RUDDY DUCK NESTING SUCCESS: DO NEST CHARACTERISTICS DETER NEST PREDATION?[1]

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Abstract. It has been hypothesized that proximity to edges, timing of nesting, nest concealment or inaccessibility, working singly or in concert, may explain variable nesting success of birds, but results have been mixed. I tested these hypotheses by determining fates and measuring nest-site features of 233 Ruddy Duck (*Oxyura jamaicensis*) nests near Minnedosa, Manitoba, Canada, during summers of 1994–1996. Mayfield nesting success averaged 41%. Discriminant function analysis was unable to segregate successful and destroyed nests. Results suggest that nesting success for this population of Ruddy Ducks is unpredictable, probably because a diversity of predators precluded choice of safe nest sites.

Key words: edge effects, nesting success, nest-site characteristics, Oxyura jamaicensis, *predation, Ruddy Duck.*

For most birds, choice of nest site is an important factor influencing fitness, because predation occurs on incubating adults and nest contents. Mortality of nesting female waterfowl due to predation can exceed 25% in some populations, and the leading cause of nest failure is predation (Sargeant and Raveling 1992). Thus, females should be under strong selection to discriminate between secure and vulnerable nest sites. Numerous investigations have attempted to determine factors influencing nesting success (Martin 1995). For a variety of avian species, researchers have tested an assortment of nest habitat characteristics, but often the single most important variable correlated with nesting success is nest concealment (Martin 1995). Other identified factors altering nest fate include nest density and initiation date, proximity of habitat edge, and habitat patch size. Similarly, water depth, a measure of nest inaccessibility, could affect nesting success of over-water nesting species. However, conflicting results from a variety of studies suggests that further research is needed to allow generalizations about the factors associated with avian nesting success.

Ruddy Ducks (*Oxyura jamaicensis*) breed extensively in the prairie pothole region of North America and build their nests over water in emergent vegetation. Ruddy Ducks should be under especially intense selection pressure to select secure nest sites because predation on incubating females and eggs can be intense (Sargeant et al. 1973, Greenwood 1981, Greenwood et al. 1995), and through a combination of small body size and large eggs, Ruddy Ducks experience extremely high energetic costs during egg production (Alisauskas and Ankney 1994). Presumably, as a consequence, few female Ruddy Ducks renest after loss of their nest (Bellrose 1976, Somerville 1985, Tome 1987).

Several investigations have estimated Ruddy Duck nesting success and four have examined differences in nest variables between successful and destroyed nests (Featherstone 1975, Somerville 1985, Krasowski and Nudds 1986, Maxson and Riggs 1996). These studies produced equivocal results, possibly due to small sample sizes, which hampered statistical analyses and interpretation of results. I tested the timing of nesting, nest concealment, nest inaccessibility, and edge effect hypotheses on the fate of 233 Ruddy Duck nests and predicted that greater nesting success would occur with (1) nests initiated earlier in the breeding season, (2) nests concealed with more vegetation, (3) nests located in deeper water, thus more inaccessible to predators, and (4) nests farther from habitat edges.

METHODS

I conducted this study during summers, 1994–1996, in the aspen parkland physiographic zone of the prairie pothole region near Minnedosa, Manitoba, Canada (50°10′N, 99°47′W), an area described in detail by Stoudt (1982) and Rounds (1982).

I found Ruddy Duck nests by systematically searching the emergent fringe of wetlands on the 15.4 km² study area 2–3 times each summer. I marked each nest with flagging placed several meters away in various directions. At each nest, I recorded clutch size and stage of incubation by egg flotation and/or candling (Weller 1956). I visited nests every 7–10 days to determine nest fate. I classified each nest as successful if ≥ 1 egg hatched as determined by the presence of eggshell caps, detached egg membranes, or ducklings. I calculated nesting success using Mayfield's (1975) technique modified by Johnson (1979). Mean clutch size of 6.6 eggs required 6–7 days to lay, and the length of the incubation period was 23 days, for a total of about 30 days for the nesting cycle.

When each nest was found, I visually estimated, from directly above the nest, the percent of the nest occluded by overhead cover. At each subsequent nest visit, I measured water depth to the nearest 0.5 cm on the shore side of the nest and estimated overhead con-

TABLE 1. Mayfield nesting success of Ruddy Ducks. Also shown are the number of nests (*n*) and exposure days (number of failed nests) used in calculating Mayfield nesting success, and 95% confidence intervals (CI).

	1994 (*n* = 45)	1995 (*n* = 91)	1996 (*n* = 93)
Nesting success[a] (%)	42.3	41.2	40.3
Exposure days	569 (16)	1,202 (35)	1,406 (42)
95% CI for nesting period[b]	27.6–65.0	30.5–55.5	30.4–53.2

[a] $\chi^2_2 = 0.04$, $P = 0.98$, following Sauer and Williams (1989).
[b] 30-day laying and incubation period, following Johnson (1979).

cealment, because these variables potentially change during a 30-day nesting period. To minimize disturbance to vegetation and possibly nest fate, I approached nests from different directions, primarily the open water side of the nest, and took care not to disturb vegetation during nest checks. I measured several nest-site variables after fate was determined. I determined vegetation density at each nest by counting the total number of live and dead stems in a 1-m² quadrat centered on the nest. I measured the maximum height of vegetation directly over the bottom of the nest bowl to the nearest cm. Concealment provided by the surrounding vegetation was estimated visually by determining the percent visibility of the nest just above the water surface from 1 m away in each cardinal direction. A nest visibility score was computed as the mean of the percent visibility value from each direction. I incorporated several measures of edge in my analysis of nest success, because I hypothesized that mammalian predators would use these edges as travel lanes during foraging. I measured distance from the nest to the closest open body of water, greater than 5 m in diameter, using a tape measure. I also measured the shortest distance from shore to the nest. I estimated the distance from the nest to the closest edge of an agricultural field to the nearest 5 m.

DATA ANALYSIS

I eliminated abandoned nests, which were undisturbed nests that had not advanced in development between nest checks, from all data analyses. I did not use data for nests found initially either hatched or destroyed, because nest-site variables can change after nest fate. Many nest-site variables were not distributed normally and were transformed. I rank transformed vegetation density, and log transformed distance to shore, open water, and field, and arcsine square-root transformed overhead cover and nest visibility. Nest-initiation dates, vegetation heights, and water depths were distributed normally. To control for the influence of season on nest-site variables, I regressed each nest-site variable against day-of-year nest measurements were made, and saved the residuals. I controlled for year effects by creating *z*-scores for the residuals within years, which allowed combining data for all years.

I used multivariate techniques to investigate the simultaneous effects of several nest-site variables as opposed to univariate comparisons, because often joint consideration of several variables can reveal interrelationships among variables and produce stronger conclusions about the data (James and McCulloch 1990). I tested for multicollinearity by performing principal

component analysis on the nine nest-site variables. The first principal component explained less variation (28%) than would be expected by chance alone (31%) (Legendre and Legendre 1983, Jackson 1993). This suggests that the nest-site variables were orthogonal, so I used the actual nest-site variables in the discriminant function analysis (DFA). I entered simultaneously all nest-site variables into the DFA and found no difference between within-group covariance matrices (*P* = 0.054, Box's M criterion), so I used these in the DFA. Because unequal sample sizes can bias classification results in DFA, I set prior classification probabilities equal to initial sample sizes (Williams 1983) and used chance-corrected classification to control for classification by chance alone (Titus et al. 1984). I used SPSS (1995) for all statistical analyses, and report means ± SE unless otherwise stated; *P*-values ≤ 0.05 are considered significant.

RESULTS

I found 58, 125, and 130 nests on the study area in 1994, 1995, and 1996, respectively, for a total of 313 Ruddy Duck nests. Ruddy Ducks nested in sedge (*Carex atherodes*), cane (*Phragmites communis*), bulrush (*Scirpus* spp.), cattail (*Typha* spp.), and whitetop grass (*Scolochloa festucacea*), or in a combination of these emergent vegetation types. Whitetop grass and cattail were present most often in quadrats at 166 (70.9%) and 144 (61.5%) sampled nests, respectively. Sedge, bulrush, and cane were present less frequently in 66 (28.6%), 46 (19.7%), and 10 (4.3%) quadrats, respectively.

I found no difference (*P* = 0.98) in nesting success among years (Table 1). Most nest-site variables were similar between successful and depredated nests (Table 2). Thus, DFA was unable to distinguish between hatched and depredated nests, although results approached significance (Wilks' Lambda, *U* = 0.94, *P* = 0.09). Nest visibility (0.77) and overhead cover (−0.72) were most correlated with the canonical discriminant function that described increasing probability of nest depredation (Table 2). Discriminant function analysis classified correctly 22.4% and 89.2% of depredated and hatched nests, respectively, for an overall correct classification rate of 64.8%, only 13.3% better than chance alone, and nonsignificant (*z* = 1.66, *P* = 0.10).

To determine the high incidence of misclassification for depredated nests, I used Spearman rank correlation to test the prediction that depredated nests would survive longer if more concealed. I found no correlation between overhead cover ($r_s = 0.11$, *n* = 86, *P* = 0.15)

TABLE 2. Characteristics of nest-site variables of successful and destroyed Ruddy Duck nests ($\bar{x} \pm$ SD) and the corresponding correlation coefficient with the canonical discriminant function. Values in parentheses are sample sizes for each representative nest fate.

Nest Site Variable	Hatched (n = 148)	Depredated (n = 85)	DFA correlation coefficients
Nest initiation date (days)	177.3 ± 11.8	178.2 ± 12.2	0.16
Distance to field (m)	20 ± 19	25 ± 14	−0.20
Distance to shore (m)	9.4 ± 4.8	9.0 ± 4.9	0.19
Distance to open water (m)	8.7 ± 7.8	9.4 ± 9.8	−0.28
Maximum vegetation height (cm)	136.2 ± 47.4	140.8 ± 42.9	0.20
Water depth at nest (cm)	39.7 ± 17.0	37.3 ± 18.7	0.30
Vegetation density (stems m⁻²)	228.6 ± 174.2	223.2 ± 171.7	−0.36
Overhead cover (%)[a]	53.0 ± 29.0	34.0 ± 30.0	−0.72
Nest visibility (%)[b]	24.0 ± 21.0	32.0 ± 23.0	0.77

[a] Larger values mean greater overhead concealment.
[b] Higher values mean less concealment from sides.

or nest visibility (r_s = 0.16, n = 86, P = 0.07) and days devoted to egg laying and incubation.

DISCUSSION

Ruddy Ducks had stable nesting success among years. Several nest-site variables were similar, thus DFA was unable to separate successful and unsuccessful nests, suggesting that nest-site variables used in this study were unpredictable indicators of nesting success. Also, the lack of correlation between nest concealment and duration of depredated nests suggests little effect of nest concealment on Ruddy Duck nesting success.

For many upland nesting ducks, nest concealment is related positively to nesting success (Livezey 1981, Guyn and Clark 1997, Clark and Shutler 1999). However, nest concealment has not been attributed to nesting success in diving ducks (Krasowski and Nudds 1986, Maxson and Riggs 1996, this study). Similarly, edge effects (Featherstone 1975) and water depth (Krasowski and Nudds 1986, Maxson and Riggs 1996, but see Featherstone 1975, Somerville 1985) have not been associated with nesting success for natural nests of diving ducks, results consistent with this study. The relatively narrow ring of emergent vegetation possibly "forces" Ruddy Ducks to be edge nesters, which may explain the inability of the DFA to separate successful and unsuccessful nests (Krasowski and Nudds 1986).

Why is nesting success in Ruddy Ducks unpredictable based on a variety of nest-site characteristics? Females in good physical condition may be more likely to nest successfully than females in poor body condition (Gloutney and Clark 1991, Arnold et al. 1995, Blums et al. 1997). Nest-site cover may influence thermal conditions, a characteristic I did not measure, in and around the nest, and influence nesting success as found by Stokes and Boersma (1998). Possibly, female condition and nest-site cover interact allowing some females to take fewer incubation breaks, thus being less conspicuous to predators. A high diversity of nest predators could prevent placement of nests in secure locations (Filliater et al. 1994). On my study area, known Ruddy Duck nest predators included raccoon (*Procyon lotor*), mink (*Mustela vison*), American Crow (*Corvus brachyrhynchos*), Red-tailed Hawk (*Buteo jamaicensis*), and Great Horned Owl (*Bubo virgi-*

nianus). This predator diversity may prevent Ruddy Ducks from identifying safe nest sites. Lastly, too much similarity in nest-site selection among co-existing species may produce random nesting success (Martin 1988a, 1988b). Ruddy Ducks, Canvasbacks (*Aythya valisineria*), and Redheads (*A. americana*), the three most common over-water nesting ducks on my study area, all use similar nest sites (Maxson and Riggs 1996) with some overlap in nesting dates. Ruddy Duck nesting success may be unpredictable because safe sites are precluded by a seasonal increase in use of wetlands by raccoons (Fritzell 1978) and a search image developed from previous foraging success on waterfowl nests placed in similar locations earlier in the season (Martin 1988a), however, this hypothesis remains to be tested using natural nests.

LITERATURE CITED

ALISAUSKAS, R. T., AND C. D. ANKNEY. 1994. Costs and rates of egg formation in Ruddy Ducks. Condor 96:11–18.

ARNOLD, T. W., M. G. ANDERSON, R. B. EMERY, M. D. SORENSON, AND S. N. DE SOBRINO. 1995. The effects of late-incubation body mass on reproductive success and survival of Canvasbacks and Redheads. Condor 97:953–962.

BELLROSE, F. C. 1976. Ducks, geese, and swans of North America. Stackpole Books, Harrisburg, PA.

BLUMS, P., A. MEDNIS, AND R. G. CLARK. 1997. Effect of incubation body mass on reproductive success and survival of two European diving ducks: a test of the nutrient reserve hypothesis. Condor 99: 916–925.

CLARK, R. G., AND D. SHUTLER. 1999. Avian habitat

selection: pattern from process in nest-site use by ducks. Ecology 80:272–287.

FEATHERSTONE, J. D. 1975. Aspects of nest site selection in three species of ducks. Ph.D. diss., Univ. Toronto, Toronto.

FILLIATER, T. S., R. BREITWISCH, AND P. M. NEALEN. 1994. Predation on Northern Cardinal nests: does choice of nest site matter? Condor 96:761–768.

FRITZELL, E. K. 1978. Habitat use by prairie raccoons during the waterfowl breeding season. J. Wildl. Manage. 42:118–127.

GLOUTNEY, M. L., AND R. G. CLARK. 1991. Significance of body mass to female dabbling ducks during late incubation. Condor 93:811–816.

GREENWOOD, R. J. 1981. Foods of prairie raccoons during the waterfowl nesting season. J. Wildl. Manage. 45:754–760.

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. Wildl. Monogr. 128.

GUYN, K. L., AND R. G. CLARK. 1997. Cover characteristics and success of natural and artificial duck nests. J. Field Ornithol. 68:33–41.

JACKSON, D. A. 1993. Stopping rules in principal components analysis: a comparison of heuristical and statistical approaches. Ecology 74:2204–2214.

JAMES, F. C., AND C. E. McCULLOCH. 1990. Multivariate analysis in ecology and systematics: panacea or Pandora's box? Annu. Rev. Ecol. Syst. 21:129–166.

JOHNSON, D. H. 1979. Estimating nest success: the Mayfield method and an alternative. Auk 96:651–661.

KRASOWSKI, T. P., AND T. D. NUDDS. 1986. Microhabitat structure of nest sites and nesting success of diving ducks. J. Wildl. Manage. 50:203–208.

LEGENDRE, L., AND P. LEGENDRE. 1983. Numerical ecology. Elsevier, Amsterdam.

LIVEZEY, B. C. 1981. Locations and success of duck nests evaluated through discriminant analysis. Wildfowl 32:23–27.

MARTIN, T. E. 1988a. On the advantage of being different: nest predation and the coexistence of bird species. Proc. Natl. Acad. Sci. 85:2196–2199.

MARTIN, T. E. 1988b. Processes organizing open-nesting bird assemblages: competition or nest predation? Evol. Ecol. 2:37–50.

MARTIN, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation and food. Ecol. Monogr. 65:101–127.

MAXSON, S. J., AND M. R. RIGGS. 1996. Habitat use and nest success of overwater nesting ducks in westcentral Minnesota. J. Wildl. Manage. 60:108–119.

MAYFIELD, H. F. 1975. Suggestions for calculating nest success. Wilson Bull. 87:456–466.

ROUNDS, R. D. 1982. Land use changes in the Minnedosa pothole region of southwestern Manitoba 1948–1970. Blue Jay 40:6–12.

SARGEANT, A. B., AND D. G. RAVELING. 1992. Mortality during the breeding season, p. 396–422. In B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu [EDS.], Ecology and management of breeding waterfowl. Univ. Minnesota Press, Minneapolis, MN.

SARGEANT, A. B., G. A. SWANSON, AND H. A. DOTY. 1973. Selective predation by mink, Mustela vison, on waterfowl. Am. Midl. Nat. 89:208–214.

SAUER, J. R., AND B. K. WILLIAMS. 1989. Generalized procedures for testing hypotheses about survival or recovery rates. J. Wildl. Manage. 53:137–142.

SOMERVILLE, A. J. 1985. Advantages to late breeding in Ruddy Ducks. Ph.D. diss., Univ. British Columbia, Vancouver.

SPSS, INC. 1995. SPSS version 6.1. SPSS, Inc., Chicago.

STOKES, D. L., AND P. D. BOERSMA. 1998. Nest-site characteristics and reproductive success in Magellanic Penguins (Spheniscus magellanicus). Auk 115:34–49.

STOUDT, J. H. 1982. Habitat use and productivity of Canvasbacks in southwestern Manitoba, 1961–1972. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Wildl. No. 248.

TITUS, K., J. A. MOSHER, AND B. K. WILLIAMS. 1984. Chance-corrected classification for use in discriminant analysis: ecological applications. Am. Midl. Nat. 111:1–7.

TOME, M. W. 1987. An observation of renesting by a Ruddy Duck, Oxyura jamaicensis. Can. Field-Nat. 101:153–154.

WELLER, M. W. 1956. A simple field candler for waterfowl eggs. J. Wildl. Manage. 20:111–113.

WILLIAMS, B. K. 1983. Some observations on the use of discriminant analysis. Ecology 64:1283–1291.