

Influence of habitat patch characteristics on the success of upland duck nests

JAIME E. JIMÉNEZ, Laboratorio de Ecología, Universidad de Los Lagos, Casilla 933, Osorno, Chile
jjimenez@ulagos.cl

MICHAEL R. CONOVER, Jack H. Berryman Institute, Department of Wildland Resources, Utah State University, Logan, UT 84322-5230, USA

RAYMOND D. DUESER, Jack H. Berryman Institute, Department of Wildland Resources, Utah State University, Logan, UT 84322-5230, USA

TERRY A. MESSMER, Jack H. Berryman Institute, Department of Wildland Resources, Utah State University, Logan, UT 84322-5230, USA

Abstract:

When there is a rich guild of nest predators that use different modalities and techniques to locate hidden nests, we hypothesized that no habitat patch characteristic will consistently predict nest success, because if such a characteristic existed then predators would develop a search image based on it and use that characteristic to increase their hunting efficiency for nests. We tested this prediction in the Prairie Pothole region of North Dakota by characterizing the features of 16 habitat patches that contained >1,800 dabbling duck nests. Nest success was monitored during both the early and late nesting season over 2 years. Nest success was generally low and highly variable among habitat patches and across seasons and years. We found that nest success was rarely correlated with patch size, nest density, predator abundance and richness, abundance of alternative prey for predators, and visual and physical obstruction provided by the vegetation. Those few habitat patch characteristics that were correlated with nest success during a particular single year or season were not correlated during other seasons or years. Hence, our results supported the hypothesis that no habitat patch characteristic can consistently predict nest success.

Key words: dense nesting cover, ducks, human–wildlife conflicts, landscape ecology, nest depredation, raccoon (*Procyon lotor*), red fox (*Vulpes vulpes*), skunk (*Mephitis mephitis*), wildlife damage management

THE GREAT PLAINS of North America has a rich guild of predators that prey upon the eggs of upland-nesting ducks. These predators include raccoons (*Procyon lotor*), red foxes (*Vulpes vulpes*), coyotes (*Canis latrans*), striped skunks (*Mephitis mephitis*), mink (*Mustela vison*), ground squirrels (*Otospermophilus beecheyi*), American crows (*Corvus brachyrhynchos*), great-horned owls (*Bubo virginianus*), black-billed magpies (*Pica pica*), and snakes (Sargeant et al. 1993, Greenwood et al. 1995). These predators are the primary reasons why duck eggs fail to hatch in upland habitats (Sargeant and Raveling 1992, Sargeant et al. 1993, Greenwood et al. 1995). Ducks lack the ability to defend their nests against most of these predators so that their chief method of avoiding nest predation is to hide their nests. However, in the conflict that arises between a duck's need to hide its nests from predators and the predator's need to find the nest for food, predators have 2 major advantages over nesting ducks (Conover 2007). First, different predator species use different techniques and modalities to locate nesting ducks. Unfortunately, the nesting behaviors

and strategies that ducks use to hide their nests from visual predators expose them to olfactory-oriented predators (Conover 2007). Because of this, there are few upland sites for nesting ducks that are not vulnerable to olfaction-oriented predators, such as mammalian carnivores.

The second advantage that predators have over nesting ducks is that predators can change their search image of where to hunt for duck nests faster than ducks can change their search image of where to hide their nests (Conover 2007). Because of this, the optimal hiding strategy for ducks is to locate their nests in the same general area used previously—provided that their prior nesting attempts were successful—and to select random sites for their nests within suitable habitat if their prior nesting attempts were unsuccessful (Conover 2007). When duck nests are accessible to predators and when nesting success is dependent upon predators not finding a nest before the eggs have hatched, no habitat characteristic should consistently be correlated with either duck nest density or successful nesting. If such a habitat existed, predators could use it themselves to

locate duck nests. Hence, it would cease to be correlated with nest success or nest density (Conover 2007).

In this paper, we test the prediction that the success of duck nests in a habitat patch is unrelated to nest success in the same patch during the prior seasons or years. We also examine whether any habitat patch characteristics are related to nest success.

Methods

Study sites

This study was conducted at 15 sites during the waterfowl breeding seasons of 1997–1998. Study sites ranged in size from 13 to 388 ha and were located in an area of about 100 km in diameter north and east of Devils Lake, North Dakota, in the Drift Plain biogeographical province of the Prairie Pothole region (Stewart 1975). The region exhibited a high density of breeding waterfowl and predators (Garrettson et al. 1996). The landscape is highly fragmented, with its 1-x 1-mile road network and planted shelterbelts that produce a grid-like mosaic of patches with sharp edges (Pasitschniak-Arts et al. 1998). Up to 95% of the landscape surface is cultivated annually (Reynolds et al. 1994), primarily for the production of small grains and sunflowers (Cowardin et al. 1985).

To select study sites, we considered all of the sites in Ramsey, Cavalier, and part of Nelson counties with dense nesting cover. Dense nesting cover is considered the best available duck nesting habitat and resembles the original prairie vegetation (Klett et al. 1984, 1988, Higgins et al. 1992). Potential sites were not subjected to plowing, tilling, grazing, or predator control during at least the 2 years prior to initiation of this study. Areas enrolled in the Conservation Reserve Program, U.S. Fish and Wildlife Service Waterfowl Production Areas, and Wildlife Development Areas met these requirements. Other criteria for site selection included abundant seasonal and temporary wetlands. Sites with large wetlands were discarded from consideration.

We stratified the available sites by the amount of upland area into small- medium- and large-sized patches. We selected 5 sites randomly from each group. To gain independence among sites, selected sites were located >5 km apart. For comparative purposes, we used all but one of the

same sites during both 1997 and 1998. Because 1 site was mowed in autumn 1997 we replaced it with another with similar characteristics. We obtained the surface area of each site (including wetlands) and upland area from the Devils Lake Fish and Wildlife Service records, and, when these were not available, we computed the area using aerial photographs. To calculate patch size, only upland surface area was used. Estimates of all habitat, prey, and predator variables were obtained early (i.e., May to early June) and late (i.e., late June to July) during each breeding season.

Estimating waterfowl nest success

As in Duebbert and Kantrud (1974) and Cowardin and Johnson (1979), we used nest success as an index of recruitment. We estimated nest success at each site on 4 16-ha blocks. We pooled information from the 4 blocks by site. Sites <64 ha were surveyed entirely. We combined data from nests of all duck species by site because of small sample sizes for individual species (Greenwood 1986). We used chain-dragging to locate nests (Higgins et al. 1977). Hatching date was estimated as described in Weller (1956) and Klett et al. (1986). We marked each nest location with a bamboo stake 4 m from the nest and recorded the position with a hand-held Global Positioning Satellite (GPS) unit with differential correction. Nest fate was assessed as abandoned, successful, or depredated (Cowardin et al. 1985, Klett et al. 1986). Abandoned nests were not used in the analyses. The predator species that destroyed a nest often could not be determined because the evidence left by predators was inconclusive. We used nest fates and exposure days to calculate daily survival rates for nests according to the Mayfield method (Mayfield 1961) as modified by Johnson (1979). Nest searching was conducted 3 times between early May and late July (Miller and Johnson 1978, Sargeant et al. 1984, Higgins et al. 1992, Greenwood et al. 1995). To determine the fate of the nests, we weekly visited those with known locations.

We calculated nest success estimates separately for the first and second halves of the breeding season. In what follows, these will be called early and late season, respectively. Splitting the breeding season into 2 periods instead of treating time as a continuous variable may seem arbitrary, but it was dictated by logistic con-

straints in sampling the other variables.

Estimating nest density

We first attempted to compute the density of nests as the ratio of the number of nests initiated to the surface of upland area searched. The number of nests initiated was computed as the ratio of the number of successful nests found to the estimated hatch rate (Miller and Johnson 1978). However, this procedure has 2 problems. Statistically, it would be incorrect to calculate the independent variable nest density, from the dependent variable nest success. Additionally, this procedure works well only within certain ranges of nest success values and will produce extreme density values if few nests were successful and nonsense values if no nest succeeded at a site. Instead, we used a more conservative approach based only on the total number of nests found. Thus, nest density at any given site will be a ratio of the number of all nests found to the upland area searched (Duebbert 1969, Higgins 1977). Even though this estimate will present negative bias for sites with intense predation—this is the essence of the Mayfield estimator—it correlates positively with estimates produced by the method described above (Spearman *rhos* for early and late seasons > 0.69 , $P < 0.001$, $n = 30$). Because this estimate is a composite of the nests found over a time span, it overestimates nest density at any given time (Hill 1984). Conversely, because only a fraction of the nests are detected (Sowls 1955, Keith 1961, Gloutney et al. 1993), the data will underestimate total nest density over the entire breeding season.

Measuring habitat patch variables

We estimated visual and physical obstruction at 20 random locations in each site from each of 4 cardinal directions. These 2 measures represent the difficulty that a mammalian predator would have to both see through and move through the vegetation. Visual obstruction was evaluated by using the method described by Robel et al. (1970). It corresponded to the mean height of the vegetation at a given site of 4-m radius measured from 0.5 m off the ground. We also measured visual obstruction at each duck nest when first found. We obtained an index of physical obstruction by measuring the force necessary to drag a 0.4-kg soccer ball through vegetation.

We pulled a ball with a 4-m string attached to a Pesola scale and determined the maximum force necessary to drag the ball at a speed of approximately 1 m/sec. Estimates for each site were the average of 80 measurements.

We obtained indices of small mammal and arthropod abundances at each site. These 2 prey categories constitute most, or an important part, of the diet of red foxes, raccoons, and striped skunks, the most common nest predators in the region (Verts 1967, Fritzell 1978, Greenwood 1981, 1982, 1986, 1993, Greenwood et al. 1985). We estimated small mammal abundance using 20 medium-sized Sherman traps baited with rolled oats and peanut butter. We placed the traps every 10 m along a line that ran across each patch beginning 50 m from an edge and running perpendicular to it. Traps were checked every morning for 3 consecutive days. The total number of individual small mammals caught during the 60 trap-nights provided an abundance index for each site.

Arthropods were captured using a line of 20 pit-fall traps without bait or preservation liquid (Sutherland 1996). A pit-fall trap was set every 10 m along the same line as the Sherman traps, equidistant between adjacent traps. Pit-fall traps were operated for 5 days. These traps selectively collect invertebrates that move above the ground, and these are more vulnerable to mammalian predators than other arthropods. We counted the number of arthropods > 5 mm in size that we collected in each trap, separating them by size into small (< 1 cm) or large (> 1 cm) groups and by taxa (Order or Family if possible). To account for differences in biomass, the smaller arthropods were weighed as 0.2 of the larger (i.e., 5 small were equivalent to 1 large). The number of arthropods collected in the 20 traps provided an index of abundance for the site.

Mammalian predators are the principal causes of nest failure in North Dakota (Duebbert and Kantrud 1974, Cowardin et al. 1985, Sargeant et al. 1993). At each site, we estimated the relative abundance of mammalian predators and the species richness of predators by using visitations to scent stations as described by Linhart and Knowlton (1975), refined by Roughton and Sweeny (1982), and used by Travaini et al. (1996). Local predator tracks were distinguished based on shape and size (Halfpenny and Biesiot 1986). At each site, a line of 6 scent stations spaced 250

m apart was placed in the patch interior. If a straight line did not fit into a site, it was curved so that no station was closer than 50 m from an edge. Another similar line of scent stations was run along the edge of each patch. We operated both lines simultaneously for 2 days and nights (Travaini et al. 1996). The predator abundance index for a site was the percentage of the 12 stations visited by predators. The species richness index was based on all the species recorded at these same scent stations combined with supplemental observations of avian and mammalian predators and their tracks, feces, or dens within 1.6 km of a site (Keith 1961). We combined local avian predators in 4 functional groups: (1) hawks, harriers, and falcons, (2) owls, (3) large-sized gulls, and (4) crows and magpies. Given that we spent similar amounts of time at all sites, data are comparable.

Statistical analyses

For all statistical tests, the site was our sample unit. We compared nest success separately for early- and late-nesting ducks because vegetation in North Dakota varies considerably as the spring and summer progresses. We used nest success as the dependent variable and habitat-patch characteristics as the independent variables. These latter included patch size, nest density, predator abundance, predator richness, arthropod abundance, small mammal abundance, visual obstruction, and physical ob-

struction. Because the variance of the Mayfield estimator is inversely related to the number of exposure days (Greenwood 1986, Klett et al. 1988, Greenwood et al. 1995, 1998), we weighted all analyses by the number of exposure days to eliminate that bias (Freund and Littell 1991).

We conducted a 2-way ANOVA to compare nest success between years and seasons (early-nesting versus late-nesting). We conducted Spearman Rank Correlation tests to compare habitat patch characteristics to nest success. Prior to conducting the Spearman Rank Correlation tests, we transformed the independent variables to better meet the assumptions of normality and homoscedasticity and to improve the linear relationships between the independent variables and the dependent variable (Table 1). Paired *t*-tests were conducted to test if the slopes of the relationships were equal to zero. All tests were 2-tailed and the significance level was $\alpha = 0.05$.

Results

Variation in nest success between consecutive seasons and years

During the 2 years of study, we found 1,865 nests representing 5 dabbling duck species (Table 2). Of these nests, 843 and 826 either hatched or were destroyed by predators during 1997 and 1998, respectively, and were thus used in the analysis (Table 2). We excluded nests when we could not determine their fate (79) or when they were abandoned (117). We included

TABLE 1. Transformations of the variables used in the statistical tests.

Variable	Unit of measurement	Transformation	Abbreviations
Nest success	% (Mayfield)	Square root	SQMAYFI
Nest density	Nests/ha	Square root	SQDENSI
Patch size (upland area)	ha	Log _e	LNUPLAN
Predator abundance	% scent stations visited	Square root	SQPREAB
Predator richness	Species detected	Not transformed	PREDSP
Arthropod abundance	Numbers trapped	Inverse	ARTHR_1
Small mammal abundance	Individuals trapped	Arcsine square root	ASSMALL
Visual obstruction	dm (Robel)	Square root	SQVISUA
Physical obstruction	kg force	Log _e (x + 0.5)	LNPHYSI

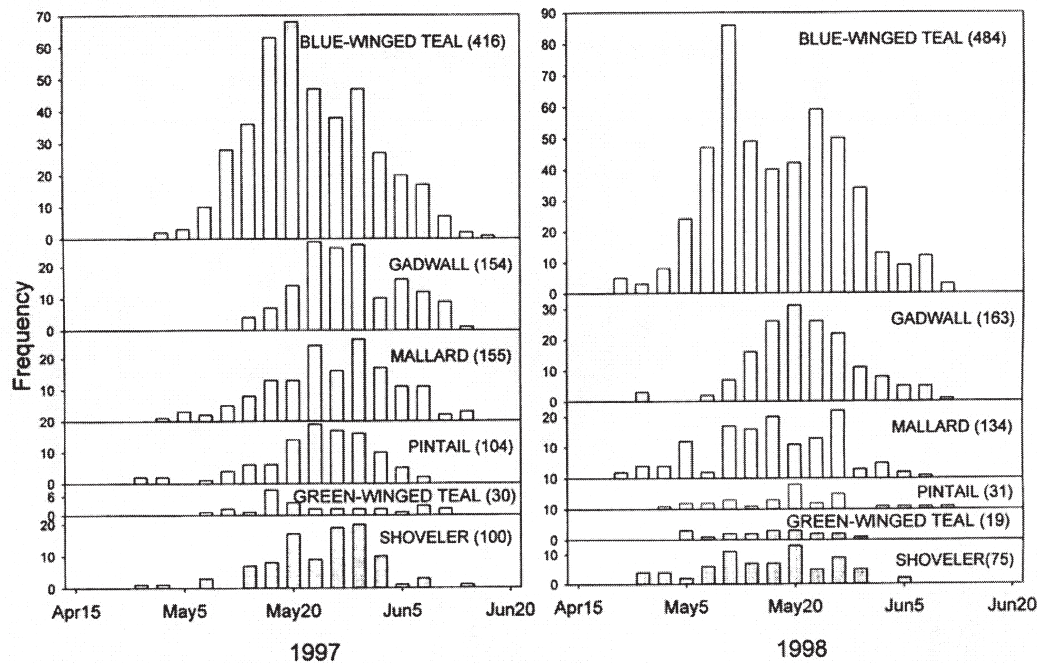
TABLE 2. Number of dabbling duck nests, by year, season, species, and fate, found on 15 sites in North Dakota.

Year	Fate	Early season						Late season						Total		
		BW ^a	GD	GW	ML	PT	SV	ST	BW	GD	GW	ML	PT		SV	ST
1997	Hatched	80	23	6	19	21	17	166	43	28	6	13	19	17	126	292
	Depredated	143	27	9	34	19	24	256	97	64	5	66	32	31	295	551
	Abandoned	20	1	1	11	5	3	41	11	2	1	9	2	5	30	71
	Unknown	13	2	2	3	3	2	25	9	7	0	0	3	1	20	45
Subtotal		256	53	18	67	48	46	488	160	101	12	88	56	54	471	959
1998	Hatched	113	21	6	28	5	17	190	90	48	3	26	11	15	193	383
	Depredated	129	28	5	39	5	17	223	118	48	2	27	6	19	220	443
	Abandoned	11	2	0	3	0	1	17	10	8	2	6	1	2	29	46
	Unknown	9	2	0	3	1	3	18	4	6	1	2	2	1	16	34
Subtotal		262	53	11	73	11	38	448	222	110	8	61	20	37	458	906
Total		518	106	29	140	59	84	936	382	211	20	149	76	91	929	1865

^a BW = Blue-winged teal, GD = Gadwall, GW = Green-winged teal, ML = Mallard, PT = Pintail, SV = Shoveler, ST = Subtotal.

TABLE 3. Means (\bar{x}) and standard errors (SE) of the variables measured in this study (see Table 1 for units).

Year	Season		Nest success	Nest density	Patch size	Predator abundance	Predator richness	Arthropod abundance	Small mammal abundance	Visual obstruction	Physical obstruction
1997	Early	\bar{x}	0.19	0.95	88.1	27.8	4.3	68.2	2.7	4.3	1.09
		SE	0.04	0.13	21.0	3.8	0.4	13.0	0.6	0.2	0.04
1997	Late	\bar{x}	0.16	0.97	88.1	27.8	4.1	93.2	5.8	5.8	1.24
		SE	0.03	0.15	21.0	4.6	0.3	32.6	1.1	0.3	0.04
1998	Early	\bar{x}	0.19	0.97	87.9	21.1	4.4	62.3	5.4	4.6	0.92
		SE	0.05	0.13	21.1	4.3	0.2	21.7	1.2	0.3	0.04
1998	Late	\bar{x}	0.24	0.99	87.9	20.0	4.5	70.6	9.7	7.0	1.18
		SE	0.05	0.14	21.1	2.5	0.3	27.9	1.3	0.4	0.06

**FIGURE 1.** Relationship of duck nest success estimated on the same sites in consecutive years (1997 and 1998) during the same season.

in the analyses 835 early-season nests and 834 late-season nests.

Nest success was low in all seasons and years (Tables 2 and 3). On average, nest success was similar between early and late seasons ($F = 0.08$; $df = 1,53$; $P = 0.79$), but differed among years ($F = 4.96$; $df = 1,53$; $P = 0.03$). There was no interaction between season and year ($F = 1.97$; $df = 1,53$; $P =$

0.17). When estimated on the same sites, nest success in 1998 was independent from that in 1997 for the corresponding seasons (regression slopes were indistinguishable from zero; $P = 0.97$, $n = 15$ and $P = 0.33$, $n = 14$, for early- and late-season, respectively; Figure 1).

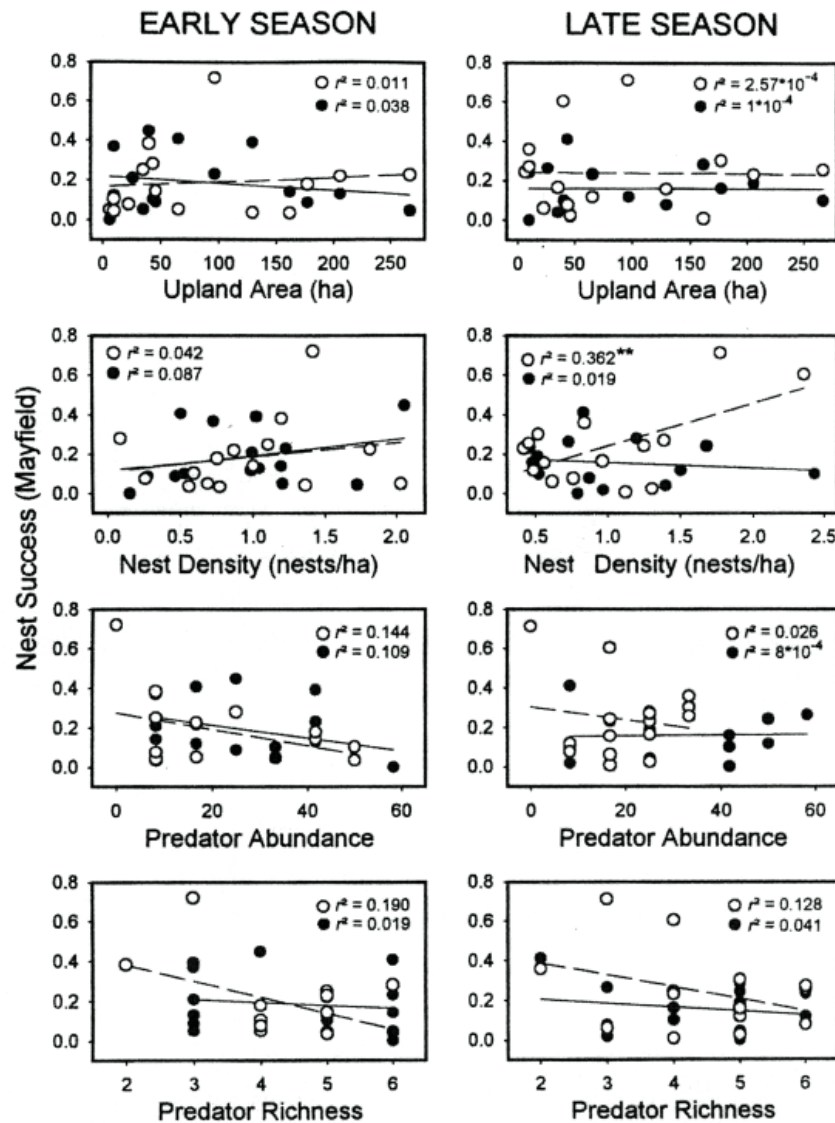


FIGURE 2 A. Relationship of duck nest success and each habitat patch characteristic measured during early and late season of 1997 (filled circles) and 1998 (open circles) in North Dakota. Significant slopes are shown as * = $P \leq 0.01$, ** = $P < 0.001$.

Relationship between nest success and habitat patch characteristics

The bivariate relationship between nest success and each of the independent variables (Figure 2) showed considerable scatter and few strong associations. Out of all 32 pairwise correlations, only 5 were significant, and all of them occurred during 1998 (Figure 2). Only 2 of these were significant for both the early-nesting and late-nesting seasons of 1998. There

were arthropod abundance (slopes = 0.0015 and 0.0013, respectively, $t_s > 3.4$, $df = 14$, $P_s < 0.01$) and small mammal abundance (slopes = 0.0234 and 0.0210, respectively, $t_s > 2.2$, $df = 14$, $P_s < 0.05$). Many of the relationships changed directions (i.e., the sign of the slope) between consecutive seasons or years (Figure 2). It should be noted that most of the significant associations were likely determined by only 1 or 2 influential points (Figure 2).

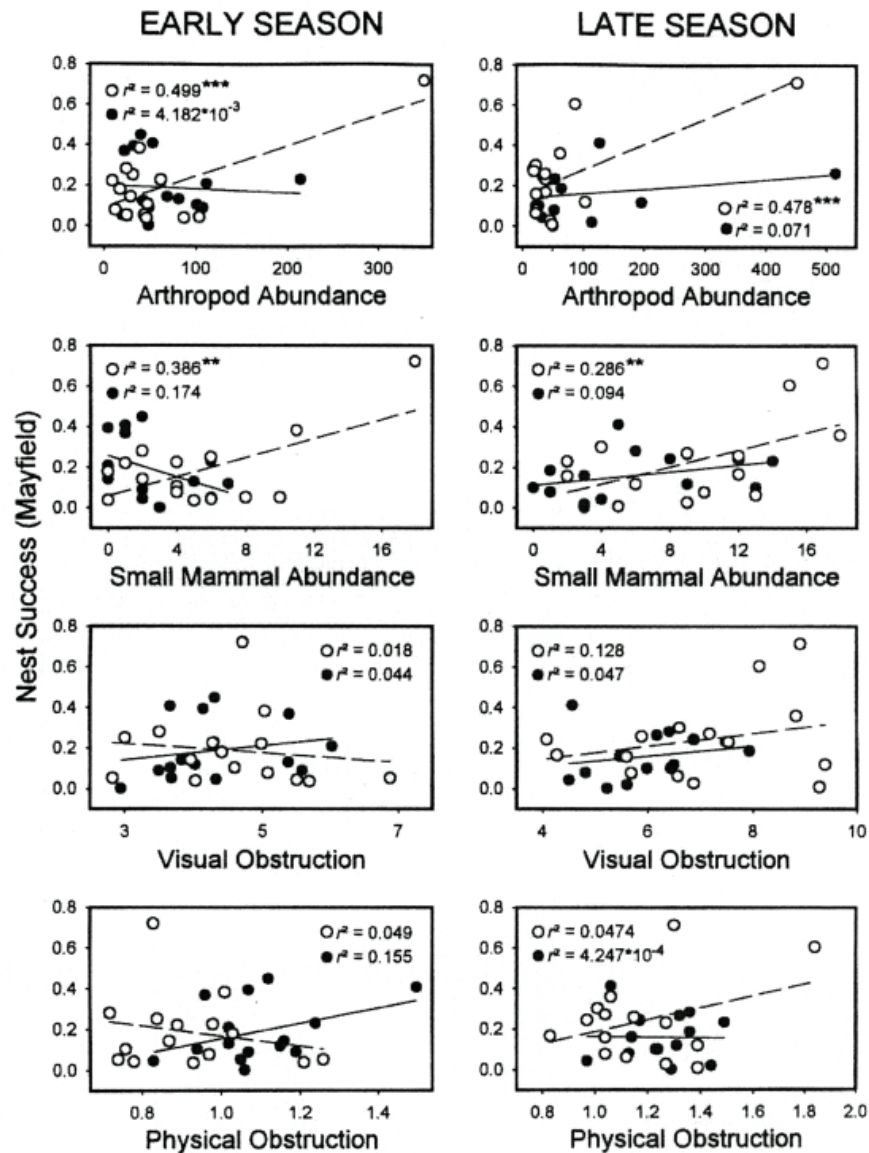


FIGURE 2 B. Relationship of duck nest success and each habitat patch characteristic measured during early and late season of 1997 (filled circles) and 1998 (open circles) in North Dakota. Significant slopes are shown as * = $P \leq 0.01$, ** = $P < 0.001$.

Discussion

Variation in nest success between seasons and years

Our results showed that predation rates on upland duck nests in the Prairie Potholes region of North Dakota are extremely variable in space and time. In fact, there was no repeated pattern between seasons or years. Sites where nest success was high the first year were often low during the second.

What is the impact of different hatch patch characteristics on nest success?

In forests, nest success of breeding birds varies with the size of the forest fragment (Burgess and Sharpe 1981, Andrén and Angelstam 1988, Andrén 1995). The mechanism implicated has been an increase in predation by generalist predators and in nest parasitism with decreasing patch size (Brittingham and Temple 1983, Wilcove 1985,

Paton 1994, Pasitschniak-Arts and Messier 1995, Robinson et al. 1995).

In grassland habitat, the effects of the interaction of predation and habitat fragmentation on the reproductive success of waterfowl have rarely been explicitly documented (Clark and Nudds 1991, Clark and Diamond 1993, Beauchamp et al. 1996), and what studies have been conducted have shown varied results (see Clark's and Nudds 1991, Horn et al. 2005 and references therein). Sovada et al. (2000) produced mixed data on whether daily survival rates (DSR) in duck nests increased with patch size. Horn et al. (2005) found a curvilinear relationship between DSRs and patch size, with DSRs being highest in small and large patches and lowest in intermediate patches. Our findings of no effect of patch size on nest success concur with Clark's and Nudds' (1991) observations and their reanalysis of Duebbert and Lokemoen's (1976) data. Given that the amount of edge decreases with patch size, these results are in line with the lack of edge effect found by Livezey (1980), Cowardin et al. (1985), and Pasitschniak-Arts et al. (1998). Horn et al. (2005) found an edge effect in landscapes where most of the habitat was in grasslands, but not in areas where only 15–20% of the landscape was occupied by grassland. Thus, as implied by Andr en (1995), it appears that the forces that control nest predation in grassland patches differ from those in forested patches, at least in relation to patch size and edge effect.

It has been speculated that large habitat patches allow waterfowl nests to be spaced out and that this reduces nest predation (Sugden and Beyersbergen 1986, Higgins et al. 1992, Greenwood et al. 1995, Larivi re and Messier 1998). Our data support neither of these propositions. We found that nest density was uncorrelated to patch size ($r_s = -0.12$, $n = 60$, $P = 0.36$) and that nest density was uncorrelated with nest success ($r_s = 0.12$, $n = 59$, $P = 0.36$; Figure 2). In turn, nest success was uncorrelated with patch size ($r_s = 0.05$, $n = 59$, $P = 0.68$; Figure 2). The same conclusions can be drawn from data from Duebbert and Lokemoen (1976).

Many studies have hypothesized that alternate prey densities affect nest success, but the few studies that actually measured abundance of alternative prey found contradictory results (Angelstam et al. 1984, Phersson 1986, Crabtree and Wolfe 1988, Vickery et al. 1992, Ackerman

2002). Likewise the only 2 large-scale replicated experiments that tested the hypothesis found mostly negative results (Greenwood et al. 1998, Conover et al. 2005). In our study, we separately quantified the abundances of arthropods and small mammals. Our assessment of the relationship of alternative prey and nest success showed that the effect varies among years, seasons, and type of alternative prey.

The number of predatory species and the relative abundance of individual predators appeared unrelated to nest success in our study. It seems that even a few predators in a site can produce a major impact on nest success. Often, studies assume a negative correlation between predator abundance and nest success (Urban 1970, Klett et al. 1988, Sovada et al. 1995). Aside from Keith (1961), no study has directly assessed the abundance of predators and its effect on nesting ducks, likely because of the difficulty of doing it. Keith (1961) found a tendency for lower nest success with increasing abundance of mammalian predators. DeLong et al. (1995) reported no relationship between predation on artificial ground-nests and predator abundance. Johnson et al. (1989) established species-specific correlations between nest predators and duck nest success, but did not provide data combining all species per site. Our results argue in favor of compensatory predation, as reflected by the lack of effect found with predator removal (Duebbert and Kantrud 1974, Duebbert and Lokemoen 1976, Parker 1984, Greenwood 1986, Clark et al. 1995, but see Horn et al. 2005). We concur with Sargeant et al. (1993) in recognizing the need to examine the effect of abundance and predator composition on nest success more closely.

The height of the vegetative cover and the index of physical obstruction at the sites were unrelated to nest success. Similar findings were reported by Crabtree et al. (1989), which was the only study we found that assessed obstruction to movement. It seems that when the primary predators are mammals, cover plays no role in protecting nests, as concluded by Clark and Nudds (1991). Further, patches of dense nesting cover apparently attract both predators and nesting hens, resulting in increased encounters between predators and nests and lower nest success (Schranck 1972, Sugden and Beyersbergen 1987, Crabtree et al. 1989, Reynolds et al. 1994).

What is the optimal hiding strategy for nesting ducks in landscapes swamped with predators?

For upland-nesting ducks, the likelihood of a predator finding their nest and consuming the eggs before they have had time to hatch is inherently high. Despite the efforts of managers to create habitats with dense nesting cover, predators were efficient in finding and destroying duck nests. The role of vegetative cover was of little importance in protecting nests. In fact, good cover may have provided good habitat for other prey species, such as arthropods and small mammals, which may have attracted predators. In contrast, prey abundance is probably low in agricultural fields. Furthermore, agricultural fields provided little cover for the predators themselves and constituted a habitat of high risk for them. Hence, predators were attracted to habitat patches of dense nesting cover. We contend that compared to the matrix of crop fields, patches of dense nesting cover provide year-round safe habitats for carnivores. It is in these patches that carnivores breed and fulfill their feeding requirements. Nesting hens are also attracted to the few same high-risk patches, which are, however, still better than cultivated fields.

The lack of consistency in the relationship of duck nest predation or nest density with any of the habitat variables we measured probably resulted from the landscape having a rich guild of predators that hunt for nests using different modalities, foraging strategies, and hunting skills. We hypothesized that there are no safe places for upland-nesting ducks to hide their nests in such areas. Predation on nests appeared unpredictable, and perhaps incidental. Our sites had a rich community of generalist predators whose home ranges were at least as large as the patches themselves. It appeared that a few predators could completely search a patch for nests in a couple of nights. Radio-telemetry data collected for another study (Jiménez, unpublished data), support this hypothesis. Jiménez (1999) documented nocturnal movements of female skunk, one of the purportedly less mobile predator species or gender. Skunks can detect nests 25 m away, and Nams (1977) experimentally determined that a single skunk could potentially find 20–30% of the nests in an average-sized patch during a

single night. Unfortunately for nesting ducks, we often observed multiple predators foraging at night within a single patch concomitantly.

What strategy should a hen use for placing her nest in a landscape that has limited suitable cover and is swamped with predators? We hypothesize that the optimal nesting strategy is to select a habitat patch for nesting at random from those available in the general area and then to select a nest site within that habitat patch at random. If a duck's nest is successful, it should return to the site next year and try again. If unsuccessful, the duck should select a new location at random and try again. By initially selecting nesting sites at random, ducks improve the odds of their nest surviving by providing no pattern or clue for predators. Inevitably, nest predators and nesting ducks play a game of hide-and-seek within the landscape, and it is the predators that usually win this game.

Acknowledgments

We thank R. King for helping to collect the data and the U.S. Fish and Wildlife Service for granting us permission to work on their property within the Devils Lake Wetland Management District. This research was funded by the Jack H. Berryman Institute, Association of Fish and Wildlife Agencies, Delta Waterfowl Foundation, and the Utah Agricultural Experiment Station.

Literature cited

- Ackerman, J. T. 2002. Of mice and mallards: positive indirect effects of coexisting prey in waterfowl nest success. *Oikos* 98:469–480.
- Andrén, H. 1995. Effect of landscape composition on predation rates at habitat edges. Pages 225–255 in L. Hansson, L. Fahrig, and G. Merriam, editors. *Mosaic landscapes and ecological processes*. Chapman and Hall, New York, New York, USA.
- Andrén, H., and P. Angelstam. 1988. Elevated predation rates as an edge effect in habitat islands: experimental evidence. *Ecology* 69:544–547.
- Beauchamp, W. D., T. D. Nudds, and R. G. Clark. 1996. Duck nest success declines with and without predator management. *Journal of Wildlife Management* 60:258–264.
- Brittingham, M. C., and S. A. Temple. 1983. Have cowbirds caused forest songbirds to decline? *BioScience* 33:31–35.
- Burgess, R. L., and M. Sharpe, editors. 1981. *Forest*

- island dynamics in man-dominated landscapes. Springer-Verlag, New York, New York, USA.
- Clark, R. G., and A. W. Diamond. 1993. Restoring upland habitats in the Canadian prairies: lost opportunity or management by design? *Transactions of the North American Wildlife and Natural Resources Conference* 58:551–564.
- Clark, R. G., D. E. Meger, and J. B. Ignatiuk. 1995. Removing American crows and duck nesting success. *Canadian Journal of Zoology* 73:518–522.
- Clark, R. G., and T. A. Nudds. 1991. Habitat patch size and duck nesting success: the crucial experiments have not been performed. *Wildlife Society Bulletin* 19:534–543.
- Conover, M. R. 2007. *Predator-prey dynamics: the use of olfaction*. CRC, Boca Raton, Florida, USA.
- Conover, M. R., R. L. King, J. E. Jiménez, and T. A. Messmer. 2005. Evaluation of supplemental feeding to reduce predation of duck nests in North Dakota. *Wildlife Society Bulletin* 33:1330–1334.
- Cowardin, L. M., S. Gilmer, and C. W. Shaiffer. 1985. Mallard recruitment in the agricultural environment of North Dakota. *Wildlife Monographs* 92:1–37.
- Cowardin, L. M., and D. H. Johnson. 1979. Mathematics and mallard management. *Journal of Wildlife Management* 43:18–35.
- Crabtree, R. L., L. S. Broome, and M. L. Wolfe. 1989. Effects of habitat characteristics on gadwall nest predation and nest-site selection. *Journal of Wildlife Management* 53:129–137.
- Crabtree, R. L., and M. L. Wolfe. 1988. Effects of alternate prey on skunk predation of waterfowl nests. *Wildlife Society Bulletin* 16:163–169.
- DeLong, A. K., J. A. Crawford, and D. C. DeLong, Jr. 1995. Relationships between vegetational structure and predation of artificial sage grouse nests. *Journal of Wildlife Management* 59:88–92.
- Duebber, H. F. 1969. High nest density and hatching success of ducks on South Dakota CAP lands. *Transactions of the North American Wildlife Conference* 24:218–229.
- Duebber, H. F., and H. A. Kantrud. 1974. Upland duck nesting related to land use and predator reduction. *Journal of Wildlife Management* 38:257–265.
- Duebber, H. F., and J. T. Lokemoen. 1976. Duck nesting in fields of undisturbed grass-legume cover. *Journal of Wildlife Management* 40:39–49.
- Freund, R. J., and R. C. Littell. 1991. *SAS system for regression*. Second edition. SAS Institute, Cary, North Carolina, USA.
- Fritzell, E. K. 1978. Habitat use by prairie raccoons during the waterfowl breeding season. *Journal of Wildlife Management* 42:118–127.
- Garrettson, P. R., F. C. Rohwer, J. M. Zimmer, B. J. Mense, and N. Dion. 1996. Effects of mammalian predator removal on waterfowl and non-game birds in North Dakota. *Transactions of the North American Wildlife and Natural Resources Conference* 61:94–101.
- Gloutney, M. L., R. G. Clark, A. D. Afton, and G. J. Huff. 1993. Timing of nest searches for upland nesting waterfowl. *Journal of Wildlife Management* 57:597–601.
- Greenwood, R. J. 1981. Foods of prairie raccoons during the waterfowl nesting season. *Journal of Wildlife Management* 45:754–760.
- Greenwood, R. J. 1982. Nocturnal activity and foraging of prairie raccoons (*Procyon lotor*) in North Dakota. *American Midland Naturalist* 107:238–243.
- Greenwood, R. J. 1986. Influence of striped skunk removal on upland duck nest success in North Dakota. *Wildlife Society Bulletin* 14:6–11.
- Greenwood, R. J., D. G. Pietruszewski, and R. D. Crawford. 1998. Effects of food supplementation on depredation of duck nests in upland habitat. *Wildlife Society Bulletin* 26:219–226.
- Greenwood, R. J., A. B. Sargeant, and D. H. Johnson. 1985. Evaluation of mark-recapture for estimating striped skunk abundance. *Journal of Wildlife Management* 49:332–340.
- Greenwood, R. J., A. B. Sargeant, D. H. Johnson, L. M. Cowardin, and T. L. Shaffer. 1995. Factors associated with duck nest success in the Prairie Pothole Region of Canada. *Wildlife Monographs* 128:1–57.
- Halfpenny, J., and E. Biesiot. 1986. *A field guide to mammal tracking in North America*. Johnson Publishing, Boulder, Colorado, USA.
- Higgins, K. F. 1977. Duck nesting in intensively farmed areas of North Dakota. *Journal of Wildlife Management* 41:232–242.
- Higgins, K. F., L. M. Kirsch, H. F. Duebber, A. T. Klett, J. T. Lokemoen, H. W. Miller, and A. D. Kruse. 1977. Construction and operation of cable-chain drag for nest searches. U.S. Fish and Wildlife Service Wildlife Leaflet 521. U.S.

- Government Printing Office, Washington, D.C., USA.
- Higgins, K. F., L. M. Kirsch, A. T. Klett, and H. W. Miller. 1992. Waterfowl production on the Woodworth Station in south-central North Dakota, 1965–1981. U.S. Fish and Wildlife Service Resource Publication 180. U.S. Government Printing Office, Washington, D.C., USA.
- Hill, D. A. 1984. Clutch predation in relation to nest density in mallard and tufted duck. *Wildfowl* 35:151–156.
- Horn, D. J., M. L. Phillips, R. R. Koford, W. R. Clark, M. A. Sovada, and R. J. Greenwood. 2005. Landscape compositions, patch size, and distance to edge: interactions affecting reproductive success. *Ecological Applications* 15:1367–1376.
- Jiménez, J. E. 1999. Nest success of dabbling ducks in a human-modified prairie: effects of predation and habitat variables at different spatial scales. Dissertation, Utah State University, Logan, Utah. USA.
- Johnson, D. H. 1979. Estimating nest success: the Mayfield method and an alternative. *Auk* 96:651–661.
- Keith, L. B. 1961. A study of waterfowl ecology on small impoundments in southeastern Alberta. *Wildlife Monographs* 6:1–88.
- Klett, A. T., H. F. Duebber, C. A. Faanes, and K. F. Higgins. 1986. Techniques for studying nest success of ducks in upland habitats in the Prairie Pothole Region. U.S. Fish and Wildlife Service Resource Publication 158. U.S. Government Printing Office, Washington, D.C., USA.
- Klett, A. T., H. F. Duebber, and G. L. Heinsmeyer. 1984. Use of seeded native grasses as nesting cover for ducks. *Wildlife Society Bulletin* 12:134–138.
- Larivière, S., and F. Messier. 1998. Effect of density and nearest neighbours on simulated waterfowl nests: can predators recognize high-density nesting patches? *Oikos* 83:12–20.
- Linhart, S. B., and F. F. Knowlton. 1975. Determining the relative abundance of coyotes by scent station lines. *Wildlife Society Bulletin* 3:119–124.
- Livezey, B. C. 1980. Effects of selected observer-related factors on fates of duck nests. *Wildlife Society Bulletin* 8:123–128.
- Mayfield, H. 1961. Nesting success calculated from exposure. *Wilson Bulletin* 73:255–261.
- Miller, H. W., and D. H. Johnson. 1978. Interpreting the results of nesting studies. *Journal of Wildlife Management* 42:471–476.
- Nams, V. O. 1997. Density-dependent predation by skunks using olfactory search images. *Oecologia* 110:440–448.
- Parker, H. 1984. Effect of corvid removal on reproduction of willow ptarmigan and black grouse. *Journal of Wildlife Management* 48:1197–1205.
- Pasitschniak-Arts, M., R. G. Clark, and F. Messier. 1998. Duck nesting success in a fragmented prairie landscape: is edge effect important? *Biological Conservation* 85:55–62.
- Pasitschniak-Arts, M., and F. Messier. 1995. Risk of predation on waterfowl nests in the Canadian prairies: effects of habitat edges and agricultural practices. *Oikos* 73:347–355.
- Paton, P. W. C. 1994. The effect of edge on avian nest success: how strong is the evidence? *Conservation Biology* 8:17–26.
- Phersson, O. 1986. Duckling production of the oldsquaw in relation to spring weather and small-rodent fluctuations. *Canadian Journal of Zoology* 64:1835–1841.
- Reynolds, R. E., T. L. Shaffer, J. R. Sauer, and B. G. Peterjohn. 1994. Conservation reserve program: benefit for grassland birds in the northern plains. *Transactions of the North American Wildlife and Natural Resources Conference* 59:328–336.
- Robel, R. J., J. N. Briggs, A. D. Dayton, and L. C. Hulbert. 1970. Relationships between visual obstruction measurements and weight of grassland vegetation. *Journal of Range Management* 23:295–297.
- Robinson, S. K., F. R. Thompson III, T. M. Donovan, D. R. Whitehead, and J. Faaborg. 1995. Regional forest fragmentation and the nesting success of migratory birds. *Science* 267:1987–1990.
- Roughton, R. D., and M. W. Sweeny. 1982. Refinements in scent-station methodology for assessing trends in carnivore populations. *Journal of Wildlife Management* 46:217–229.
- Sargeant, A. B., S. H. Allen, and R. T. Eberhardt. 1984. Red fox predation on breeding ducks in midcontinent North America. *Wildlife Monographs* 89:1–41.
- Sargeant, A. B., R. J. Greenwood, M. A. Sovada, and T. L. Shaffer. 1993. Distribution and abundance of predators that affect duck production—Prairie Pothole Region. U.S. Fish and Wildlife Service Resource Publication 194. U.S. Government Printing Office, Washington, D.C., USA.
- Schranck, B. W. 1972. Waterfowl nest cover and some predation relationships. *Journal of Wildlife Management* 36:182–186.

- Sovada, M. A., A. B. Sargeant, and J. W. Grier. 1995. Differential effects of coyotes and red foxes on duck nesting success. *Journal of Wildlife Management* 59:1–9.
- Sovada, M. A., M. C. Zicus, R. J. Greenwood, D. P. Rave, W. E. Newton, R. O. Woodward, and J. A. Beiser. 2000. Relationship of habitat patch size to predator community and survival of duck nests. *Journal of Wildlife Management* 64:820–831.
- Sowls, L. K. 1955. *Prairie ducks*. Stackpole, Harrisburg, Pennsylvania, USA.
- Stewart, R. E. 1975. *Breeding birds of North Dakota*. Tri-College Center for Environmental Studies, Fargo, North Dakota, USA.
- Sugden, L. G., and G. W. Beyersbergen. 1986. Effect of density and concealment on American crow predation of simulated duck nests. *Journal of Wildlife Management* 50:9–14.
- Sugden, L. G., and G. W. Beyersbergen. 1987. Effect of nesting cover density on American crow predation of simulated duck nests. *Journal of Wildlife Management* 51:481–485.
- Sutherland, W. J. 1996. *Ecological census techniques: a handbook*. Cambridge University Press, New York, New York, USA.
- Traviani, A., R. Laffitte, and M. Delibes. 1996. Determining the relative abundance of European red foxes by scent-station methodology. *Wildlife Society Bulletin* 24:500–504.
- Urban, D. 1970. Raccoon populations, movement patterns, and predation on a managed waterfowl marsh. *Journal of Wildlife Management* 34:372–382.
- Verts, B. J. 1967. *The biology of the striped skunk*. University of Chicago Press, Chicago, Illinois, USA.
- Vickery, P. D., M. L. Hunter, Jr., and J. V. Wells. 1992. Evidence of incidental nest predation and its effects on nests of threatened grassland birds. *Oikos* 63:281–288.
- Weller, M. W. 1956. A simple field candler for waterfowl eggs. *Journal of Wildlife Management* 20:111–113.
- Wilcove, D. S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. *Ecology* 66:1211–1214.



JAIME E. JIMÉNEZ (photo) studied ecology at Universidad Católica de Chile in Santiago. He obtained an M.S. degree in conservation of natural resources from the University of Florida (1993) and a Ph.D. degree in wildlife ecology from Utah State University (1999). Currently, he is head of the school of graduate studies at the Universidad de Los Lagos, in southern Chile. His interests are broad and deal mainly with endangered species and predation ecology. They range from studying raptors in Torres del Paine and other localities, passerine birds, pudu deer, mouse opossums and Darwin's foxes in the southern rainforests, culpeo foxes and chinchillas in the highland deserts of northern Chile, voles in New York, red foxes and raccoons in Virginia, and nesting ducks in the prairies of North Dakota.

MICHAEL R. CONOVER, TERRY A. MESSMER, and RAYMOND D. DUESER are professors in the Department of Wildland Resources at Utah State University.