Of mice and mallards: positive indirect effects of coexisting prey on waterfowl nest success

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Coexisting prey species interact indirectly via their shared predators when one prey type influences predation rates of the second prey type. In a temperate system where the predominant shared predator is a generalist, I studied the indirect effects of rodent populations on waterfowl nest success, both within the nesting season among sites and among years. Among six to ten upland fields (14 to 27 ha), mallard (*Anas platyrhynchos*) nest success was positively correlated with rodent abundance in all three years of the study. After removing year effects, mallard nest success remained positively correlated with the relative abundance of rodents. Of the rodent species present, California voles (*Microtus californicus*) were the most important coexisting prey type influencing nest success. Among years, mallard nest success was positively correlated with vole abundance; the asymptotic relationship suggests a threshold response to vole abundance, beyond which predators become satiated and additional voles do little to affect nest success. I tested and rejected three alternative explanations for the observed positive correlation between mallard nest success and rodent abundance that do not involve an indirect effect of coexisting prey populations. The influences of dense nesting cover, nesting density, and predator activity did not explain the observed patterns of nest success. These results suggest that rodent populations buffer predation on waterfowl nests, both within and among years, via the behavioral responses of shared predators to coexisting prey.

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Indirect effects are defined as the influence that one species has on a second species via their interactions with a third species, the key feature being that indirect effects require an intermediary species (Strauss 1991). Indirect effects can arise when one species alters the abundance of an intermediary species or modifies the interaction between the intermediary species and the third species (Wootton 1994). One class of indirect effects involves interactions between coexisting prey species whose relationship is mediated by shared predators when one prey type influences predation rates of the second prey type (Holt 1977, Holt and Lawton 1994). In the case of nesting birds, the indirect effects of coexisting prey may be particularly important since nest contents are an ephemeral food resource for predators,

available only a few months out of the year, and prey types regularly consumed during other times of the year likely will influence nest predation rates during the nesting season.

Nest predation is recognized as the most important factor influencing avian nest success (Nice 1957, Ricklefs 1969, Martin 1993), particularly for waterfowl (Greenwood et al. 1987, Klett et al. 1988). Although the direct effects of nest predation have been well studied (Sargeant and Raveling 1992), the indirect effects of coexisting prey on nest success are poorly understood. In some cases, shared predation may promote antagonism between nesting species and coexisting prey populations via apparent competition and may lead to the local extinction of the less tolerant prey species (Holt

1977, Jeffries and Lawton 1984, Holt and Lawton 1994). In other cases, coexisting prey species may benefit a nesting species by focusing predation away from nests (e.g. apparent mutualism; Holt and Lawton 1994). For example, weasels (*Mustela nivalis*) switched from foraging on the eggs of tits (*Parus* spp.) to rodents (*Clethrionomys glareolus* and *Apodemus sylvaticus*) when rodents were abundant, presumably because small mammals are weasels' preferred prey (Erlinge 1975, Dunn 1977). Finally, the presence of a coexisting prey species may have no effect on a nesting species.

In the Arctic and sub-Arctic, many bird populations fluctuate synchronously with rodent populations possibly due to the numerical and behavioral responses of shared predators to these coexisting prey (Hörnfeldt 1978, Angelstam et al. 1984, 1985, Pehrsson 1986, Summers 1986, Greenwood 1987, Summers and Underhill 1987, Sutherland 1988, Hogstad 2000). At lower latitudes where generalist predators are more numerous, coexisting prey tend not to cycle, apparently due to the dampening effect of generalist predators on a cycle driven by specialist predators (Hanski et al. 1991, Turchin and Hanski 1997). Despite this lack of cycling, it has been suggested that the indirect effects of coexisting prey on bird populations are also important in temperate regions, although few studies have investigated these interactions (Byers 1974, Crabtree and Wolfe 1988, Greenwood et al. 1998).

Regardless of location, no study has examined the indirect effects of rodent populations on nest success among different sites within the same year. The distinction between within-year (among sites) and among-year

effects of coexisting prey on nest success is important in determining the indirect effects involved. Within-year studies tend to highlight the importance of predator behavior (i.e. functional responses) whereas among-year studies emphasize the role of predator abundance (i.e. numerical responses) on nest predation rates (Schmidt 1999). Thus, the indirect effects of coexisting prey on nest success can differ depending on the spatiotemporal scale under study, and the lack of within-year studies may have underemphasized the influence of predator behavior on nest predation rates.

In this paper, I present evidence for positive indirect effects of rodent populations on waterfowl nest success, both within the nesting season among sites and among years, in a temperate system where the predominant shared predator is a generalist, the striped skunk (*Mephitis mephitis*). I test and reject alternative explanations for the observed positive correlation between waterfowl nest success and rodent densities, including the influences of dense nesting cover, nesting density, and predator activity on nest predation rates.

Methods

Study area

The Grizzly Island Wildlife Area (GIWA) is located in the Suisun Marsh, a large ($\sim$ 34 000 ha) brackish estuary at the downstream end of the Sacramento-San Joaquin Delta in California (38°14′ N, 121°97′ W; Fig. 1). Approximately one-third of the marsh is tidally influenced, with the remainder consisting of diked wetlands managed to attract waterfowl. GIWA contains roughly 2000 ha of wetlands and 1600 ha of uplands. A large block of these uplands (800 ha) is divided into fields, each 14 to 27 ha in size. I conducted this study within these upland fields and considered each field an independent replicate (see below).

Waterfowl nest success

Waterfowl nest search procedures were designed following Klett et al. (1986) as modified by McLandress et al. (1996) for this study site. Nest searches were initiated in early April and continued until July to ensure finding both early-nesting and late-nesting ducks (McLandress et al. 1996). Each field was searched at three-week intervals until no new nests were found (about four to five times). Nest searches began at least two hours after sunrise and were finished by 1400 hours to avoid missing nests due to morning and afternoon nest breaks by hens (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
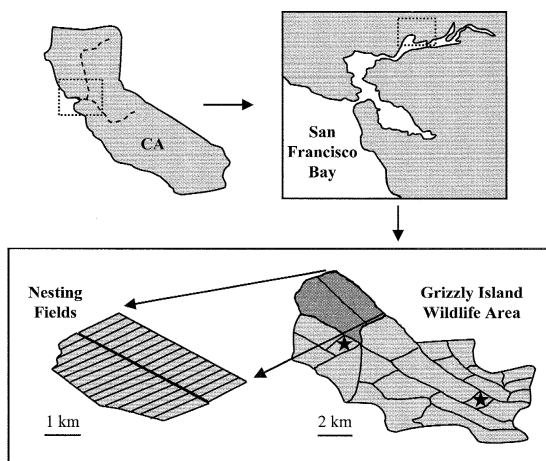

Fig. 1. The Grizzly Island Wildlife Area (GIWA) is located within the Suisun Marsh, CA, at the northeastern edge of the San Francisco Bay estuary. Within GIWA, 800 ha of upland habitat is linearly divided into rectangular fields, each 14 to 27 ha, and is managed by the California Dept of Fish and Game on a per-field basis. I conducted this study within these upland fields. Stars indicate additional field locations monitored in 1998.

vehicles (ATV). 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 hens to flush from their nests, thus enabling observers to find those nests by searching a restricted area. Each nest 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. 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 (hatched, destroyed, or abandoned) were recorded. A nest was considered successful if at least one egg hatched (as determined from shell remains; Klett et al. 1986). If the nest contained the same number of eggs as on the day it was found, embryo development had not advanced, the eggs were cold, and the hen was absent during the second nest visit, then the nest was considered abandoned on the day it was found due to investigator disturbance (Klett et al. 1986). These nests were excluded from calculations of nest success (Klett et al. 1986). Nest success was determined for each field using Mayfield (1961, 1975) techniques modified for waterfowl (Johnson 1979, Klett et al. 1986). Total duck nest success was calculated using an average clutch age at hatching of 35 days.

I used Mayfield nest-success rates to estimate nesting densities (Miller and Johnson 1978). Briefly, I divided the number of hatched nests by the Mayfield nest-success rate to estimate the total number of nests initiated in each field. I 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.

Small mammal abundance

Rodent abundance was estimated during two sampling periods each year; the first was conducted just prior to the mallard-nesting season (late March to early April), and the second immediately followed the mallard-nesting season (early July). Conducting rodent sampling both prior to and after the mallard-nesting season reduced intrusion and observer bias when estimating nest success. Sherman live traps (Model LF9, 3 × 3.5 × 9 inches) were placed in two 7 × 7 grids (10 m spacing, 0.49 ha sampling area each) systematically placed > 20 m from any field edge and > 200 m apart within habitat that was representative of each field. Two fields were sampled simultaneously for rodents; upon completion, the traps were immediately relocated to two differ-

ent fields and this procedure was continued until all fields were sampled. Traps were baited with millet seed and were checked each morning (and thereafter closed and reset in the late afternoon) for three consecutive days. Animals were identified to species except shrews (*Sorex* spp.), which were identified to genus (Shellhammer 1982, 1984, Jameson and Peeters 1988). Rodents were permanently marked with individually numbered ear tags for the purpose of distinguishing individuals and evaluating population densities. For each field, abundance estimates were calculated as the minimum number known alive (MNKA) for each sampling period, both periods were summed, and this quantity was divided by the total number of trap nights. Indices of rodent abundance per 100 trap nights were calculated by multiplying each index by 100. Rodent sampling was conducted under California Department of Fish and Game Scientific Collection Permit numbers 803017-03, 803026-03, and 803011-04, and University of California, Davis, animal welfare protocol number 8506.

I was not able to sample rodents in one field in 1998 because of permit restrictions, so I used Finfrock's (1998) rodent data for this field. Our sampling methodologies were similar, except that Finfrock's sampling session was conducted one month after my second sampling period. I combined western harvest mice (*Reithrodontomys megalotis*) and salt marsh harvest mice (*R. raviventris*) data for this field's analysis because they are morphologically and behaviorally similar and difficult to distinguish between (Shellhammer 1982, 1984).

Predator activity

During the 2000 waterfowl-nesting season, I deployed covered track-plates and remote cameras in 10 rectangular-shaped upland fields that were simultaneously monitored for waterfowl nesting and rodent populations. I used three to five stations per field to distribute sampling effort per unit area equally among fields (range: 0.18 to 0.25 stations per ha, mean: 0.21 stations per ha).

Stations were placed systematically within each field by (1) dividing the field's length by six, eight, or 10 for fields having three, four, or five stations, respectively, to obtain a distance d, (2) separating each station by twice that distance ($2d$), or from the field's edge by $1d$, and (3) alternating the stations' positions on one of two ATV tracks that each divide the field's length. ATV tracks were created during searches for duck nests, with each field divided three times along its length. Predator sampling stations were set along the outer two of these three ATV tracks. This methodology allowed each predator station to sample about the same amount of area.

Each predator sampling station consisted of a covered track-plate and a remote camera system. Covered track-plate boxes were built and used following Zielinski (1995), except that, rather than using soot, I sprayed each aluminum track-plate with a thin layer of blue carpenter's chalk mixed with ethanol. I baited each predator station in a "non-reward" manner to limit the influence of baiting on predators' foraging behavior and indices of predator activity level. I baited each predator station with two tablespoons of moist cat food in sealed plastic containers, punched five holes in the lid, and attached the container to the end of the aluminum track-plate with duct tape. I replaced the bait with fresh cat food during each subsequent visit to the station.

Active infrared sensing units with remotely-triggered 35-mm cameras (TrailMaster® TM1500 and TM35-1, Goodson and Associates, Inc., Lenexa, KS, USA; reviewed by Zielinski 1995) were positioned at each station such that the infrared beam crossed the 4 m ATV path (a presumed animal pathway) about 5 inches off the ground. The sensitivity of the TrailMaster® units was set to record both small carnivores and brief interruptions of the infrared beam typical of the legs of larger carnivores. The camera was positioned 1.2 m behind the receiver and faced the transmitter and the enclosed track-plate. The track-plate box's opening was positioned next to the infrared transmitter and slightly off and parallel to the ATV path, so that any animal traveling along the ATV path or entering the box would interrupt the infrared beam and trigger the camera to record the event. All vegetation was cleared from the infrared beam's path.

Predator sampling stations in each field were exposed during two eight-day sessions and were checked every other day. In the first session, two fields were sampled simultaneously for an eight-day period, after which the stations were immediately relocated to two different fields. This procedure was repeated until all 10 fields were sampled (40 days total). The second session immediately followed the first and repeated the sampling order of fields. In total, each sampling station was active for a total of 16 days during the waterfowl-nesting season (about 24% of the time during the central span of nest initiations; McLandress et al. 1996).

For each field, indices of predator activity were calculated by enumerating predator visits and dividing by sampling effort (station nights). I used two indices of predator activity levels. The first, called predator activity level per station night, was calculated for each field by totaling the number of nights a predator was present for each station, summing this quantity for all stations in the field, and dividing this quantity by the total number of station nights for each field. The second, called predator activity level per hour station night, was calculated for each field by totaling the number of times a predator was present at each station separated by

more than an hour from a previous visit (by either the same or different predator), summing this quantity for all stations in the field, and dividing this quantity by the total number of station nights for each field. Predator activity per 100 station nights was calculated by multiplying each index by 100. These two indices each use a different temporal scale for predator activity, either presence/absence per night or how often the predator was present, and may indicate different aspects of a predator's foraging behavior important to nest success.

Vegetation measurements

Each year, nest site vegetation was measured using a Robel pole (Robel et al. 1970) when each duck nest was initially found; measurements included the vegetation's visual obstruction height (dm), lateral density, and canopy density. Lateral and canopy densities were a subjective estimate of the nest site's vegetation density from a ground or aerial predator's view, respectively. Vegetation density was ranked from partial (vegetation only partially covered the nest site, a rank of 1) to complete (vegetation completely covered the nest site, a rank of 6). For each year, I used principal components analysis to extract the first principal component (PC 1) for the three vegetation measurements. PC 1 accounted for 55.4%, 56.9%, and 50.2% of the variance in 1998, 1999, and 2000, respectively, and was used as an index of waterfowl nest site vegetation complexity for each field. In 2000, I also collected vegetation data at 25 randomly chosen sites (not nest sites) within each field during early- to mid-June for field-level vegetation analysis. Vegetation data at nest sites, or randomly chosen sites for the field-level analysis, were analyzed by pooling data for each field. By doing so, I was able to determine the relationship between nest success and vegetation among fields. Although pooling vegetation data in each field reduces sample size and, hence, the statistical power to detect an effect of vegetation on nest success, it is necessary because the observed relationship between nest success and rodent abundance (see Results) was based on pooled data for each field. PC 1 scores increased with vegetation measurements for both nest site and field-level vegetation analyses; thus, larger PC 1 scores mean more complex vegetation.

Statistical analysis

Nest success (Mayfield estimate) was normalized with arcsine square root transformation. Indices of rodent abundance and nesting density were log transformed (log [value + 1]). Nest site vegetation measurements, field-level vegetation measurements, and predator activity levels were normally distributed (Kolmogorov-Smirnov test for normality, all $p > 0.10$) and therefore

Table 1. Sample size and species composition of duck nests and small mammals from 1998 to 2000 in the Suisun Marsh, CA.

Species	1998		1999		2000		Total	
	N	Frequency	N	Frequency	N	Frequency	N	Frequency
ducks								
mallard	294	67.7%	225	79.2%	427	80.4%	946	75.7%
gadwall	109	25.1%	52	18.3%	95	17.9%	256	20.5%
northern pintail	25	5.8%	4	1.4%	7	1.3%	36	2.9%
cinnamon teal	4	0.9%	3	1.1%	2	0.4%	9	0.7%
northern shoveler	2	0.5%	0	0%	0	0%	2	0.2%
total	434		284		531		1249	
small mammals								
California vole	25	47.2%	35	1.9%	409	44.3%	469	16.4%
house mouse	16	30.2%	1586	84.0%	342	37.1%	1944	67.9%
harvest mouse[1]	12	22.6%	266	14.1%	170	18.4%	448	15.6%
shrew	0	0%	0	0%	2	0.2%	2	0.1%
total	53		1887		923		2863	

[1] Includes both western harvest mice and salt marsh harvest mice in 1998.

were not transformed. I used analysis of covariance to determine if the relationship between nest success and rodent abundance differed among years, with nest success as the dependent variable, rodent abundance as the covariate, and year as the factor. There was a significant interaction between the effects of year and rodent abundance on nest success (see Results; Table 3). Therefore, to analyze the effect of the relative abundance of rodents on nest success among years, I standardized for year using z-scores. Z-scores 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. Pearson product-moment correlation analyses were used to test the strength of association between variables both within each year and combining all years using z-scores. Similar patterns were found using rodent biomass instead of rodent abundance and therefore are not reported. I used partial correlation (of z-scores) to test simultaneously the influence of rodent abundance, nesting density, and nest site vegetation complexity on nest success. Analysis of variance was used to test for differences in nesting densities among years.

Using fields as independent replicates

I examined a broad range of representative habitats within the study area, totaling 104, 128, and 198 ha in 1998, 1999, and 2000, respectively, although fields were not randomly selected due to logistical constraints. The upland fields are linearly divided by levees, ditches, canals, or dirt roads and 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.). Consequently, adjacent fields typically are highly diverse in vegetation structure and habitat. Since sampled fields either were adjacent or non-adjacent and some were sampled in multiple years, I tested for statistical independence (i.e. no autocorrelation) among fields, both spatially and across years. I tested whether pairs of residuals (from a linear regression model of mallard nest success vs. rodent abundance for each year) for spatially contiguous points were more similar than pairs of residuals that were spatially more widely spread (either within or across years) by plotting the absolute difference of residual errors versus the distance between the fields' centers (N. Willits, UC Davis statistical consulting services, pers. comm.). If there was spatial autocorrelation either within or among years, then the absolute difference in residuals would increase as the distance between fields' centers increased (i.e. a positive correlation). However, I found no correlation between the absolute difference in residual errors and distance among fields for all pair-wise comparisons in any year (1998: $r = -0.28$; 1999: $r = -0.17$; 2000: $r = -0.05$) or for all years combined ($r = -0.03$). Moreover, the trends were negative in all years, opposite to the trends expected if adjacent fields were more similar than non-adjacent fields. Additionally, fields that were sampled in multiple years were not more similar from year to year than fields sampled in different years that were widely spaced ($r = -0.09$). Accordingly, I used each field as an independent replicate.

Results

Coexisting prey abundance

Mallards were the most numerous nesting duck in each year, comprising 75.7% of all nests over the three years (Table 1). Other waterfowl nesting within the uplands

were gadwall (20.5%, *A. strepera*), northern pintail (2.9%, *A. acuta*), cinnamon teal (0.7%, *A. cyanoptera*), and northern shoveler (0.2%, *A. clypeata*). Nesting densities varied considerably within each nesting season among fields and among years ($F = 6.23$, $p = 0.008$). Nesting densities were highest in 1998 and lowest in 1999 (Table 2).

Five species of rodents were captured during the study, although species composition varied dramatically among years (Table 1). Overall, rodent populations were low in 1998, high in 1999, and at intermediate levels in 2000 (Table 2). California voles were the most common rodent species captured in 1998 and 2000 and the least common species in 1999 (Table 1). Among fields, mean vole abundance was greater than house mice (*Mus musculus*) and harvest mice in 2000 and lower in 1998 and 1999 (Table 2). Voles exhibited a 20-fold increase in abundance from 1998 through 2000. House mice were the most common species captured in 1999 and the second most common species in 1998 and 2000 (Table 1).

Indirect effects of coexisting prey

Mallard nest success was positively correlated with rodent abundance in 1998 ($r = 0.82$, $p = 0.048$), 1999 ($r = 0.93$, $p = 0.004$), and 2000 ($r = 0.65$, $p = 0.04$; Fig. 2). Among years, mallard nest success tended to be higher with increasing rodent abundance, although

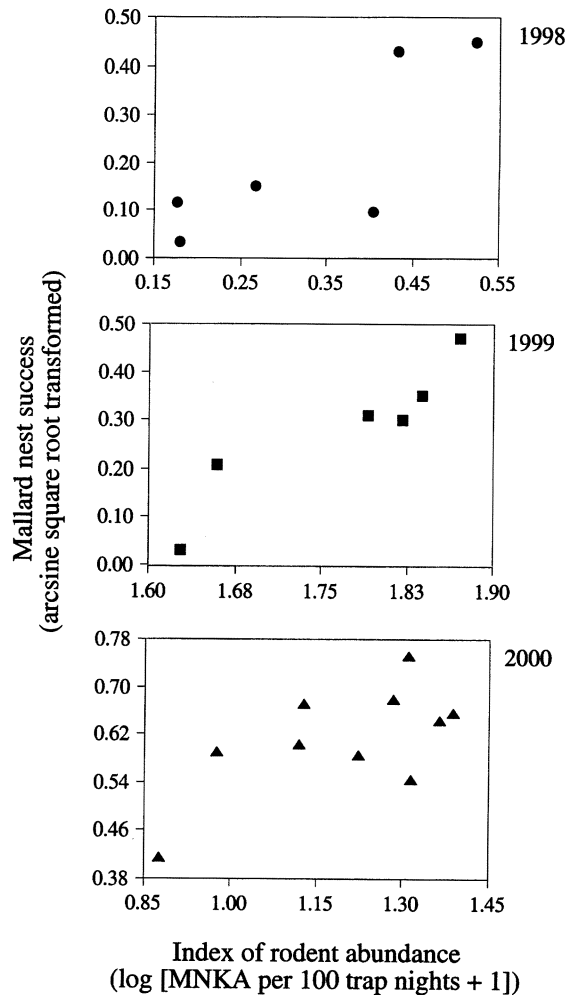Index of rodent abundance
(log [MNKA per 100 trap nights + 1])

Fig. 2. Relationships between mallard nest success (arcsine square root transformed) and rodent abundance (log [MNKA per 100 trap nights + 1]) in the Suisun Marsh, CA, from 1998 to 2000. Each data point represents an entire upland field. Axis scales differ between panels.

Table 2. Summary data (mean $\pm$ SE) of potential factors influencing duck nest success from 1998 to 2000 in the Suisun Marsh, CA. Each sample represents an entire upland field.

	1998	1999	2000
Number of fields	6	6	10
Mayfield nest success (% successful)			
mallard	6.8 $\pm$ 3.6%	9.1 $\pm$ 2.9%	33.3 $\pm$ 2.6%
all ducks	8.6 $\pm$ 4.3%	6.4 $\pm$ 2.5%	32.7 $\pm$ 2.6%
Rodent abundance (number per 100 trap nights)			
total rodent	1.24 $\pm$ 0.30	58.82 $\pm$ 5.27	15.82 $\pm$ 1.82
California vole	0.35 $\pm$ 0.15	1.06 $\pm$ 0.23	7.03 $\pm$ 1.06
house mouse	0.37 $\pm$ 0.18	48.74 $\pm$ 6.16	5.83 $\pm$ 1.03
harvest mouse [1]	0.52 $\pm$ 0.36	9.02 $\pm$ 4.00	2.92 $\pm$ 0.68
Nesting density (Mayfield nests initiated per ha)			
mallard	14.57 $\pm$ 7.53	1.55 $\pm$ 0.73	2.78 $\pm$ 0.36
all ducks	14.20 $\pm$ 4.53	2.97 $\pm$ 0.96	3.52 $\pm$ 0.39
Mallard nest site vegetation			
vegetation height (dm)	3.99 $\pm$ 0.14	4.65 $\pm$ 0.27	4.83 $\pm$ 0.27
lateral density rank	4.74 $\pm$ 0.14	4.41 $\pm$ 0.18	4.52 $\pm$ 0.15
canopy density rank	4.44 $\pm$ 0.19	3.72 $\pm$ 0.18	4.22 $\pm$ 0.12

[1] Includes both western harvest mice and salt marsh harvest mice in 1998.

there was a significant interaction between the effects of year and rodent abundance on nest success ($F = 4.54$, $p = 0.03$; Table 3). I therefore removed the effect of year by using z-scores. Combining all data using z-scores, mallard nest success was positively correlated with the relative abundance of rodents ($r = 0.73$, $p < 0.0001$; Fig. 3). Similarly, using z-scores, total duck nest success (i.e. all duck species combined) was positively correlated with rodent abundance ($r = 0.63$, $p = 0.001$), although the strength of the relationship was less than that for mallards alone.

Of all the rodent species, California vole abundance was most strongly correlated with mallard nest success. Mallard nest success was positively correlated with California vole abundance ($r = 0.79$, $p = 0.005$) in 2000 when mean vole abundance was greater than the abundance of each other rodent species, but not in 1998 or 1999 (all $r < |0.3|$, $p > 0.5$) when mean vole abundance

Table 3. Analysis of covariance of the relationship between mallard nest success (arcsine square root transformed) and rodent abundance (log transformed) among years.

	df	Sum of squares	Mean square	F	p-value
year	2	0.08	0.04	5.90	0.01
rodent abundance	1	0.22	0.22	31.90	<0.0001
year × rodent abundance	2	0.06	0.03	4.54	0.03
residual	16	0.11	0.01		

was smaller than each other species. There was no significant interaction between year and vole abundance on nest success; therefore I pooled all years to investigate the effect of vole abundance on nest success. Mallard nest success was positively correlated with vole abundance among years ($r = 0.83$, $p < 0.0001$; Fig. 4).

Alternative explanations

I tested three alternative explanations that could produce a spurious correlation between nest success and rodent abundance that do not involve an indirect effect between coexisting prey populations via shared predation.

Dense nesting cover

One possibility is that dense vegetative cover both reduced nest predation rates and promoted increased rodent abundance, thereby explaining the observed positive correlation between nest success and rodent abundance. Dense nesting cover could either influence nest success at (1) the nest site by affecting a predator's visual or olfactory ability to find nests, or (2) the field level by inhibiting a predator's movements and reducing its foraging efficiency.

Vegetation at the nest site: Mallard nest success was not significantly correlated with any nest site vegetation measurement, including vegetation height, lateral density, and canopy density, in any year or for all years combined using z-scores (all $p > 0.10$). Similarly, mallard nest success was not significantly correlated with vegetation complexity in any year (i.e. PC 1; 1998: $r = -0.53$, $p = 0.31$; 1999: $r = -0.30$, $p = 0.59$; 2000: $r = -0.09$, $p = 0.82$; Fig. 5) or for all years combined using z-scores ($r = -0.22$, $p = 0.34$). Furthermore, the trends were negative, opposite to those predicted if dense nesting cover increased nest success.

Vegetation at the field level: In 2000, mallard nest success was not correlated with any vegetation measurement at the field level, including vegetation height, lateral density, canopy density (all $p \gg 0.10$), or vegetation complexity ($r = 0.18$, $p = 0.63$).

Nesting density

Another possibility is that nesting density influenced nest predation rates. A positive correlation between nest success and rodent abundance could result if nest

predation was density-dependent and nesting densities were correlated with rodent abundance because of similar habitat requirements. However, mallard nest success was not significantly correlated with nesting density in 1998 or 2000 (all $p > 0.10$, see below; Fig. 6) or when all years were combined using z-scores ($r = 0.24$, $p = 0.29$). In 1998, the trend between mallard nest success and nesting density was negative ($r = -0.64$, $p = 0.19$), whereas there was no trend in 2000 ($r = 0.33$, $p = 0.36$). In 1999, mallard nest success was positively correlated with nesting density ($r = 0.81$, $p = 0.05$; Fig. 6). However, in that year, mallard nesting density also was positively correlated with rodent abundance ($r = 0.88$, $p = 0.02$), so an ecological effect of rodents may have contributed to the positive trend observed between nest success and nesting density. I therefore used partial correlation to simultaneously test the effects of rodent abundance, nesting density, and nest site vegetation complexity on nest success, after controlling for year effects by using z-scores. Rodent abundance was the only significant predictor of mallard nest success ($r = 0.69$, $p < 0.001$; Table 4).

Predator activity

Differential predator activity among fields might lead to lower nest success in fields with greater predator activity and vice versa. In 2000, I sampled predators in the 10 upland fields for a total of 640 station nights. I obtained 606.5 station nights of photographic data and
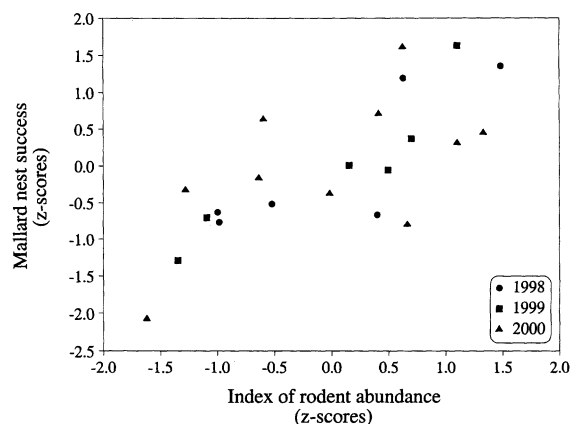

Fig. 3. Relationship between mallard nest success and relative abundance of rodents, after controlling for year effects using z-scores. Each data point represents an entire upland field.
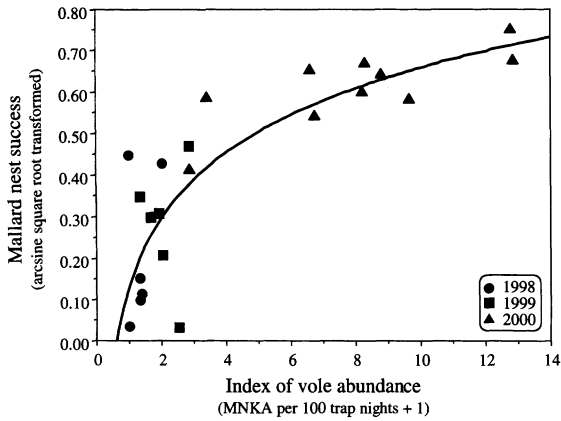
Fig. 4. Relationship between mallard nest success (arcsine square root transformed) and vole abundance (MNKA per 100 trap nights + 1) among years. Logarithmic regression line illustrates the asymptotic relationship. Statistical analyses were performed on log transformed vole abundance to linearize the relationship. Each data point represents an entire upland field.

detected numerous striped skunks (*Mephitis mephitis*), one raccoon (*Procyon lotor*), one coyote (*Canis latrans*), and one feral cat (*Felis silvestris*), whereas with covered track-plates I detected only striped skunks. Although rarely detected at predator stations, I observed coyotes (range: one to three) within the upland nesting fields on 15 separate occasions on 12 different days, and considered them to be common. Because raccoons, coyotes, and feral cats were detected so infre-
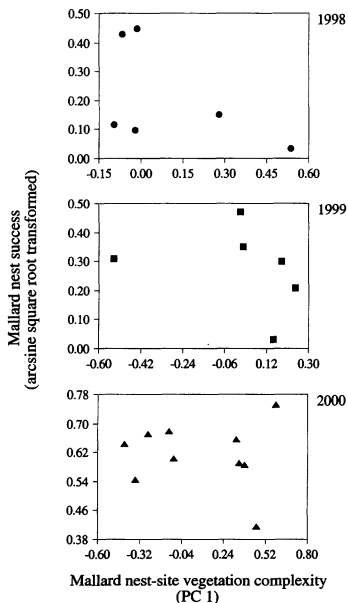

Fig. 5. Relationships between mallard nest success (arcsine square root transformed) and vegetation complexity (PC 1) from 1998 to 2000. Each data point represents an entire upland field. Axis scales differ between panels.
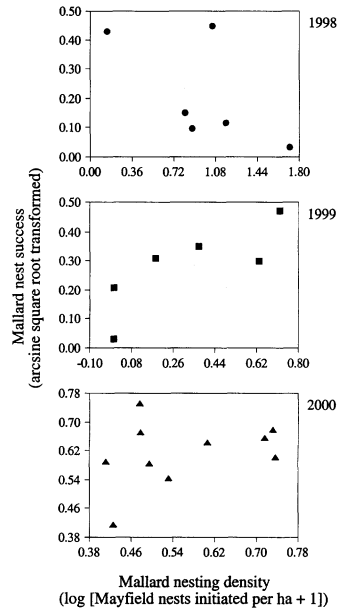

Fig. 6. Relationships between mallard nest success (arcsine square root transformed) and nesting density (log [Mayfield nests initiated per ha + 1]) from 1998 to 2000. Each data point represents an entire upland field. Axis scales differ between panels.

quently, I excluded them from further analyses. Among fields, the indices of skunk activity obtained using camera data and covered track-plate data were highly correlated (presence/absence data for each method, $r = 0.87$, $p \ll 0.01$). In all further analyses I used only camera data because it provided more detailed resolution of skunk activity levels.

Mallard nest success was not correlated with skunk activity per station night ($r = -0.04$, $p = 0.93$, Fig. 7) or skunk activity per hour station night ($r = 0.21$, $p = 0.57$). Similarly, total duck nest success was not correlated with either metric (skunk activity per station night: $r = -0.04$, $p = 0.91$; skunk activity per hour station night: $r = 0.09$, $p = 0.81$). Additionally, neither index of skunk activity was correlated with nesting density, rodent abundance, nor vole abundance (all $p > 0.10$).

Table 4. Partial correlation matrix for the effects of rodent abundance, mallard nesting density, and mallard nest site vegetation complexity (PC 1) on mallard nest success after controlling for the effect of year by using z-scores (df = 18).

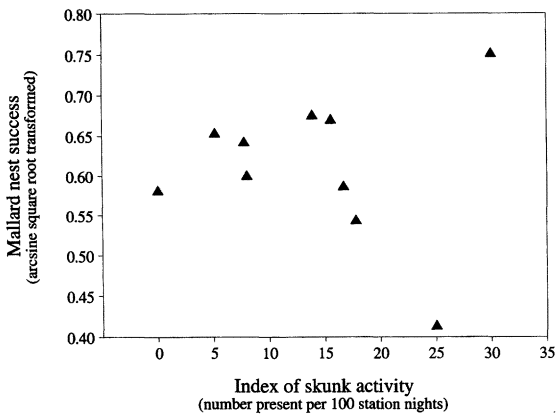|	Mallard nest success	
	Correlation	*p*-value
rodent abundance	+0.69	<0.001
nesting density	+0.02	>0.25
nest site vegetation complexity	−0.05	>0.25

Fig. 7. Relationship between mallard nest success (arcsine square root transformed) and skunk activity (number present per 100 station nights) in 2000. Each data point represents an entire upland field.

Discussion

Mallard nest success was positively correlated with rodent abundance during all three years of this study (Fig. 2). After controlling for year effects and combining all years, mallard nest success remained positively correlated with the relative abundance of rodents (Fig. 3). Among years, mallard nest success was positively correlated with vole abundance (Fig. 4). Thus, it appears that rodent populations indirectly affect nest success. However, because I was unable to experimentally manipulate rodent densities, cause and effect can only be inferred. Therefore, I evaluated three alternative explanations that might lead to a spurious correlation between nest success and rodent abundance that do not involve an indirect effect between duck nests and rodent populations via shared predation.

Alternative explanations

First, nest site vegetation is thought to influence nest success by affecting a predator's visual or olfactory ability to find nests (Crabtree et al. 1989). Dense nesting cover might also inhibit a predator's movements (Duebbert 1969, Schrank 1972) and reduce its foraging efficiency (Crabtree et al. 1989). Large rodent populations may therefore be indicative of a field's dense nesting cover or enhanced nest site vegetation, which could lead to increased nest success by reducing a predator's ability to find nests, and vice versa. I found no evidence for this alternate explanation. Mallard nest success was not correlated with any nest site vegetation measurement in any year or for all years combined (Fig. 5). Furthermore, mallard nest success in 2000 was not correlated with any vegetation measurement at the field-level. These results are consistent with other studies on the effect of dense nesting cover on nest success;

few have documented increased nest success in habitats managed for dense nesting cover and the effect of dense nesting cover on nest success remains unclear (reviews by Schrank 1972, Cowardin et al. 1985, McKinnon and Duncan 1999). Thus, the positive relationship between nest success and rodent densities likely was not caused by nest site or field-level vegetation characteristics.

Second, nesting density could influence nest success via density-dependent predation. For example, some predators will concentrate their searching effort after finding a prey item, resulting in low nest success at high nesting densities (Tinbergen et al. 1967). In this study, nesting density may have influenced nest predation rates and could explain the observed positive correlation between nest success and rodent abundance if, for instance, nest predation was density-dependent (either positively or negatively) and nesting densities were correlated with rodent abundance because of similar habitat requirements. However, mallard nest success was not correlated with nesting density in 1998 or 2000 (Fig. 6) or when all years were combined. Mallard nest success was positively correlated with nesting density in 1999 (Fig. 6). Although this relationship could have been caused by density-dependent predation, it also could have been caused by the positive correlation between mallard-nesting density and rodent abundance in that year. Using partial correlation to test simultaneously the effects of rodent abundance, nesting density, and nest site vegetation complexity on nest success, I found that rodent abundance was the only significant predictor of mallard nest success (Table 4). Similarly, Andrén (1991) found no difference in nearest neighbor distance (a correlate of nesting density) between successful and unsuccessful mallard nests. Conversely, other studies using simulated duck nests found evidence consistent with density-dependent predation (Sugden and Beyersbergen 1986, Larivière and Messier 1998). Thus, although nest density probably influences nest predation rates and warrants further research, in this study rodent abundance explained the pattern of nest success better than nesting density.

Third, differential predator activity among fields also could lead to a spurious correlation between nest success and rodent abundance. Large rodent populations might result from low rodent mortality rates because of low predator activity levels in those fields, and vice versa. Accordingly, if predator activity levels are low, then nest predation rates might also be low and result in high nesting success. Hence, a positive correlation between nest success and rodent abundance would be observed. According to this alternative explanation, rodent populations do not indirectly affect nest predation rates; rather, large rodent populations and low nest predation rates (i.e. high nesting success) each are a result of low predator activity levels in those fields. Striped skunk activity levels were not correlated with mallard nest success and therefore do not support this

alternate explanation (Fig. 7). In contrast, Johnson et al. (1989) reported correlations between predation rates of duck nests and indices of predator activity in the Canadian prairie and pothole region, including a positive correlation between striped skunk activity and nest predation rates. Removal of striped skunks also has resulted in increased nest success (Greenwood 1986). However, at the spatial and temporal scales of this study it appears that nest success depends not so much on where the predators are, but on how they forage and upon what prey. The primary factor influencing mallard nest success is the indirect effects of coexisting prey and, specifically, how alternate prey types influence predator foraging behavior.

Indirect effects of coexisting prey

Predators are the primary cause of duck nest failure and significantly limit recruitment (Sargeant and Raveling 1992), potentially below replacement levels for mallards (Cowardin et al. 1985) and other duck species (Greenwood et al. 1987, Klett et al. 1988). The striped skunk is a predominant predator of duck nests in various habitats throughout its range (Greenwood 1986, Crabtree et al. 1989, Johnson et al. 1989, Pasitschniak-Arts and Messier 1995, Larivière and Messier 1998), despite preying extensively on other food resources (Verts 1967, Greenwood et al. 1999). McLandress et al. (1996) implicated striped skunks as a major predator of duck nests in the Suisun Marsh. I also documented skunks as the most active predators within the nesting fields during 2000, and believe they were the major predator of duck nests in 1998 and 1999 as well. Other predators of duck nests that are common in the Suisun Marsh but generally were not detected at predator stations include coyotes, gopher snakes (*Pituophis melanoleucus*), and common ravens (*Corvus corax*), but these species are rarely implicated as principal predators of ducks nests (Johnson et al. 1989, Pasitschniak-Arts and Messier 1995, Sovada et al. 1995, Larivière and Messier 1998) and were suspected to have only a minor influence on estimates of nest success.

Striped skunks primarily consume small mammals and invertebrates (Hamilton 1936, Verts 1967, Crabtree and Wolfe 1988, Greenwood et al. 1999) and incidentally depredate grassland songbird nests (Roseberry and Klimstra 1970, Vickery et al. 1992). Skunks might consume duck eggs opportunistically while foraging for prey that are unpredictably located and largely immobile (e.g. nestling rodents, insects, carrion; Crabtree and Wolfe 1988), although they also may actively search for duck nests, resulting in density-dependent nest predation (Larivière and Messier 1998). Diet studies of striped skunks conducted in areas with nesting waterfowl find that rodents, especially voles (Arvicolinae), constitute a large proportion of the diet (Crabtree and Wolfe 1988, Greenwood et al. 1999).

It is unclear whether predators, predominantly skunks, were keying specifically on overall rodent abundance, biomass, or a particular species. Although the effect of rodent populations on nest success depended on the year (Table 3), the relative abundance of rodents was positively correlated with mallard nest success (Fig. 3). This suggests that each year predators were responding to the spatial variability in rodent densities and sought food accordingly. Yet, despite the positive effects of rodent abundance on nest success, overall mallard nest success in 1998 and 1999 was similar, and well below the 15% suggested for population stability (Cowardin et al. 1985), even though overall rodent abundance had increased considerably between these years (Table 2). Thus, the overall abundance of rodents alone cannot explain the yearly trends in mallard nest success, indicating that the specific (rodent) prey type may be important. Of the rodent species present, California vole abundance was most strongly correlated with mallard nest success, indicating that voles may be a major food resource for nest predators. Additionally, when voles were the most abundant rodent species (2000), mallard nest success was positively correlated with vole abundance. Others have noted the importance of voles in the diet of skunks throughout their range (Hamilton 1936, Pearson 1971), including in duck nesting areas (Byers 1974, Crabtree and Wolfe 1988, Greenwood et al. 1999). Although capture rates and handling times may differ among prey species, voles may be a more profitable food resource for skunks than other rodent species due to their size, which at 42 g was 3–4 times that of house mice (15 g) and harvest mice (11 g).

If voles are a preferred prey of skunks, then vole abundance alone can explain the yearly trends in nest success. Both mallard nest success and vole abundance increased consecutively in each year of the study, whereas the abundance of other rodent species did not (Table 2). Among years, mallard nest success was significantly correlated with vole abundance (Fig. 4). The relationship between mallard nest success and vole abundance is positive and asymptotic; nest success increases rapidly as vole abundance increases, but gradually decelerates towards a plateau (Fig. 4). This relationship has a form similar to a Type II functional response (Holling 1959), although it is unknown whether nest success is a reliable proxy for the consumption rate of voles, and suggests that there may be a threshold response to vole abundance beyond which skunks become satiated and additional voles do little to affect nest success.

The few studies that have examined the influence of coexisting prey densities on waterfowl nest success each have found that nest success is positively correlated with rodent densities among years. In Iowa (USA), Byers (1974) found that blue-winged teal (*Anas discors*) nest success was positively correlated with rodent abundance (predominantly *Microtus pennsylvanicus*) among

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years. Pehrsson (1986) demonstrated a positive correlation between oldsquaw (*Clangula hyemalis*) duckling production and rodent density (predominantly *Lemmus lemmus* and *Microtus rufocanus*) in northern Sweden. In fact, twice as many ducklings were produced in rodent-peak years compared to intervening years, and oldsquaw populations were highest in years following rodent-peaks. On the Taimyr Peninsula in arctic Russia, the breeding success of dark-bellied brent geese (*Branta bernicla bernicla*) and wading birds (Charadii) also was strongly correlated with lemming densities (*Lemmus sibiricus* and *Dicrostonyx torquatus*), both among breeding years and when a lag effect was included (Summers 1986, Summers and Underhill 1987, Greenwood 1987, Sutherland 1988). Daily survival rates of wading birds' nests in Dutch agricultural grasslands also were positively correlated with densities of voles among years (*Microtus* spp.; Beintema and Müskens 1987). Similarly, positive relationships exist between grouse and vole populations in boreal Fennoscandia (Myrberget 1972, Hörnfeldt 1978, Angelstam et al. 1984, 1985, Lindström et al. 1987). Synchronized 3- to 4-year population fluctuations of voles and grouse apparently are caused by predators shifting predation pressure from declining vole populations to grouse, and vice versa. My results are consistent with these studies; mallard nest success was positively correlated with vole abundance among years. Additionally, mallard nest success was positively correlated with rodent abundance among sites within each year, a result that has not been reported previously.

Although I did not identify the specific mechanism by which coexisting prey influenced nest success, the results of this study suggest that rodent populations, especially voles, indirectly affect waterfowl nests via shared predation. There are multiple mechanisms by which coexisting prey species can indirectly affect nest predation rates, including altering the habitat use of predators (Stickney 1991, Larivière and Messier 2000), influencing the foraging mode of predators (Crabtree and Wolfe 1988, Crabtree et al. 1989, Vickery et al. 1992), or diluting predation (Foster and Treherne 1981). My results suggest that nest success depends not only on predator abundance and location, but also on predator behavior and, specifically, how predators forage and what they eat. Whether large rodent populations can buffer predation on waterfowl nests over the long term is unclear (e.g. predator populations might numerically respond to an increased prey base; Holt 1977, Holt and Lawton 1994) and remains an important avenue for future research.

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