. Finally, either through prospecting in the previous year or conspecific attraction in the current year high-density successful areas tend to attract more ducks. The mechanisms by which ducks and other animals adaptively select breeding locations, and the degree to which they are successful in avoiding a dynamic predator community deserves continued attention from behavioral ecologists, especially in systems of conservation and management concern.

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Supplementary material (available online as Appendix oik-03728 at <[www.oikosjournal.org/appendix/oik-03728](http://www.oikosjournal.org/appendix/oik-03728)>). Appendix 1.