

TESTING COMPETING HYPOTHESES FOR THE SEASONAL VARIATION IN
NESTING SUCCESS OF A LATE-NESTING WATERFOWL

by

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ABSTRACT

Populations of lesser scaup and greater scaup have been below the North American Waterfowl Management Plan goal of 6.3 million since 1984. As of 2013, scaup populations are down 12% from their long term average (1955-2013) of 4.7 million birds (Walker 2005). Nesting success has shown to be an important factor in determining population growth. If the mechanisms of nesting success can be identified wildlife managers can make the necessary changes to increase scaup nesting success and thus increase the population. Nests were located during nest searches conducted from May through July and monitored until fate was determined. Nest age, nest location, vegetation height, distance to water and depth of water were recorded at each nest. Program MARK was used to determine known fate models. The model that incorporated both nest age and the effect of nest date showed the greatest support. I found a greater influence of date on nesting daily survival rate than age during this study, although both positively influenced scaup nest daily survival rate. The positive relationship between scaup nest daily survival rate and date, provided support for the nest concealment hypothesis. This posits that increasing vegetation height and density throughout the nesting season decreases predation. Sugden and Beyersbergen (1987) found similar results that artificial nests in tall, dense nesting cover escaped predation from crows for longer than those in sparse cover. The positive effect of nest age on nest survival supports the nest heterogeneity hypothesis, i.e., that low quality nests are depredated at a higher rate than nests of higher quality. Although these results have been supported by others (Klett and Johnson 1982) it has not received

unanimous support. It is possible that these results might be influenced by the lack of heterogeneity in vegetation and differences in predator community at Red Rock Lakes National Wildlife Refuge compared to other sites.

Introduction:

The annual change in the number of individuals in a population, i.e., population growth (λ), is the product of multiple vital rates during the annual life cycle of a species. In ground nesting birds, nesting success has been shown to be an important determinant of recruitment, and resultantly, population growth. For example, nesting success in mid-continent mallards (*Anas platyrhynchos*) demonstrated the greatest influence on λ relative to other vital rates examined (Hoekman et al. 2002). Moreover, studies of nesting ducks conducted in the United States portion of the Prairie Pothole Region (PPR) indicated that duck populations were not self-sustaining (i.e., $\lambda < 1.0$) due to low nesting success (Klett et al. 1988, Greenwood et al. 1995). The strong influence of nesting success on λ in ground nesting birds underscores the need for a thorough understanding of the mechanisms of nest mortality.

Nesting success of birds varies in space and time. Temporal variation in nesting success occurs from year to year (inter-seasonal) as well as within a year (intra-seasonal). Variation in nesting success among years is well documented (McKinnon and Duncan 1999, Stephens et al. 2005 Walker et al. 2005, Haffele et al. 2013). For example, in the boreal forests of Alaska, lesser scaup (*Aythya affinis*) nesting success ranged from 1–61% during a 5 year period (Walker et al. 2005). In the PPR, nesting success of upland-nesting ducks ranged from 20% during 1966–1974 to 41% during 1980–1984 (Klett et al. 1988). Intra-seasonal increases in nesting success have been similarly well documented (Klett and Johnson 1982, Greenwood et al. 1995, Walker et al. 2005). Emery et al. (2005) found nesting success in the Canadian PPR varied within the nesting season, decreasing during the nesting season in managed cover (i.e., planted cover, delayed haying), but increasing

in unmanaged cover. Garrettson and Rohwer (2001) found nesting success increased during the nesting season in North Dakota on sites where predator removal occurred and control sites. Walker et al. (2005) found the relationship between nest survival and date to be variable among years at Minto Flats, Alaska but positive in 5 of the 7 years. Multiple hypotheses have been posited to describe the commonly observed pattern of increasing intra-seasonal nesting success. Nesting success could increase intra-seasonally as the result of 1) increasing vegetation density and height, 2) changes in nest predator behavior patterns, 3) heterogeneity in nest quality that results in “higher” quality nests surviving at a higher rate, or a combination of these (Klett and Johnson 1982, Montgomerie and Weatherhead 1988, Borgmann 2010, Haffele et al. 2013).

One of the most commonly cited drivers of intra-seasonal increases in nesting success for ground nesting birds is increasing vegetation height and density as the nesting season progresses. Known as the nest-concealment hypothesis, this hypothesis posits that birds nesting earlier in the year do so in less dense vegetation, and thus nests are more easily found by nest predators. Using artificial nests, Dwernychuk and Boag (1972) demonstrated egg loss from avian predators was negatively correlated with presence of overhead cover. Furthermore, Sugden and Beyersbergen (1987) found that artificial nests in tall, dense nesting cover escaped predation from crows for longer than those in sparse cover. Warren et al. (2008) found that as nest-site vegetation density increased so did nesting success for upland-nesting ducks in the western Aspen Parkland of the Canadian PPR. Assuming consistent vegetative growth across years and habitats, the nest-concealment hypothesis predicts nesting success would be most closely correlated with date.

Intra-seasonal increases in nesting success could also be linked to changes in predator behavior. The number of nests available for a nest predator increases non-linearly during the nesting season with nest density low early and late in the nesting season and at its greatest mid-season. Assuming a threshold nest density exists where predators respond positively either numerically or functionally, nesting success would be predicted to be high early and late in the season, then would decline mid-season as nests peak in. This hypothesis, the predator search-image hypothesis, predicts nesting success is negatively related to nest density due to predators developing search images in response to increased nest densities (Borgmann 2010). Daily nest survival of willow ptarmigan (*Lagopus lagopus*) was high early in the season (23 May–11 June), decreased to a low mid-season (early June to early July), then increased again late in the season (Wilson et al. 2007). Seasonal patterns in nest survival of ptarmigans may be due to predators responding to the profitability of finding nests; nest survival was negatively correlated with nest density (Wilson et al. 2007). Similarly, Larivière and Messier (1988) observed daily survival rates of simulated mallard nests were at their highest at low density (2.5 nest/ha).

A third observed pattern in nesting success is increased survival with nest age (Hoekman et al. 2006), which could result from heterogeneity in nest quality. Nesting success would increase with progression of the nesting season as low-quality nests (i.e., low likelihood of successfully hatching) are removed by depredation at a higher rate than high-quality nests. In this scenario the culling of low-quality nests by predation leads to a correlation between nest-age and nesting success. Klett and Johnson (1982) found that age effects were present in their studies of mallards in North Dakota and Alaska. They

proposed that the effect of age was related to nest location during their study, with areas predators were believed to avoid (i.e., roadsides) having higher nesting success than other areas. Hoekman et al. (2006) found support for an effect of nest age on nest survival and speculated that heterogeneity in nest success was due to nest placement relative to home ranges of nest predators and habitat edges. Supporting the idea that nests vary in quality, Martin et al. (2000) were able to demonstrate passerine nest sites with a high risk of predation in one year had a consistently high risk the subsequent year.

I used a six year data set to explore inter- and intra-annual variation in nesting success in lesser scaup. Lesser scaup are a small-bodied diving duck that are one of the latest nesting ducks in North American (Bellrose 1980). I tested three competing hypotheses and their resulting predictions for the observed intra-seasonal increase in nest daily survival rate (DSR). First, the nest-concealment hypothesis was tested based on the prediction that nest DSR should be most highly correlated with calendar date. Second, the predator search-image hypothesis, which posits a negative correlation between nest DSR and nest density, was tested using total apparent duck nest density on the study site. Lastly, the nest heterogeneity hypothesis posits that nest DSR increases linearly with nest age as low quality nest are removed from the sample population by predation at a higher rate than higher quality nests.

Study Area:

The study was conducted on Lower Red Rock Lake and the associated River Marsh (hereafter Lower Lake), which sit in the eastern extent of the Centennial Valley of southwest Montana, USA (Fig. 1). Lower Lake is a large (2,332 ha), high elevation (2014 m above mean sea level) wetland encompassed by Red Rock Lakes National Wildlife Refuge (Refuge). Lower Lake is part of a larger shallow lake/wetland complex that is a remnant of Pleistocene Lake Centennial, a prehistoric lake that was believed to have formerly covered the valley floor to a depth of ca. 20 m (Sonderegger et al. 1982).

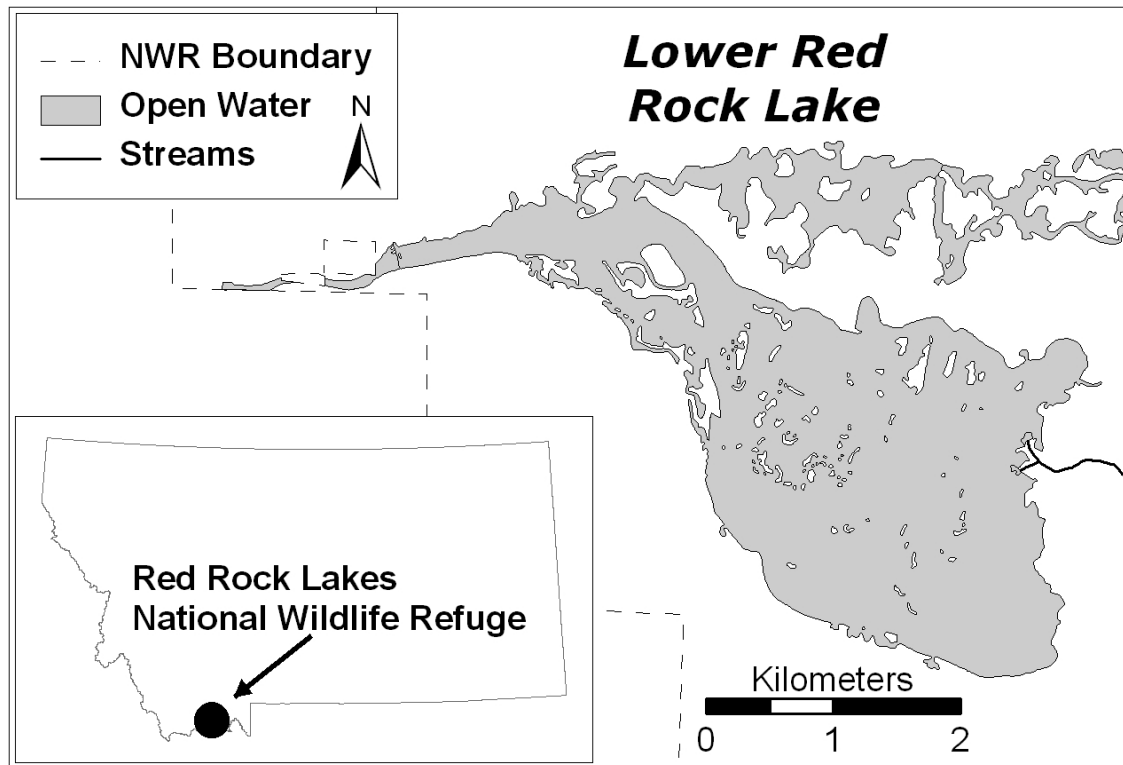


Figure 1. Lower Red Rock Lake study area within Red Rock Lakes National Wildlife Refuge, southwest Montana, USA.

Lower Lake water depths typically do not exceed 1.5 m, with large open water areas interspersed with hardstem bulrush (*Schoenoplectus acutus*) islands. Nearly half of

the area is extensive stands of seasonally flooded beaked sedge (*Carex utriculata*) that contain small (<2 ha), scattered open water areas. Based on specific conductance and salinity, Lower Lake is classified as a fresh water wetland (Stewart and Kantrud 1972, Gleason et al. 2009) of intermediate alkalinity.

Average annual precipitation is 49.5 cm with 27% occurring during May and June. Annual average temperature is 1.7°C. Climatic patterns in southwestern Montana have followed those of northwestern North America, namely warmer springs and drier winters. For example, mean March temperatures, as measured at Refuge headquarters, increased 4.3°C ($P < 0.01$) between 1948 and 2005 (USFWS 2009). Moreover, mean annual precipitation has declined 9.6 cm ($P = 0.042$) during this same period, driven largely by declines in January and December precipitation (USFWS 2009).

Methods:

Field Data Collection—Nest searching was conducted from late May/early June through mid-July to locate scaup nests. The study area was divided into 750 m × 750 m blocks for a capture-mark-recapture (CMR) study of scaup survival (USFWS unpublished data). Blocks were aggregated into 16 survey plots compromising one to four survey blocks such that each survey plot had approximately the same area of open water. Survey plots were randomly ordered for CMR surveys. Plots were also used to organize nest searches, following the original randomization.

Two nest searches were conducted in *Carex* spp. dominated habitats each year. Nest searching was conducted between 0700 and 1300 hrs. Investigators (1–3) used observational cues and trained dogs to locate scaup nests. Two person-mornings of nest searching occurred for each block within a survey plot. All nests found were marked with a stick placed 4 m north of the nest bowl. Habitat type, Universal Transverse Mercator (UTM) position, and nest initiation date, estimated by field-candling eggs (Weller 1956), were recorded. Nest age (NAGE) was calculated by determining the difference between nest initiation date and current date. All nest data was recorded on Red Rocks Lakes NWR Nest Record Cards. Nests were revisited every 6 to 10 days until fate was determined (i.e. abandoned, destroyed, or successful). To test for a potential relationship between nest density and scaup nest DSR, I calculated total apparent duck nest density (TOTDEN) as the number of known active duck nests on the study area each day divided by the area of potential nesting habitat (2332 ha total area – 836 ha open water).

Data Analysis—I used nest survival models in program MARK (White and Burnham 1999) implemented with package RMark (Laake 2013) in R version 3.0.3 (R

Development Core Team 2014) to explore variation in nest DSR. Based on my hypotheses and predictions described above, I developed an a priori suite of candidate models. Akaike's Information Criterion adjusted for small sample size (AIC_c) was used to rank models; Akaike weights were used to assess the relative likelihood of models (Anderson et al. 2000, Burnham and Anderson 2002).

Results

During 2008–2013, 353 scaup nests were found and monitored. Seventeen nests were abandoned, damaged or destroyed by investigator activity, resulting in 336 nests used for analysis. The number of nests monitored annually ranged from 25 nests in 2011 to 82 nests in 2008. Clutch size varied from 6.7 (SD=2.0) in 2011 to 9.1 (SD=1.3) in 2012. The median initiation date varied from June 13th (SD=9.5) in 2012 to July 4th (SD=8.8) in 2011 (Table 1). Total apparent duck nest density (TOTDEN) was highly variable within and among the years studied (Fig. 2). 2008 had the greatest TOTDEN with 0.081 nest/ha, whereas 2011 had the least with only 0.014 nest/ha.

I found support for an influence of both nest age and date within the nesting season on nest DSR. The top two models included DATE and NAGE; the top model included these variables additively, while the second best model had an interaction between these variables (Table 2). Although our top model included Date and NAGE additively, Date did have a larger effect on nest DSR ($\beta_{\text{Date}} = 0.064$, SE= 0.012) compared to the effect of nest age ($\beta_{\text{NAGE}} = 0.041$, SD=0.013; Table 3). Total apparent duck nest density on the study site was not correlated with lesser scaup nest DSR, providing little support for the predator search-image hypothesis. Models containing TOTDEN were > 28 AIC_c units from the top model. Similarly, inter-annual variation in nest DSR was poorly supported as models containing YEAR were > 10 AIC_c units from the top model (Table 2).

My top model suggested DSR was positively affected by NAGE and DATE. For example, a nest initiated on the overall median nest initiation date for scaup (June 23rd, 22 days later than the earliest known scaup initiation date) was predicted to have a nest DSR

of 0.968 (95% CI=0.954–0.981). A nest 20 days old on the same day was predicted to have a DSR of 0.985 (95% CI=0.986-0.999) (Fig 3).

Discussion

My results revealed a positive relationship between scaup nest DSR and nest age and date, providing support for the nest concealment and nest heterogeneity hypotheses. I found a greater influence of date on nesting DSR than age during this study, although both positively influenced scaup nest DSR. Klett and Johnson (1982) and Walker et al. (2005) found a similar increase in nest survival with increasing date in the PPR of North Dakota and boreal forest of Alaska, respectively. My results are not consistent with Jobin and Picman (1997), who found predation of nests increased as the season progressed on simulated waterfowl nests in marshes within a matrix of agricultural land. This discrepancy in results could result from differences in predator community as suggested by Clark and Nudds (1991) and Wilson et al. (2007). Predators that rely more on olfactory senses might locate some nests easier than predators that rely on visual cues. Clark and Nudds (1991) compared 38 studies and found that the influence of nest concealment on nest survival was dependent on predator community. When a predator community was dominated by avian predators nest concealment was important. My study area consists of a large wetland complex, with scaup nests located primarily in seasonally-flooded emergent vegetation. Common ravens (*Corvus corax*) and California gulls (*Larus californicus*) are presumed to be the predominate predator of scaup nests, which may explain the strong influence of date on nest DSR. The ability of these avian predators to locate nest would be reduced as the nesting season progresses and the vegetation density increases.

Differences in cover type could also lead to the observed differences in the effect of date on nest DSR. Dense cover types could provide better protection to nests by

limiting ability of predator movements through vegetation and by reducing the transmission of auditory, visual or olfactory cues (Borgmann 2010). Emery et al. (2005) showed that nesting success can increase as the season progressed in managed cover, but decrease in unmanaged cover in the same year, providing support that cover type variation could lead to variation in correlation between DSR and date.

I found that nest DSR increased with nest age. This supports the nest heterogeneity hypothesis, i.e., that low quality nests are depredated at a higher rate than nests of higher quality. This is supported by Martin et al. (2000) that showed nests sites have an effect on predation rates; nests that had high risk of predation one year had similarly high risk in subsequent years. Furthermore, Hoekman et al. (2006) found a strong increase in nest survival with nest age and speculated that this was due to heterogeneity in the quality of nest sites. They could not rule out attributes of the female, nesting habitat and behavior of predators, however. On my study site female scaup selected pre-breeding habitat in close proximity to areas of successful nesting in the previous year, providing support for the idea that females can recognize, and select, areas of higher quality than others (O'Neil et al. 2014).

The positive relationship between nest DSR and nest age could also be caused by an increasing value of a nest to the parent(s). Parental investment in a nest increases with nest age, while for single-brooded species the likelihood of another nesting attempt decreases if the current effort fails. This is corroborated by evidence of increasing nest defense as a nest ages (Forbes et al. 1994, Dassow et al. 2012) Moreover, because quality of young declines with progression of the nesting season (Verboven and Visser 1998, Lepage et al. 2000), the probability of a nest leading to successful recruitment of young

also declines within the season, resulting in declining value of subsequent nesting attempts if the current one should fail. Forbes et al. (1994) found that flushing distances of females decreased as incubation advanced. This could lead to a correlation between nest age and nest DSR if decreased flushing distance reduced the likelihood of a predator finding a nest.

I did not find support for the predator search-image hypothesis, i.e., that predators develop search images in response to increases in nest density. Apparent duck nest density on the study area was highly variable within and among years of this study, but nest density was a poor predictor of scaup nest DSR. This contradicts the results of Wilson et al. (2007) and Lariviere and Messier (1998), who demonstrated a negative relationship between nest density and nest DSR. Discrepancies in results may be due to my quantification of nest density at the study area scale, which resulted in densities lower than the lowest density of simulated nests ($2.5 \text{ nests ha}^{-1}$) included in Lariviere and Messier (1998) work.

I found weak support for intra-annual variation in scaup nest DSR during the six years of study. This differs from studies conducted in the PPR that found highly variable nest DSR among years (McKinnon and Duncan 1999, Stephens et al. 2005). The PPR has been shown to vary greatly in its predator community from year to year (Johnson et al. 1989), which could result from its highly fragmented landscape and periodic drought cycles that result in the “boom and bust” duck production the region is known for (Lynch et al. 1963). My study was conducted within a snow melt runoff driven system that’s within a largely intact landscape, i.e., habitat– fragmentation or loss has not occurred.

My results provide indirect support for the nest concealment and nest heterogeneity hypotheses; scaup nest DSR increased consistently with date and nest age among the six years studied. Hoekman et al. (2006) found similar results and suggested heterogeneity of nest survival could result from attributes of females and/or, nesting habitat, such as nest placement relative to home ranges of nest predators or habitat edges. Evidence of variation in quality of nesting areas on my study area exist (O'Neil et al. 2014, Stetter 2014), providing ancillary support for nest heterogeneity as a driver of the observed relationship between nest DSR and nest age. The intra-seasonal increases in nest DSR among years observed during this study is also consistent with the prediction of increasing vegetation density positively influencing nest survival. The increase in nest DSR with the progression of the season has not received unanimous support from all studies (Jobin and Picman 1997, Haffele et al. 2013).

Table 1. Number of nests, mean clutch size and nest initiation dates for lesser scaup in the Lower Red Rock Lake study area 2008-2013. Standard deviations are presented parenthetically.

Year	Number of Nest	Clutch Size	Initiation date
2008	82	8.4 (1.44)	175 (6.1)
2009	42	7.2 (1.23)	172 (8.6)
2010	65	8.2 (1.37)	174 (9.5)
2011	25	6.7 (2.00)	186 (8.8)
2012	55	9.1 (1.33)	165 (9.5)
2013	66	8.0 (1.72)	175 (7.9)

Table 2. Model rankings for analysis of nesting success in lesser scaup. Covariates include, date, nest age (NAGE), year and total duck nest abundance (TOTDEN).

Model	ΔAIC_c	Model Weight
Date + NAGE	0.00	0.652
Date * NAGE	1.43	0.319
Date	7.10	0.019
Date * NAGE ²	9.45	0.006
Date + Year	10.3	0.004
Date * Year	12.9	0.001
Null	27.2	0.001
NAGE	27.2	0.001
TOTDEN	28.2	0.001

Table 3. Coefficient estimates, and standard errors (SE) for the most supported model of lesser scaup nest daily survival rates at Red Rock Lakes National Wildlife Refuge, Montana, 2008–2013.

Model Parameter	β	SE
Intercept	1.953	0.321
Date	0.064	0.012
NAGE	0.041	0.013

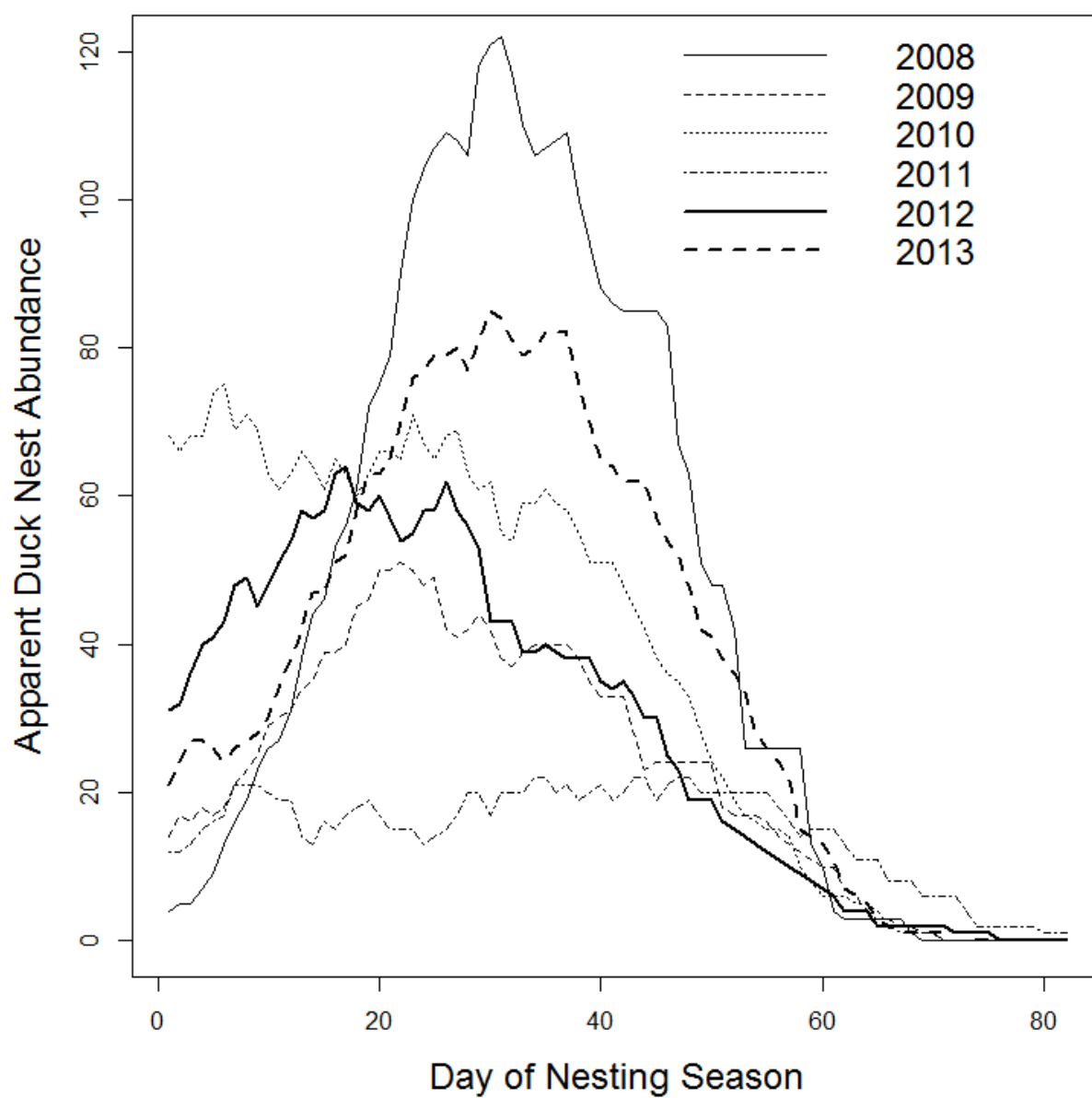


Figure 2. Duck nest abundance throughout the nesting season at Red Rock Lakes National Wildlife Refuge, Montana, 2008–2013.

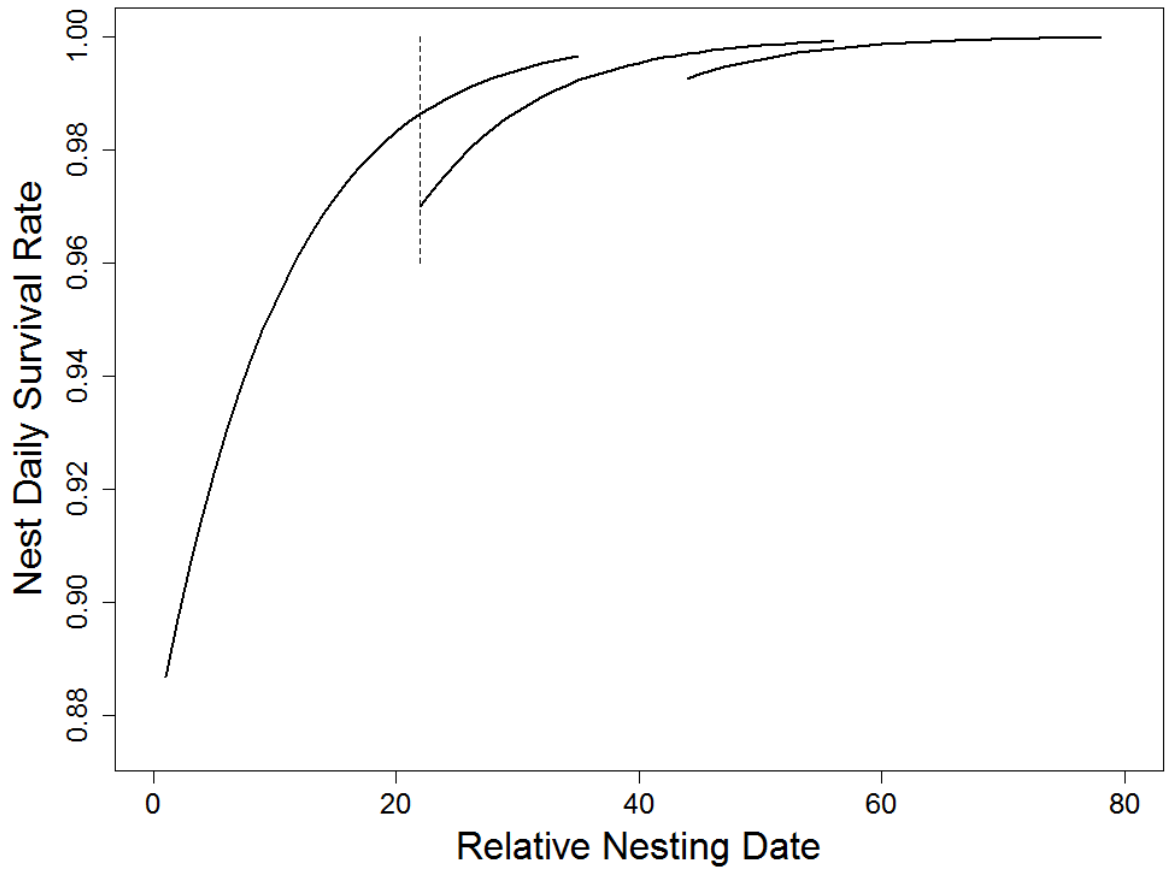


Figure 3. Comparison of lesser scaup nest daily survival rate for nests initiated on 1) the first relative nesting date , 2) median relative nesting (day 22), and 3) the last day a female could initiate a nest and have it hatch by the end of the season (day 44) at Red Rock Lakes National Wildlife Refuge, Montana, 2008–2013. The vertical dashed line represents the overall median nest initiation date for lesser scaup for the years studied.

Literature Cited:

- ARNOLD, T.W., E.A. ROCHE, J.H. DEVRIES, D.W. HOWERTER. 2012. Costs of reproduction in breeding female mallards: predations risk during incubation drives annual mortality. *Avian Conservation and Ecology* 7: 1
- BELLROSE, F.C. 1980. Ducks, geese and swans of North America, 2nd ed. – Stackpole Books.
- BORGMANN, K. L. 2010. Mechanisms underlying intra-seasonal variation in the risk of avian nest predation: implications for breeding phenology. Dissertation, University of Arizona, Tucson.
- BURNHAM, K.P., AND D.R. ANDERSON. 2002. Model selection and multimodel interference: a practical information-theoretic approach, second edition. Springer-Verlag, New York, New York, USA
- CLARK, R.G., AND T.D. NUDDS. 1991. Habitat patch size and duck nesting success: the crucial experiments have not been preformed. *Wildlife Society Bulletin* 19:534-543
- COWARDIN, L. M., D. S. GILMER, and C. W. SHAIFFER. 1985. Mallard recruitment in the agricultural environment of North Dakota. *Wildlife Monographs* 92.
- DASSOW, J.A., M.W. EICHHOLZ, J.D.STAFFORD, P.J. WEATHERHEAD. 2012. Increased nest defence of upland-nesting ducks in response to experimentally reduced risk of nest predation. *Journal of Avian Biology* 43:61-67
- DWERNYCHUK, L.W., AND D.A. BOAG. 1972. How vegetative cover protects duck nests from egg-eating birds. *Journal of Wildlife Management* 36:955-958
- EMERY, R. B., D. W. HOWERTER, L. M. ARMSTRONG, M. G. ANDERSON, J. H. DEVRIES, AND B. L. JOYNT. 2005. Seasonal variation in waterfowl nesting success and its relation to cover management in the Canadian Prairies. *Journal of Wildlife Management* 69:1181–1193.
- FORBES, R.L., R.G. CLARK, P.J. WEATHERHEAD, T. ARMSTRONG. 1994. Risk-taking by female ducks: intra- and interspecific tests of nest defense theory. *Behaviors Ecology and Sociobiology* 34:79-85
- GARRETTSON, P.R., F.C. ROHWER. 2001. Effects of mammalian predator removal on production of upland-nesting ducks in North Dakota. *Journal of Wildlife Management* 65:398-405
- 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.

HAFFELE, R.D., M.W. EICHHOLZ, AND C.S. DIXON. 2013. Duck productivity in restored species-rich native and species-poor non-native plantings. *PLoS ONE*, 8:1-10

HOEKMAN, S. T., MILLS, L. S.,HOWERTER, D. W., DEVRIES, J. H., and BALL, I.J. 2002 Sensitivity analyses of the life cycle of midcontinent mallards. *Journal of Wildlife Management* 66:883–900

JOBIN, B., J. PICMAN. 1997. Factors affecting predation on artificial nests in marshes. *Journal of Wildlife Management* 61:792-800.

JOHNSON, D.H., A.B. SARGEANT, AND R.J. GREENWOOD. 1986. Importance of individual species of predators on nesting success of ducks in the Canadian perairie pothole region. *Canadian Journal of Zoology* 67:291-297

KLETT, A.T., T. L. SHAFFER, and D. H. JOHNSON. 1988. Duck nest success in the Prairie Pothole Region. *Journal of Wildlife Management* 52:431–440.

KLETT, A.T., and D.H. JOHNSON. 1982. Variability in nest survival rates and implications to nesting studies. *Auk* 99:77–87.

LYNCH, J.J., C.D. EVANS, AND V.C. CONOVER. 1963. Inventory of waterfowl environments of prairie Canada. Transactions of the North American Wildlife and Natural Resources Conference 28:93-109.

LAAKE, J.L. 2013. RMark: An R interface for analysis of capture-recapture data with MARK. AFSC Processed Report 2013-01, 25p. Alaska Fisheries Science Center,

LEPAGE, D., G. GAUTHIER, AND S. MENU. 2000. Reproductive consequences of egg-laying decisions in Snow Geese. *Journal of Animal Ecology* 69:414-427.

LARIVIÈRE, S. and F. MESSIER. 1998. Effects of density and nearest neighbours on simulated waterfowl nests: can predators recognize high-density nesting patches? *Oikos*

MARTIN, T.E., J. SCOTT, AND C.MENGE. 2000. Nest predation increases with parental activity: separating nest site and parental activity effects. *The Royal Society B* 267:2287-2293.

MCKINNON, D.T., AND D.C.DUNCAN. 1999. Effectiveness of dense nesting cover for increasing duck production in Saskatchewan. *Journal of Wildlife Management*, 63:382-389

MONTGOMERIE, R.D., AND P.J. WEATHERHEAD. 1988. Risks and rewards of nest defense by parent birds. *The Quarterly Review of Biology*, 63:167-187

National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Seattle WA.

O'NEIL, S.D., J.M. WARREN, J.Y. TAKEKAWA, S.E. DE LA CRUZ, K.A. CUTTING, M.W. PARKER, J.L. YEE. 2014. Behavioural cues surpass habitat factors in explaining prebreeding resource selection by a migratory diving duck. *Animal Behavior*, 90: 21-29

R DEVELOPMENT CORE TEAM. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org/>.

SONDEREGGER, J. L., R. B. SCHOFIELD, R. B. BERG, and M. L. MANNICK. 1982. The upper Centennial Valley, Beaverhead and Madison Counties, Montana. Montana Bureau of Mines and Geology Memoir 50.

STEPHENS, S.E., J.J. ROTELLA, M.S. LINDBERG, M.L. TAPER, AND J.K. RINGELMAN. 2005. Duck nest survival in the Missouri coteau of North Dakota: Landscape effects at multiple spatial scales. *Ecological Applications*, 15:2137-2149

STEWART, R. E., AND H. A. KANTRUD. 1972. Vegetation of prairie potholes, North Dakota, in relation to quality of water and other environmental factors. U. S. Geological Survey Professional Paper 585-D.

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 ducks nest. *Journal of Wildlife Management* 51:481-485

[USFWS] U.S. FISH AND WILDLIFE SERVICE. 2009. Comprehensive Conservation Plan, Red Rock Lakes National Wildlife Refuge. U. S. Fish and Wildlife Service, Region 6, Denver, Colorado.

VERBOVEN, D.L., AND M.E. VISSER. 1998. Seasonal variation in local recruitment of Great Tits: The importance of being early. *Oikos* 81:511-524

WALKER, J., M. S. LINDBERG, M. C. MACCLUSKIE, M. J. PETRULA, and J. S. SEDINGER. 2005. Nest survival of scaup and other ducks in the boreal forests of Alaska. *Journal of Wildlife Management*, 67:582-591.

WARREN, J.M., AND K. CUTTING. 2008. Breeding ecology of lesser scaup at Red Rock Lakes National Wildlife Refuge. U.S. Fish and Wildlife Service unpublished report.

- WARREN, J.M., J. ROTELLA, AND J.E. THOMPSON. 2008. Contrasting effects of cattle grazing intensity on upland-nesting duck production at nest and field scales in the Aspen Parkland, Canada. *Avian Conservation and Ecology*. 3(2): 6
- WELLER, M. W. 1956. A simple field candler for waterfowl eggs. *Journal of Wildlife Management*, 20:111–113.
- WHITE, G.C., AND K.P. BURNHAM. 1999. Program MARK: Survival estimation from populations of marked animals. *Bird Study* 46 Supplement: 120-138.
- WILSON, S., K. MARTIN, and S. J. HANNON. 2007 Nest survival patterns in willow ptarmigan: influence of time, nesting stage, and female characteristics. *Condor* 109:377–388