

## Is predation on waterfowl nests density dependent? – Tests at three spatial scales

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We tested whether predation on duck nests (*Anas* spp.) was density dependent at three spatial scales using artificial and natural nests in the Suisun Marsh, California, USA. At the largest spatial scale, we used 5 years (1998–2002) of data to examine the natural variation in duck nest success and nest densities among 8–16 fields per year, each 5–33 ha in size ( $n = 62$  fields). At an intermediate spatial scale, we deployed artificial nests (2000,  $n = 280$ ) within 1-ha plots at three experimental densities (5, 10, and 20 nests  $\text{ha}^{-1}$ ) in a complete randomized block design and examined differences in nest predation. At the smallest spatial scale, we examined nest success in relation to nearest-neighbor fates and distances for artificial (2000,  $n = 280$ ) and natural nests (2000,  $n = 507$ ). We detected no relationship between nest success and the density of natural nests among fields in any year, nor when we pooled data for all years after controlling for year effects. The proportion of artificial nests that survived also did not depend on experimental nest densities within 1-ha plots. Overall,  $15.0 \pm 12.4\%$ ,  $15.0 \pm 11.0\%$ , and  $6.2 \pm 4.3\%$  of artificial nests survived the 32-day exposure period in the low, intermediate, and high nest densities, respectively. Additionally, we detected no consistent effect of nearest-neighbor fate or distance on the success of artificial or natural nests. Thus, our results provide no evidence of density-dependent predation on duck nests at any scale of analysis, in contrast to a number of previous studies. Variation among geographical locations in the degree to which predation is density-dependent may reflect the composition of the predator community and the availability of alternate prey.

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Nest predation is the primary cause of reproductive failure for many bird species (Ricklefs 1969, Böhning-Gaese et al. 1993, Martin 1993), including waterfowl (Cowardin et al. 1985, Klett et al. 1988, Greenwood et al. 1995). As a result, birds have evolved numerous tactics to reduce the risk of predation, such as concealment of nest sites (Schieck and Hannon 1993) and spacing nests away from neighbors (Tinbergen et al. 1967, Page et al. 1983, Martin 1988). The effectiveness of these tactics depends, in part, on whether predation risk

varies with nest density. Density-dependent predation can be caused by both functional responses (e.g. development of search images, area-restricted searching; Tinbergen et al. 1967, Smith 1974) and numerical responses of predators (e.g. aggregation of predators in areas with higher nest densities; Holt 1977). For cryptically colored animals such as female dabbling ducks, dispersion of nests has been proposed as an important mechanism employed to counteract density-dependent predation (Tinbergen et al. 1967, André

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1991). Yet, despite the apparent advantages of nest spacing for cryptic birds (Taylor 1976), it remains unclear whether nest predation generally is density dependent or independent (Andr n 1991, Major and Kendall 1996, Schmidt and Whelan 1999).

The scale at which predators perceive and respond to prey density will have an important influence on whether predation on nests is density dependent. At a large spatial scale, predators might aggregate in habitat blocks with high nest densities. Alternatively, predators might concentrate their foraging behavior in smaller patches within habitat blocks where nests are clustered. At the smallest spatial scale, predators might simply increase their searching behavior within a restricted area after encountering a nest, leading to nearest-neighbor effects regardless of the overall density of nests within the habitat patch. In many cases, nest densities at each of these spatial scales will be correlated; for example, higher densities of nests within a habitat will often lead to shorter distances between nests. However, density-dependent effects may be detected at some scales and not at others even if density-dependent nest predation is occurring (Schmidt et al. 2001). Thus, a multi-scale approach should improve our ability to detect density-dependence and could provide managers with information about the appropriate habitat patch size with which to maximize nest densities without increasing nest predation via density-dependence. However, few studies have attempted to investigate these processes at multiple scales (Morgan et al. 1997, Schmidt et al. 2001).

A second concern with previous studies is the type of nest employed. For example, artificial nests commonly are used to experimentally study the effects of density on nest success (reviews by Andr n 1991, Paton 1994, Major and Kendall 1996). However, recent studies have raised concerns about whether predation rates on artificial nests accurately reflect patterns of predation on natural nests (Major and Kendall 1996, Butler and Rotella 1998, Ortega et al. 1998, Wilson et al. 1998, King et al. 1999, Zanette 2002). Although artificial nests permit an experimental approach, they differ from natural nests in a number of potentially important ways. For example, the absence of an incubating adult at artificial nests may alter a predator's ability to find the nest. In contrast, natural nests provide little potential for experimentation and predation rates could be confounded by uncontrolled variables such as parental quality, effort, and nest-site selection. Thus, methodological approaches that incorporate both artificial and natural nests may provide a more thorough test of density-dependent predation.

Here, we use both artificial and natural waterfowl nests to examine the effects of density on nest predation rates at different spatial scales in grassland habitat where striped skunks (*Mephitis mephitis*) are the predominant predator of duck eggs. Waterfowl nesting habitat has

been severely reduced and fragmented due to the widespread conversion of natural grasslands into agricultural production, potentially concentrating duck nests into smaller habitat patches (reviewed by Clark and Nudds 1991). This concentration of nests presumably has increased the foraging efficiency of predators (Clark and Nudds 1991), and the nest success of many waterfowl species has declined over time at the landscape level (Beauchamp et al. 1996). Although numerous studies have addressed the effects of density on nest predation in birds (Major and Kendall 1996), few studies have investigated these effects in waterfowl (Sugden and Beyersbergen 1986, Andr n 1991, Larivi re and Messier 1998). Predators of duck nests such as striped skunks are thought to depredate nests incidentally while foraging for alternative prey (Crabtree and Wolfe 1988, Vickery et al. 1992), and it is unclear whether duck nest predators will recognize and respond to high nest density patches (Larivi re and Messier 1998). However, medium-sized generalist predators (which are typical predators of duck nests) are considered more likely to exhibit density-dependent nest predation because they have home ranges and daily movement patterns that are large enough to be able to detect and respond to heterogeneity in nest densities (Schmidt and Whelan 1999).

We tested whether predation on duck nests was density dependent at three spatial scales. First, at the largest spatial scale, we used 5 years (1998–2002) of data to assess whether natural nest densities influenced nest success in fields 5–33 ha in size. We predicted that duck nest success would decrease with increasing densities of natural nests due to the numerical responses of predators to nest abundance. Second, in different fields during 2000, we conducted a complete randomized block design experiment using artificial duck nests at three nest densities in 1-ha plots. We predicted that (1) predation on artificial nests would be density dependent, such that sites with higher densities would suffer greater predation rates, (2) artificial nest success would increase with the distance to the nearest neighboring nest and depend on the nearest-neighbor's fate, and (3) predators would be more likely to partially depredate, rather than completely destroy, artificial nests at increasing nest densities. This last prediction is based on the observation that striped skunks often are satiated after eating an entire duck clutch (Nams 1997) and frequently do not eat all of the eggs in a clutch (Larivi re and Messier 1997, Greenwood et al. 1999, Ackerman et al. 2003a, b). Therefore, predators might be more likely to partially depredate, rather than completely destroy, artificial nests at increasing nest densities due to satiation. Third, in areas separate from the artificial nest experiment, we monitored natural duck nests in 2000 to examine nearest-neighbor effects on predation rates of natural nests. We predicted that nest sites in close proximity would be more likely to be depredated than those spaced further apart and that the

fates of neighboring nests would be related due to area-restricted searching behavior by successful predators. Finally, we evaluated whether artificial nests reliably reflected patterns of predation on natural nests by comparing predation rates between artificial and natural nests among experimental replicates.

## Methods

### Study area

We conducted our study at the Grizzly Island Wildlife Area in the Suisun Marsh of California (38°08' N, 121°59' W). The Suisun Marsh is a large (~34,000 ha) brackish estuary at the downstream end of the Sacramento-San Joaquin Delta. The Grizzly Island Wildlife Area contains roughly 2,000 ha of wetlands and 1,600 ha of uplands managed for waterfowl production. Our experiments were conducted in a large block of uplands (800 ha) divided into fields (5–33 ha each) by levees, ditches, canals, or dirt roads. These uplands are managed by the California Department of Fish and Game on a per-field basis for different vegetation types and structure, including fields dominated by pickleweed (*Salicornia virginica*), vetch (*Vicia* spp.), herbs (*Atriplex patula*, *Lotus corniculatus*), mid-height (<1 m) grasses (*Lolium* spp., *Hordeum* spp., *Bromus* spp., *Polypogon monspeliensis*), or taller (>1 m) grasses (*Elytrigia* spp., *Phalaris* spp.). We considered each field to be an independent replicate because there is no spatial or temporal autocorrelation of duck nest success among fields (Ackerman 2002). Striped skunks are the major predator of duck nests in this area, but coyotes (*Canis latrans*), raccoons (*Procyon lotor*), gopher snakes (*Pituophis melanoleucus*), and common ravens (*Corvus corax*) also occur in the area (McLandsress et al. 1996, Ackerman 2002).

### Large scale: observational study using natural duck nests

#### *Natural nest success and nest densities*

During 1998 to 2002, we monitored the natural variation in nest success and nest densities among 8–16 upland fields each year (a total of 62 field-years). Waterfowl nest search procedures were designed following Klett et al. (1986), modified by McLandsress et al. (1996) for this study site. Nest searches were initiated in early April and continued until July to ensure finding both early- and late-nesting ducks (McLandsress et al. 1996). The date of nest initiation was calculated by subtracting the age of the nest when found (i.e. the number of eggs when found plus the incubation stage when found) from the date the nest was discovered (Klett et al. 1986). Each field was

searched four to five times at 3-week intervals until no new nests were found. Nest searches began at least 2 hours after sunrise and were finished by 2:00 pm hours to avoid missing nests due to morning and afternoon incubation recesses by females (Caldwell and Cornwell 1975, Gloutney et al. 1993). Nest searches were conducted using a 50-m nylon rope strung between two slow-moving all-terrain vehicles. Tin cans containing stones to generate noise were attached at 1.5-m intervals along the length of the rope. The rope was dragged through the vegetation, causing females to flush from their nests, thus enabling observers to locate nests by searching a restricted area. Nests were marked with a 2-m bamboo stake placed 4 m north of the nest bowl and a shorter stake placed just south of the nest bowl, level with the vegetation height. Each nest was revisited on foot once every seven days, the stage of embryo development was determined by candling (Weller 1956), and clutch size and nest fate were recorded. After each visit, we covered the eggs with nest materials (i.e. down and contour feathers from the nest), as the female would have done before leaving for an incubation recess.

We calculated nest success for each field using Mayfield (1975) techniques modified for waterfowl (Johnson 1979). Total duck nest success was calculated using an average clutch age at hatching of 35 days. We considered a nest successful if at least one egg hatched (as determined from shell remains; Klett et al. 1986). Nests that were abandoned on the day we found them, or were partially depredated before we found them, were excluded from analyses (Klett et al. 1986). We also excluded nests that were disturbed by investigators, such as nests that were altered by clutch size manipulations (Ackerman and Eadie 2003) and those damaged by nest searching or egg handling procedures (Klett et al. 1986).

#### *Statistical analysis*

We used Mayfield nest-success rates to estimate nesting densities in each field (Miller and Johnson 1978). We divided the number of successful nests ( $\geq 1$  egg hatched) by the Mayfield nest-success rate to estimate the total number of nests initiated in each field. We then divided the number of nests initiated by the field's area (ha) to determine the density of initiated nests. The Mayfield estimate takes into account the limitations of the nest searching methodology; specifically, nests depredated early in incubation are often not found, causing apparent nesting densities (number of nests found divided by area) to be underestimated.

Pearson product-moment correlation analysis was used to test the strength of association between (natural) nest success and nest densities among fields, both within each year and after combining all years using z-scores. Z-scores were used to standardize for year effects and were calculated each year by taking the difference between each field and the mean value of all fields,

and dividing that quantity by the standard deviation for that year. For the within-year analyses, we arcsine-square-root-transformed Mayfield nest success data and log-transformed Mayfield nest density data ( $\log[\text{value} + 1]$ ) to improve normality.

### Intermediate scale: experimental study using artificial duck nests

#### *Experimental design*

We used a complete randomized block design, where each block (8 replicates total) consisted of an upland field managed for nesting ducks in 2000. Fields for the experiment were not randomly selected due to logistical constraints and the monitoring of natural nests in additional fields (above), but we examined a broad range of representative habitats within the study area. Fields used for the artificial nest experiment were not used in other studies. Within each field (hereafter called replicates), three 1-ha treatment plots were arranged systematically along the length of the replicate. We randomly selected one end of the replicate then positioned the first treatment plot 50 m from the replicate's end and  $> 40$  m from either side of the replicate to reduce any potential edge effects (Pasitschniak-Arts and Messier 1995). The second and third treatment plots also were positioned  $> 40$  m from either side of the replicate, and each treatment plot was separated by 200 m.

For each replicate, we randomly assigned one of three nest densities to each treatment plot. We randomly positioned either 5, 10, or 20 nests within each 1-ha treatment plot to simulate low, intermediate, and high nest densities. These treatments approximate current nest densities ( $10\text{--}20$  nests  $\text{ha}^{-1}$ ) that occur at small spatial scales (i.e.  $< 1$  ha; California Waterfowl Ass., unpubl.). Densities of 5 nests  $\text{ha}^{-1}$  commonly occur over larger spatial scales. For example, duck nest densities in the other fields ( $n = 14$ ) at our study site that year ranged from 1.9 to 11.3 nests  $\text{ha}^{-1}$ , with an overall nest density of 4.4 nests  $\text{ha}^{-1}$ . Our experimental nest densities also are similar to those used by Larivière and Messier (1998) and were chosen to facilitate comparisons between studies.

Artificial nest locations were marked with numbered bamboo stakes 7–10 days before beginning the experiment. To reduce the potential that predators could respond to nest markers (Picozzi 1975, Hein and Hein 1996, but see Greenwood and Sargeant 1995), we randomly positioned a total of 20 nest markers in each treatment plot. In the low-density treatment plot, only 5 of these markers were associated with nests whereas in the high-density treatment plot all of the markers were associated with an artificial nest (following Martin 1988). Each actual or potential nest site was marked with a 2-m bamboo stake placed 4 m north of the nest bowl and a shorter stake placed just south of the nest bowl level with the vegetation height. To control for the

amount of human scent in each treatment plot (Donalby and Henke 2001), we visited each of the 20 markers and disturbed the vegetation with our hands similarly around the shorter stake during each nest visit, regardless of whether an artificial nest was associated with the marker (Sieving 1992). Additionally, we wore rubber gloves at all times during artificial nest construction and nest visits. Thus, there were no differences among treatment plots in the amount of human scent or the number of markers.

#### *Artificial nests*

To increase the likelihood that predation on artificial nests would simulate patterns of predation on natural nests, artificial nests were constructed and located to resemble natural duck nests. We positioned artificial nests within 1 m of the randomly selected location, in sites that appeared similar to natural nest sites (J.T. Ackerman, pers. obs.). We constructed artificial nests by creating a circular depression in the ground (20 cm diameter), and encircling it with dead vegetation (collected away from the nest site). We placed nine chicken eggs in each nest bowl and covered the eggs with down and contour feathers, as a hen would have done before leaving for an incubation recess. Mallards (*Anas platyrhynchos*) have an average clutch size of 8.6 eggs and are the most numerous nesting species at our study site (McLandress et al. 1996, Ackerman et al. 2003a, b); therefore a clutch of nine eggs represents a typical duck nest in the Suisun Marsh. Eggs were dyed with tea to a dull-brown color to resemble natural duck eggs (Clark and Wobeser 1997, Larivière and Messier 1998). Down and contour feathers were collected from wild female mallards harvested in California the preceding winter, and the feathers were stored in paper bags until the spring nesting season. Care was taken to avoid feathers stained with blood as predators could cue on this scent. Natural nest material was collected from deserted mallard nests early in the nesting season before the experiments were conducted and was mixed and stored with the other feathers in an attempt to distribute the scent of a natural nest to all the nest materials (Clark and Wobeser 1997). In addition, three drops of commercial duck scent (Cabela's Inc., Sidney, NE) were deposited at each nest visit to simulate the presence of an incubating female (Clark and Wobeser 1997, Larivière and Messier 1998).

Artificial nests were visited every 8 days over a 32-day exposure period. This exposure period is typical for dabbling ducks, whose clutches have an average age at hatching of 32 to 35 days (Klett et al. 1986). A nest was considered depredated if  $\geq 1$  egg was missing or destroyed (Sugden and Beyersbergen 1986, Larivière and Messier 1998). We calculated daily survival rates for nests in each treatment plot following Mayfield (1975) techniques modified for waterfowl (Johnson 1979).

### *Natural nests*

Before constructing artificial nests, we searched for natural duck nests within each replicate to compare their survival to the artificial nests. Each nest was marked and visited similarly to artificial nests. To increase our sample size, we monitored both active natural nests and natural nests that were abandoned on the day they were found to determine the proportion of survivors at each nest visit.

### *Statistical analysis*

Daily survival rates and the proportion of survivors were arcsine-square-root-transformed. We were unable to calculate daily survival rates for each exposure interval (between nest visits) because often few or no nests were still intact at later exposure intervals for such an estimate to be calculated (due to high nest depredation rates). Therefore, we used the proportion of survivors at each of the four nest visits and repeated measures analysis of variance (ANOVA) to test for effects among the nest density treatments and replicates. In addition to using the proportion of nests surviving, which is an all-or-none measurement of nest success, we tested for effects of nest density using two measures of partial clutch depredation. First, G-tests with Williams' correction ( $G_w$  statistic) were used to compare the number of partially versus completely depredated nests (during the initial depredation event) among nest density treatments. Second, ANOVA was used to compare the average number of eggs depredated (during the initial depredation event) in each nest density treatment. Finally, to determine if artificial and natural nests exhibited the same relative rates of survival among replicates, we compared artificial and natural nests' daily survival rates (after 32 days of exposure) among replicates using Pearson product-moment correlation analysis. All means are reported  $\pm 1$  SE.

### **Small scale: nearest-neighbor effects**

#### *Artificial nests*

Nearest-neighbor distances (m) between artificial nests in 2000 were measured with a tape meter. A nest was considered depredated if  $\geq 1$  egg was missing or destroyed after the 32-day exposure period (Sugden and Beyersbergen 1986, Larivière and Messier 1998). We also analyzed nearest-neighbor effects for each exposure interval (day 0–8, day 8–16, day 16–24, day 24–32) and used only those nests with clutches that were completely intact at the beginning of each exposure interval. For this analysis, a nest was considered depredated if  $\geq 1$  egg was missing or destroyed after the 8-day exposure interval.

### *Natural nests*

In addition to the fields used in the artificial nest experiment, we also searched for natural duck nests in separate fields during the 2000 nesting season for the nearest-neighbor analysis. Natural nest locations were recorded using a Trimble TDC-2 (Trimble Navigation, Sunnyvale, CA, USA) global positioning system (GPS). The GPS positions (latitude and longitude) of the nest sites were used to calculate nearest-neighbor distances with ArcView GIS (ESRI 1996). Natural nests that were deserted on the day they were found (i.e. research-induced nest desertion), heavily disturbed by investigators, or damaged by nest searching or egg-handling procedures were excluded from all analyses of nest fate (Klett et al. 1986). However, these nests were used to calculate nearest-neighbor distances since they still were an available food resource for predators. As with artificial nests, a natural nest was considered depredated if  $\geq 1$  egg was missing or destroyed (Sugden and Beyersbergen 1986, Larivière and Messier 1998).

### *Statistical analysis*

For both artificial and natural nests, nearest-neighbor effects were tested using logistic regression, where the nest's fate (successful or unsuccessful) was the dependent variable and the distance to the nearest neighbor was the predictor variable. We included date in the logistic model when assessing the effect of nearest neighbors on nest fate because the date when the artificial nests were deployed or when the natural nests were initiated significantly influenced nest fate (Results). In addition to the possibility that nest fate could depend on the distance to its nearest neighbor, nest fate could depend on the fate (and not necessarily the distance) of its nearest neighbor. Therefore, we also tested whether nest fate was associated with the fate of the nearest neighboring nest using a  $2 \times 2$  contingency table and G-test with Williams' correction ( $G_w$  statistic; Sokal and Rohlf 1995). Because we tested nearest-neighbor effects for artificial nests at low, intermediate, and high densities, we controlled for the three statistical comparisons using the Bonferroni correction factor; p values  $\leq 0.017$  (i.e.  $\alpha = 0.05/3$ ) were considered statistically significant. All means are reported  $\pm 1$  SE.

## **Results**

### **Large scale: observational study using natural duck nests**

From 1998 to 2002 we monitored 2,294 duck nests (*Anas* spp.). Total duck nest success was not correlated

with duck nest densities among fields in any of the five years (Pearson correlation: 1998:  $r = 0.08$ ,  $n = 16$ ,  $p = 0.78$ ; 1999:  $r = 0.44$ ,  $n = 12$ ,  $p = 0.16$ ; 2000:  $r = -0.38$ ,  $n = 14$ ,  $p = 0.19$ ; 2001:  $r = 0.48$ ,  $n = 12$ ,  $p = 0.12$ ; 2002:  $r = -0.11$ ,  $n = 8$ ,  $p = 0.80$ ; Fig. 1). Because our yearly sample sizes were relatively small, we combined all years using z-scores and found that duck nest success still was not correlated with the relative density of duck nests (Pearson correlation:  $r = -0.10$ ,  $n = 62$ ,  $p = 0.47$ ; Fig. 1). Field size (5–33 ha) was not correlated with the relative density of duck nests within a field (Pearson correlation:  $r = 0.02$ ,  $n = 62$ ,  $p = 0.85$ ), indicating that field size did not confound the analysis between nest success and nest density.

### Intermediate scale: experimental study using artificial duck nests

#### Artificial nest survival in relation to nest density

Overall, 28 of 280 (10%) artificial nests survived the 32-day exposure period. Daily survival rates declined in relation to the date in the season on which the artificial nests were deployed at intermediate (Pearson correlation:  $r = -0.89$ ,  $n = 8$ ,  $p = 0.002$ ) and high (Pearson correlation:  $r = -0.77$ ,  $n = 8$ ,  $p = 0.02$ ) nest densities, and a similar but non-significant trend was detected at low nest densities (Pearson correlation:  $r = -0.63$ ,  $n = 8$ ,  $p = 0.10$ ; Table 1). The proportion of survivors was highest in replicate one, where 21 of the 35 (60%) artificial nests were successful, and lowest in replicate

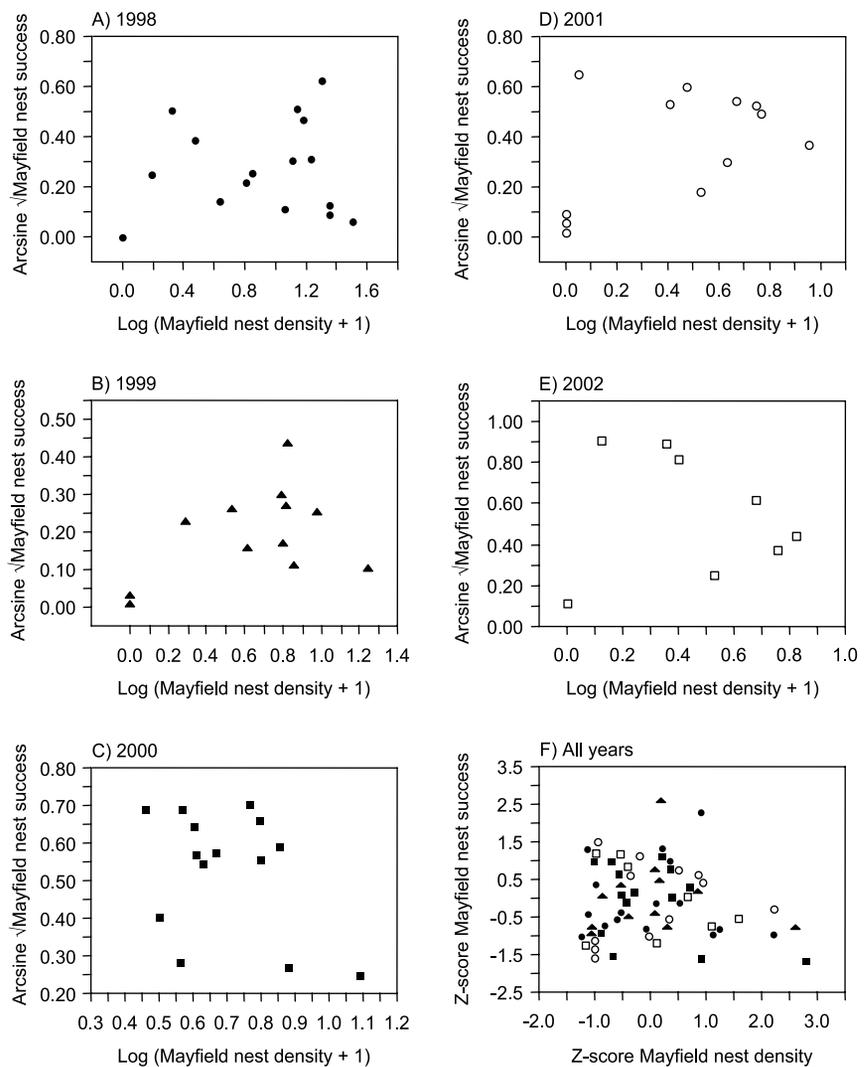


Fig. 1. Duck nest success (*Anas* spp.) was not correlated with the density of natural nests among 5–33 ha fields in any year (1998–2002), nor when all five years were combined using z-scores. For the within-year analyses, we arcsine-square-root-transformed Mayfield nest success data and log-transformed Mayfield nest density data ( $\log[\text{value} + 1]$ ) to improve normality. Data were collected in the Suisun Marsh, California, USA. Each data point represents an entire 5–33 ha upland field.

eight, where all of the artificial nests were depredated within 8 days. We controlled for the effect of date by including the blocking variable (i.e. replicate) when analyzing the effect of the treatment density on predation of artificial nests. The proportion of nests surviving differed among replicates (repeated measures ANOVA:  $F_{7,14} = 5.88$ ,  $p = 0.003$ ) and there was an interaction between the exposure interval and replicate (repeated measures ANOVA:  $F_{21,42} = 4.03$ ,  $p < 0.0001$ ). However, the proportion of nests surviving was not influenced by the nest density treatment (repeated measures ANOVA:  $F_{2,14} = 0.14$ ,  $p = 0.87$ ) and there was no interaction between the exposure interval and density treatment (repeated measures ANOVA:  $F_{6,42} = 0.48$ ,  $p = 0.82$ ). The proportion of nests surviving after 32 days was  $15.0 \pm 12.4\%$ ,  $15.0 \pm 11.0\%$ , and  $6.2 \pm 4.3\%$  for the low, intermediate, and high nest densities, respectively (Fig. 2).

#### Partial clutch depredation in relation to nest density

Artificial nests often were partially depredated rather than completely destroyed during the initial depredation event. Of the nests experiencing a depredation event (i.e. partial or complete clutch loss), 44%, 46%, and 53% of nests were partially depredated in low, intermediate, and high nest density treatments, respectively (G-test:  $G_w = 1.63$ ,  $df = 2$ ,  $p = 0.44$ ). The number of eggs depredated during the initial depredation event also was similar among treatments (ANOVA:  $F_{2,277} = 0.14$ ,  $p = 0.87$ ), averaging  $5.5 \pm 0.6$  eggs,  $5.4 \pm 0.4$  eggs, and  $5.7 \pm 0.3$  eggs in the low, intermediate, and high nest densities, respectively.

#### Artificial nests versus natural nests within replicates

Since there was no difference in the proportion of survivors among nest density treatments, we pooled the artificial nests for each replicate to determine whether patterns of predation on artificial nests were similar to natural nests. Natural duck nests within the experimental replicates consistently had a higher proportion of survivors than artificial nests at each visit (repeated measures ANOVA:  $F_{1,14} = 5.68$ ,  $p = 0.03$ ; Fig. 2) and we detected no interaction between the treatment (artificial or natural nest) and exposure interval (repeated mea-

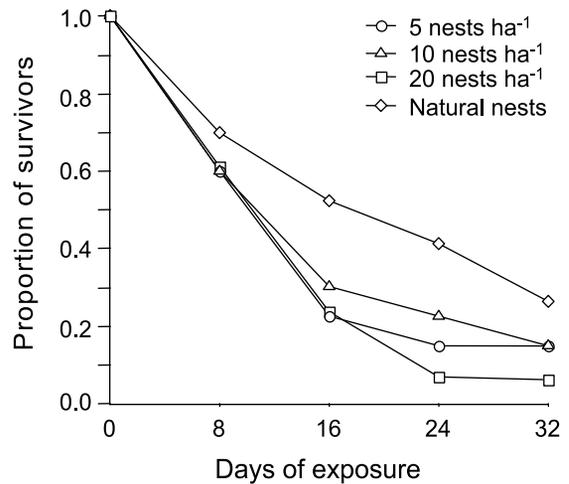


Fig. 2. Survivorship curves for artificial duck nests deployed at three experimental densities in 1-ha plots and exposed for 32 days in a complete randomized block design experiment during the 2000 nesting season in the Suisun Marsh, California, USA. The survivorship curve for natural duck nests (*Anas* spp.) that were exposed during the same 32-day period within the experimental fields is shown for comparison. A nest was considered unsuccessful if  $\geq 1$  egg was depredated.

asures ANOVA:  $F_{3,42} = 1.92$ ,  $p = 0.14$ ). However, the daily survival rates (after 32 days of exposure) of artificial and natural nests tended to be positively correlated among replicates (Pearson correlation:  $r = 0.67$ ,  $n = 8$ ,  $p = 0.07$ ).

### Small scale: nearest-neighbor effects

#### Artificial nests

Distances between nearest neighbors averaged  $27.4 \pm 2.1$  m,  $16.2 \pm 1.0$  m, and  $12.1 \pm 0.6$  m in the low, intermediate, and high nest densities, respectively. Because of high nest depredation rates and few successful nests, we pooled the nest density treatments to examine the effects of nearest-neighbor distance. We controlled for date by including it in the nearest-neighbor analysis because daily survival rates declined with the date the artificial

Table 1. Daily survival rates of artificial waterfowl nests deployed at three densities and exposed for 32 days during the 2000 waterfowl nesting season in the Suisun Marsh, California, USA.

Replicate	Dates nests exposed	Nest density treatment		
		5 nests ha <sup>-1</sup>	10 nests ha <sup>-1</sup>	20 nests ha <sup>-1</sup>
1	April 12–May 14	1.000	0.997	0.965
2	April 17–May 19	0.917	0.917	0.922
3	April 26–May 28	0.821	0.962	0.926
4	May 3–June 4	0.926	0.958	0.925
5	May 8–June 9	0.886	0.904	0.903
6	May 13–June 14	0.917	0.821	0.944
7	May 17–June 18	0.929	0.792	0.750
8	May 24–June 25	0.750	0.750	0.750
mean $\pm$ SE		0.893 $\pm$ 0.027	0.887 $\pm$ 0.032	0.886 $\pm$ 0.030

nests were deployed (above). The fate of artificial nests did not depend on the distance to nearest neighbors (logistic regression,  $n = 280$ : Wald  $\chi^2_1 = 0.79$ ,  $p = 0.37$ ; Fig. 3a); successful nests averaged  $16.0 \pm 1.5$  m ( $n = 28$ ) and unsuccessful nests  $15.4 \pm 0.7$  m ( $n = 252$ ) from their nearest neighbors.

We further assessed nearest-neighbor effects by examining predation at a shorter temporal scale. The previous analysis considered the nearest neighboring nest, regardless of the timing of predation. However, the identity of the nearest neighboring nest can change over time if a neighboring nest has been depredated. Therefore, we analyzed nearest-neighbor effects for each exposure interval (day 0–8, day 8–16, day 16–24, day 24–32) and used only those nests with clutches that remained completely intact at the beginning of each exposure interval. At this shorter temporal scale, we still did not detect an influence of nearest-neighbor distance on nest fate during any of the exposure intervals (logistic

regressions: day 0–8,  $n = 280$ : Wald  $\chi^2_1 = 0.76$ ,  $p = 0.38$ ; day 8–16,  $n = 169$ : Wald  $\chi^2_1 = 0.10$ ,  $p = 0.75$ ; day 16–24,  $n = 71$ : Wald  $\chi^2_1 = 3.34$ ,  $p = 0.07$ ; day 24–32,  $n = 33$ : Wald  $\chi^2_1 = 0.41$ ,  $p = 0.52$ ).

Regardless of nearest-neighbor distance, nest fate could depend on the fate of its nearest neighbor. Successful nests were more likely to have successful than unsuccessful nests as neighbors (and vice versa) for low (G-test:  $G_w = 16.22$ ,  $df = 1$ ,  $p < 0.0001$ ), intermediate (G-test:  $G_w = 24.16$ ,  $df = 1$ ,  $p < 0.0001$ ), and high densities (G-test:  $G_w = 12.97$ ,  $df = 1$ ,  $p < 0.0001$ ). However, 21 of the 28 successful artificial nests were located within a single field (replicate one) where 60% (21/35) of the artificial nests survived compared to only 3% (7/245) of artificial nests surviving in the seven other replicates combined. Since this replicate had a large effect on the number of successful nests with successful nearest neighbors (16/18), we excluded it from analysis to determine if the observed nearest-neighbor effects were robust. Without this replicate, nearest-neighbor effects were no longer statistically significant at low (G-test:  $G_w = 0.02$ ,  $df = 1$ ,  $p = 0.90$ ), intermediate (G-test:  $G_w = 0.02$ ,  $df = 1$ ,  $p = 0.89$ ), or high densities (G-test:  $G_w = 4.09$ ,  $df = 1$ ,  $p = 0.04$ ).

#### Natural nests

We monitored natural duck nests in additional fields that were not used for the artificial nest experiment in 2000. As with artificial nests, we controlled for date when assessing nearest-neighbor effects on natural duck nests because the likelihood of being successful declined with nest initiation date (logistic regression,  $n = 513$ : Wald  $\chi^2_1 = 30.51$ ,  $p < 0.0001$ ). The fate of natural nests did not depend on the distance to nearest neighbors (logistic regression,  $n = 507$ : Wald  $\chi^2_1 = 2.62$ ,  $p = 0.11$ ; Fig. 3b); successful nests averaged  $29.8 \pm 1.6$  m ( $n = 183$ ) and unsuccessful nests  $28.2 \pm 1.1$  m ( $n = 324$ ) from their nearest neighbors. The fate of natural nests also did not depend on the fate of neighboring nests (G-test:  $G_w = 0.35$ ,  $df = 1$ ,  $p = 0.56$ ).

## Discussion

We found little evidence of density-dependent predation on waterfowl nests. At the largest spatial scale, we detected no relationship between duck nest success and the relative density of natural nests among 5–33 ha fields in any of the five years, nor when we combined all years using z-scores (Fig. 1). At the intermediate spatial scale, experimental nest densities (5, 10, and 20 nests  $ha^{-1}$ ) in 1-ha plots had no effect on the proportion of the artificial nests that survived the 32-day exposure period (Fig. 2). Likewise, at the smallest spatial scale, we detected no effect of nearest-neighbor distance on the fate of artificial or natural duck nests (Fig. 3). Since

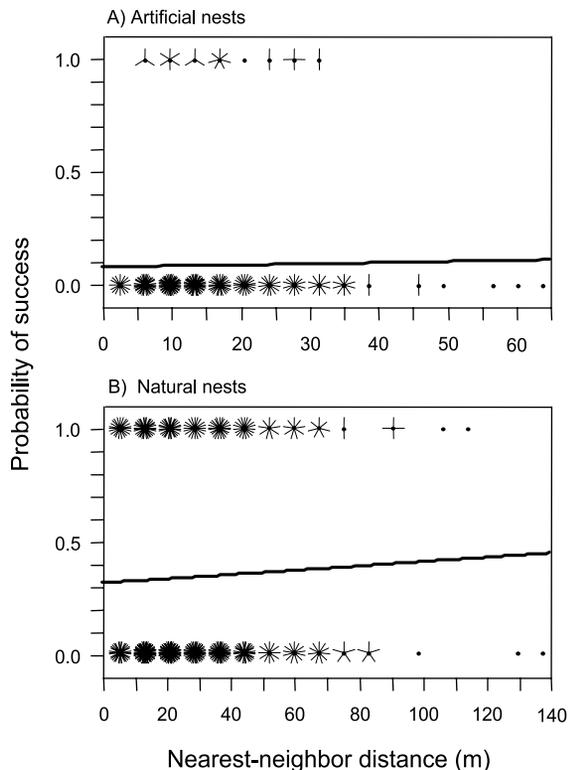


Fig. 3. Effect of nearest-neighbor distance on the success of (A) artificial duck nests (successful  $n = 28$ , unsuccessful  $n = 252$ ) and (B) natural duck (*Anas* spp.) nests (successful  $n = 183$ , unsuccessful  $n = 324$ ) during the 2000 nesting season in the Suisun Marsh, California, USA. Artificial nests were considered successful if the nine-egg clutch was still completely intact after the 32-day exposure period, whereas natural duck nests were considered successful if the complete clutch remained intact (i.e. no partial clutch depredation) and hatched. The lines indicate the logistic regressions between the distance to the nearest neighboring nest and the probability that a nest would be successful. Each leg of a star indicates one data point.

nearest-neighbor effects often occur via area-restricted searching once an initial prey item is found, predation on neighboring nests should be temporally related (Larivière and Messier 2001a). Therefore, in addition to assessing nearest-neighbor effects over a 32-day exposure period for artificial nests and over the entire breeding season for natural nests, we also explored potential nearest-neighbor effects among simultaneously active artificial nests (i.e., only those nests with clutches that were completely intact at the beginning of each exposure interval). At this shorter temporal scale, we still did not detect any effect of nearest-neighbor distance on the fate of artificial duck nests. Finally, we considered whether the fate of a nest was associated with the fate of its nearest neighbor regardless of the distance between nests. We found no relationship for natural nests, whereas the results for artificial nests were less clear. When all fields were considered, the fate of a nest was related to the fate of its neighboring nest at all experimental densities. However, a single field (replicate one) had a large influence on this pattern. In this field, 60% of the artificial nests survived compared to only 3% of the artificial nests surviving in the seven other replicates combined. Consequently, there were a large number of successful nests with successful neighbors in this field. An apparent association between nest fate and nearest neighbor fate could have resulted simply as an artifact of very low predation in this one field, rather than any nearest-neighbor effects per se. When we excluded this field from analysis, nearest-neighbor effects were not significant suggesting that the fate of nests generally was not related to the fate of neighboring nests.

Few studies have investigated whether predation on waterfowl nests is density dependent, but, for those that have, the results have been mixed (Table 2). Using an experimental design similar to ours, Larivière and Messier (1998) found that predation on artificial duck nests was density dependent late, but not early, in the nesting season. Additionally, they frequently detected nearest-neighbor effects at densities of 10 and 25 nests  $\text{ha}^{-1}$ , but rarely at densities of 2.5 nests  $\text{ha}^{-1}$ . Sugden and Beyersbergen (1986) found that American crow (*Corvus brachyrhynchos*) predation on artificial duck nests was density dependent and negatively related to the distance to neighboring nests. Esler and Grand (1993) found higher predation rates on artificial waterfowl nests in a plot with 10 nests  $\text{ha}^{-1}$  than in a plot with 2 nests  $\text{ha}^{-1}$ . In multiple experiments testing the effects of odors on predation rates of artificial duck nests, Clark and Wobeser (1997) found nearest-neighbor effects in only two of the six experiments conducted. In contrast to these experiments with artificial nests, Andrén (1991) found no difference in nearest-neighbor distances between successful and unsuccessful wild mallard nests. Duebbert and Lokemoen (1976) also found no relationship between nest success and the density of natural

duck nests among sites. However, studies testing density-dependence among years found higher predation rates on natural duck nests in years with higher nest densities (Weller 1979, Hill 1984). These contrasting results might be due to several factors, including the type of nest used, the scale of study, and the major predators involved (Table 2).

Although artificial nests may not be a reliable surrogate for natural nests, we found that patterns of nest predation were consistent among artificial and natural duck nests. First, the results for both types of nests indicated that predation was independent of density and nearest-neighbor distance. Second, although natural nests were more successful than artificial nests (Fig. 2; King et al. 1999, Zanette 2002), the daily survival rates of artificial and natural nests were correlated among replicates. Butler and Rotella (1998) also found that the success of artificial and natural duck nests was positively related among sites. These results suggest that, although artificial nests may not accurately indicate actual rates of nest predation, they are useful in detecting comparable patterns of nest predation (Wilson et al. 1998, Buler and Hamilton 2000, Davison and Bollinger 2000, Zanette 2002). Furthermore, by using both artificial and natural duck nests, our results cannot be attributed to methodology.

Detecting density-dependent predation on duck nests is likely to depend on the geographic scale at which the study was conducted (particularly with reference to the predominant egg predator) and the availability of alternate prey resources. Since predators probably perceive prey patches differently, density-dependent effects should be examined at the appropriate scale at which the major predators forage (Morgan et al. 1997, Schmidt et al. 2001). Striped skunks are the main predator of duck nests at our study site (McLandress et al. 1996, Ackerman 2002), as they are in many waterfowl breeding areas (Greenwood 1986, Crabtree et al. 1989, Johnson et al. 1989, Pasitschniak-Arts and Messier 1995, Larivière and Messier 1998). Striped skunks do not exhibit area-restricted searching behavior immediately following the depredation of a duck nest (Larivière and Messier 2001a), but instead tend to reduce their home range sizes and activity levels when exposed to high densities of nests, probably because they become satiated faster (Larivière and Messier 2001b). Striped skunks often become satiated after eating an average sized duck clutch (Nams 1997) and frequently do not finish eating an entire clutch (Larivière and Messier 1997, Greenwood et al. 1999, Ackerman et al. 2003a, b). Thus, density-dependent predation on duck nests may be unlikely to occur over short temporal scales and more likely to occur at larger scales. However, we did not detect density-dependent effects at larger spatial and temporal scales (Fig. 1, 2), and striped skunks did not concentrate

Table 2. Summary of studies that have investigated the effects of nest density and nearest-neighbor distance on predation rates of duck nests.

Scale	Nest type	Density of nests ha <sup>-1</sup> or inter-nest distance	Nest spacing	Density-dependent predation?	Major nest predators <sup>1</sup>	Reference
small						
nearest-neighbor	artificial	11–38 m (range means)	random	yes (high density), no (low density)	striped skunks	Larivière and Messier 1998
nearest-neighbor	artificial	1000 m	linear transect	no (4 tests), yes (2 tests)	not reported	Clark and Wobeser 1997
nearest-neighbor	mallard	51 m (mean)	natural	no	hooded crows <sup>2</sup>	Andrén 1991
nearest-neighbor	artificial	10–80 m (range)	uniform	yes	American crows	Sugden and Beyersbergen 1986
nearest-neighbor	artificial	12–27 m (range means)	random	no	striped skunks <sup>2</sup>	This study
nearest-neighbor	<i>Anas</i> spp.	29 m (mean)	natural	no	striped skunks <sup>2</sup>	This study
intermediate						
2–4 ha plots	artificial	2.5, 10, 25	random	no (early season), yes (late season)	striped skunks	Larivière and Messier 1998
10 ha plots	artificial	2, 10	uniform	yes	red foxes <sup>2</sup> , mew gulls <sup>2</sup>	Esler and Grand 1993
0.8–10.2 ha plots	artificial	1.5–102 (range)	uniform	yes	American crows	Sugden and Beyersbergen 1986
1 ha plots	artificial	5, 10, 20	random	no	striped skunks <sup>2</sup>	This study
large						
12–54 ha fields	<i>Anas</i> spp.	5.0–10.9 (yearly means) <sup>3</sup>	natural	no <sup>4</sup>	red foxes, raccoons	Duebbert and Lokemoen 1976
5–33 ha fields	<i>Anas</i> spp.	2.4–11.1 (yearly means) <sup>5</sup>	natural	no	striped skunks <sup>2</sup>	This study
among years	mallard	not reported	natural	yes <sup>4,6</sup>	carrion crows <sup>2</sup> , magpies <sup>2</sup>	Hill 1984
among years	blue-winged teal	not reported	natural	yes <sup>4,6,7</sup>	striped skunks <sup>2</sup>	Weller 1979

<sup>1</sup> Striped skunks, *Mephitis mephitis*; hooded crows, *Corvus corone*; American crows, *Corvus brachyrhynchos*; red foxes, *Vulpes vulpes*; mew gulls, *Larus canus*; raccoons, *Procyon lotor*; carrion crows, *Corvus corone*; magpies, *Pica pica*.

<sup>2</sup> Suspected.

<sup>3</sup> Range of (apparent) duck nest density among fields by year: 1971: 1.2–10.4 nests ha<sup>-1</sup>, 1972: 3.0–21.7 nests ha<sup>-1</sup>, 1973: 0.5–11.9 nests ha<sup>-1</sup>.

<sup>4</sup> These studies used apparent nest density rather than the Mayfield estimate of nest density and are therefore considered weaker tests (Methods).

<sup>5</sup> Range of (Mayfield) duck nest density among fields by year: 1998: 0.1–31.3 nests ha<sup>-1</sup>, 1999: 0.1–16.6 nests ha<sup>-1</sup>, 2000: 1.9–11.3 nests ha<sup>-1</sup>, 2001: 0.1–8.0 nests ha<sup>-1</sup>, 2002: 0.1–5.6 nests ha<sup>-1</sup>.

<sup>6</sup> Negative relationship between yearly nest success and the total number of nests found each year.

<sup>7</sup> It is unknown whether this relationship was caused by density-dependent predation across years because nest success also was correlated with alternate prey densities (Byers 1974, Weller 1979).

their activity within areas that had high densities of natural nests in 2000 (Ackerman 2002).

Rather than predators focusing on duck eggs, another possibility is that predators focus their foraging efforts on alternate prey, such that predation on duck nests occurs only incidentally. Striped skunks primarily consume invertebrates and small mammals, especially voles (Crabtree and Wolfe 1988, Greenwood et al. 1999), and are thought to depredate bird nests opportunistically while foraging for alternative prey (Crabtree and Wolfe 1988, Vickery et al. 1992, Larivière and Messier 1997). If so, then striped skunks may not typically respond to variation in nest densities, especially when alternative prey are abundant. In accordance, we found that mallard nest success was predominately influenced by the relative abundance of rodents, especially voles (*Microtus californicus*), among 14–27 ha fields, rather than by nest density (Ackerman 2002).

Density-dependent predation on bird nests often is more evident, when it does occur, in years when alternate prey densities are low and nest densities are high. For example, Hogstad (1995) found that weasel predation on fieldfare (*Turdus pilaris*) nests was density dependent in years with low rodent densities, but density-independent when rodent densities were high. Bêty et al. (2001) showed that the nest success of greater snow geese (*Anser caerulescens atlanticus*) was inversely density-dependent (i.e. nest success improved with increasing density) at high breeding densities, whereas nest success depended on lemming abundance when nest densities were low. Dunn (1977) found that weasel predation on tit (*Parus* spp.) nests occurred earlier in the nesting season in years with high nest densities and later in years when rodent densities were high. In an artificial nest experiment, Schmidt and Whelan (1999) also documented shifts from density-dependent to density-independent predation (and vice versa) depending on the distribution and abundance of alternative prey. Perhaps predation on duck nests might also be more prevalent in years when alternative foods are scarce and predation is focused on nests. However, we documented a 20-fold increase in vole abundance from 1998 to 2000 (Ackerman 2002) but we did not detect density-dependent predation on natural nests in either year (Fig. 1). In fact, we did not find density-dependent predation on duck nests in any of the five years (Fig. 1) despite large fluctuations in yearly duck nest success (range of yearly means: 6.5–31.4%). Density-dependent predation also may depend on the overall abundance of duck nests. Average duck nest densities during each year of our study (1998–2002) were all lower than the 18-year average at our study site (1985–2002; California Waterfowl Ass., unpubl.), possibly further reducing predators' search images for duck nests and contributing to density-independent predation (Dunn 1977, Hogstad 1995).

With the further expansion of agriculture and the fragmentation of grassland habitats, understanding density-dependent nest predation will become increasingly important as duck nests are concentrated into smaller habitat patches. Although our results conflict with previous studies that used artificial nests (Sugden and Beyersbergen 1986, Larivière and Messier 1998), they are consistent with André's (1991) results using natural nests. By using both artificial and natural nests, conducting tests at three different spatial scales, and analyzing patterns among fields over a five-year period, we are confident that our results are not simply an artifact of scale or experimental methodology. Apparently, the importance of density-dependent predation on duck nests varies considerably among study locations (Table 2). Given the importance of predation to the design of conservation and habitat management programs, it would be fruitful to understand why predation on waterfowl nests is sometimes density-dependent and at other times density-independent. In particular, future research might profitably examine density-dependent predation at a landscape scale (e.g. 10 km<sup>2</sup> habitat blocks; Reynolds et al. 2001) and as a function of the availability of alternate prey.

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