2006

Mallard Brood Movements, Wetland Use, and Duckling Survival During and Following a Prairie Drought

Gary L. Krapu
USGS Northern Prairie Wildlife Research Center, gkrapu@usgs.gov

Pamela J. Pietz
USGS Northern Prairie Wildlife Research Center, ppietz@usgs.gov

David A. Brandt
USGS Northern Prairie Wildlife Research Center, dbrandt@usgs.gov

Robert R. Cox Jr.
USGS Northern Prairie Wildlife Research Center

Research Article

Mallard Brood Movements, Wetland Use, and Duckling Survival During and Following a Prairie Drought

GARY L. KRAPU,[1] *United States Geological Survey, Northern Prairie Wildlife Research Center, Jamestown, ND 58401, USA*

PAMELA J. PIETZ, *United States Geological Survey, Northern Prairie Wildlife Research Center, Jamestown, ND 58401, USA*

DAVID A. BRANDT, *United States Geological Survey, Northern Prairie Wildlife Research Center, Jamestown, ND 58401, USA*

ROBERT R. COX JR., *United States Geological Survey, Northern Prairie Wildlife Research Center, Jamestown, ND 58401, USA*

Abstract

We used radiotelemetry to study mallard (Anas platyrhynchos) brood movements, wetland use, and duckling survival during a major drought (1988–1992) and during the first 2 years of the subsequent wet period (1993–1994) at 4 51-km^2 sites in prairie pothole landscapes in eastern North Dakota, USA. About two-thirds of 69 radiomarked mallard broods initiated moves from the nest to water before noon, and all left the nest during daylight. On average, broods used fewer wetlands, but moved greater distances during the dry period than the wet period. Broods of all ages were more likely to make inter-wetland moves during the wet period and probabilities of inter-wetland moves decreased as duckling age increased, especially during the dry period. Brood use of seasonal wetlands nearly doubled from 22% to 43% and use of semi-permanent wetlands declined from 73% to 50% from the dry to the wet period. Eighty-one of 150 radiomarked ducklings died during 1,604 exposure days. We evaluated survival models containing variables related to water conditions, weather, duckling age, and hatch date. Model-averaged risk ratios indicated that, on any given date, radiomarked ducklings were 1.5 (95% CI = 0.8–2.8) times more likely to die when the percentage of seasonal basins containing water (WETSEAS) was ≤18% than when WETSEAS was >40%. An interaction between duckling age and occurrence of rain on the current or 2 previous days indicated that rain effects were pronounced when ducklings were 0–7 days old but negligible when they were 8–30 days old. The TMIN (mean daily minimum temperature on the current and 2 previous days) effects generally were consistent between duckling age classes, and the risk of duckling death increased 9.3% for each 1°C decrease in TMIN across both age classes. Overall, the 30-day survival rate of ducklings equipped with radiotransmitters was about 0.23 lower than the survival rate of those without radiotransmitters. Unmarked ducklings were 7.6 (95% CI = 2.7–21.3) times more likely to die on any given day when WETSEAS was ≤18% than when WETSEAS was >40%. Higher duckling survival and increased use of seasonal wetlands during the wet period suggest that mallard production will benefit from programs that conserve and restore seasonal wetland habitat. Given adverse effects of low temperatures on duckling survival, managers may want to include this stochastic variable in models used to predict annual production of mallards in the Prairie Pothole Region. (JOURNAL OF WILDLIFE MANAGEMENT 70(5):1436–1444; 2006)

Key words

Decisions concerning conservation and management of mallard (*Anas platyrhynchos*) populations require a clear understanding of factors limiting reproductive success in the Prairie Pothole Region (PPR; Reynolds et al. 2001), the primary breeding ground of this species in North America (Anderson and Henny 1972). Mallards breed under a wide range of water conditions in the northern Great Plains (Krapu et al. 1983), and over the past several centuries, wet and dry years in North Dakota, USA, have occurred with similar frequencies (Will 1946). Survival of mallard broods generally is higher in wet years in the PPR (Rotella and Ratti 1992*a*, Dzus and Clark 1998, Krapu et al. 2000), but the factors underlying this effect are not well understood. We evaluated effects of dry and wet years on mallard brood movements and wetland use to understand better why brood and duckling survival increases in wet periods.

To set appropriate hunting seasons and bag limits, waterfowl managers need to estimate annual production of

mallards reliably before seasons begin. To do this, they need reliable predictors of mallard duckling survival in the PPR. As candidate predictors, we chose to test environmental parameters that previous research has suggested might influence duckling survival and those that managers can measure accurately with limited effort. Seasonal wetlands account for most variation in numbers of ponds in prairie pothole landscapes (Pietz et al. 2003) and, thus, are a good indicator of water conditions and potentially of duckling survival. We selected daily minimum temperature and rainfall for evaluation because researchers have identified adverse weather conditions as potentially important causes of mallard duckling mortality (Johnson et al. 1992), but their influence has remained poorly understood. Previous studies have shown higher duckling mortality during the first week after hatch (Talent et al. 1983, Gendron and Clark 2002) and noted that adverse weather conditions are more likely to affect younger ducklings (Korschgen et al. 1996). In addition, mallard broods hatch over a wide range of environmental conditions from mid-May to August and,

thus, hatch date may influence survival rates of ducklings, as well as broods (e.g., Krapu et al. 2000). For these reasons, we selected the percentages of seasonal basins holding water, minimum daily temperature, rain, duckling age, and hatch date as the parameters to consider in our evaluation of potentially useful predictors of duckling survival.

To address these information needs, we monitored radiomarked mallard brood hens and radiomarked ducklings during a dry period (1988–1992) and the first 2 years of the subsequent wet period (1993–1994) in eastern North Dakota. Specifically, our objectives were to 1) determine times of departure of radiomarked broods from nests to water and lengths and frequencies of inter-wetland moves in dry and wet periods in prairie pothole landscapes, 2) estimate types and numbers of ponds used by radiomarked broods during dry and wet periods, and 3) evaluate effects of wetland condition, daily minimum temperature, rainfall, duckling age, and hatch date on survival of radiomarked ducklings to 30 days.

Study Area

We monitored radiomarked hen mallards and their broods on 4 51-km^2 circular study areas located in 2 glacial landforms in the PPR. We collected data for 6 years (1988–1991, 1993–1994) at study areas 1 and 2, which were located in dead-ice moraine in the Missouri Coteau (Bluemle 1977) near Kulm, North Dakota. We collected data for 5 years (1988, 1990–1992, 1994) at study areas 3 and 4 on the glaciated drift plain near Jamestown, North Dakota (see table 1 in Krapu et al. 2000).

Most lands within the study areas were privately owned; public lands were limited primarily to scattered Waterfowl Production Areas (WPAs) owned and managed by the United States Fish and Wildlife Service. Uplands on study areas were largely for production of cereal grains, row crops, hay, and livestock grazing (Krapu et al. 1997). Wetland habitats included temporarily, seasonally, and semi-permanently flooded basins and lakes (Cowardin et al. 1995), which are about equivalent to classes II–V of Stewart and Kantrud (1971). Krapu et al. (2000) previously presented quantitative descriptions of upland and wetland habitat types on the Kulm and Jamestown study areas.

Methods

Field Procedures

During 1988–1991, we captured hen mallards from mid-April through early May with decoy-hen traps (Sharp and Lokemoen 1987). We fitted each hen with a 23-g harness transmitter (Dwyer 1972) and a uniquely identifiable combination of nylon nasal markers (Lokemoen and Sharp 1985). We monitored hens daily to assess nesting activity (Krapu et al. 1997). At nest sites of radiomarked hens, we captured all ducklings in newly hatched broods when possible, attached web tags following a procedure modified from Haramis and Nice (1980), and attached 2-g radio-transmitters using sutures and glue to 1–4 randomly selected ducklings per brood. We also radiomarked ducklings in newly hatched broods of unmarked hens inside predator exclosures (Cowardin et al. 1998) when opportunities existed.

In 1992–1994, we located nests by systematically searching WPAs and privately owned Conservation Reserve Program fields. We searched for nests by dragging a chain between 2 vehicles to flush hens from nests (Higgins et al. 1969). We determined developmental stages of eggs by candling (Weller 1956). Beginning about 15 days after the onset of incubation, we used modified bow traps (Salyer 1962) or walk-in traps (Dietz et al. 1994) to capture nesting hens. We fitted each captured hen with a 4-g anchor transmitter (Pietz et al. 1995) and a uniquely identifiable nasal marker. After marking, we anesthetized the hen with methoxyflur-ane to reduce risks of nest abandonment (Rotella and Ratti 1990). We marked newly hatched ducklings of radiomarked and unmarked hens at nests inside and outside predator exclosures. We web-tagged all ducklings and fitted 1–4 (usually 2) ducklings per brood with 1.5–1.8-g anchor transmitters modified from Mauser and Jarvis (1991). Transmitters weighed 4.4–5.3% of masses of newly hatched ducklings ($\bar{x} = 34.5 \pm 0.26$ [SE], $n = 171$). All capture and marking procedures conformed to recommendations of the American Ornithologists' Union (1988) and were approved by the Northern Prairie Wildlife Research Center Animal Care and Use Committee.

From ground-tracking vehicles, we could consistently detect signals of duckling transmitters within 1.5 km, 4-g hen transmitters within 2 km, and 23-g hen transmitters within 3 km. We tracked each brood continuously from nest to wetland, and then we attempted to check broods (visually) daily to detect radio failures and losses of unmarked ducklings. If we obtained no sightings, we recorded the brood location and radio status using standard telemetry methods (Mech 1983). We aerially searched (Gilmer et al. 1981) for signals from missing ducklings weekly. We attempted to monitor broods with radiomarked hens or ducklings daily until all ducklings were either lost or fledged.

Explanatory Variables for Survival Analyses

Wet seasonal basins.—The National Wetland Inventory (NWI) delineated wetland habitats on our study areas from high-altitude color-infrared photographs prior to our study. We classified each wetland basin by the most permanent water regime assigned to part or that entire basin (temporary, seasonal, semi-permanent, and lake) by the NWI (Cowardin et al. 1979, Cowardin 1982). Using aerial video data (Cowardin et al. 1988), and the feature-mapping process from Map and Imaging Processing Systems software (Miller et al. 1990), we estimated the percentage of seasonal basins containing ponds (WET-SEAS) on each study area at monthly intervals from May to September each year. We defined ponds as basins that contained water (Cowardin 1982) and we categorized them according to basin class (e.g., water within a basin with a seasonally flooded water regime was termed a seasonal pond). During June and July, the peak months of mallard

brood-rearing, seasonal ponds accounted for 94–97% of the annual variation in pond numbers on North Dakota study sites (Pietz et al. 2003).

To assess water conditions in the immediate vicinity of each duckling on a given exposure day, we calculated WETSEAS for the area within a 1.61-km radius of a duckling's location or the centroid of a cluster of locations (Pietz et al. 2003). To do this, we first determined the spatial distribution of each duckling's daily locations using cluster analysis (PROC CLUSTER; SAS Institute 1990). We considered a location or group of locations to be distinct clusters if they were separate from the centroid of adjacent clusters by ≥640 m. We chose 640 m as the minimum distance to separate clusters because shorter distances produced >75% overlap in surrounding areas. If a duckling was not located for >1 day, and then was located in the same cluster, we assumed that the duckling had stayed in that cluster throughout the interval. If a duckling was subsequently located in a different cluster, we assigned values to the first half of the interval from the preceding cluster and to the second half of the interval from the succeeding cluster. In cases where part of the area surrounding the cluster was unclassified (fell outside the study area), we retained and calculated proportional landscape variables only in clusters with ≥50% of the area classified. Seventeen percent (24 clusters) of duckling exposure days were <50% classified (and were excluded from analyses), 31% (37 clusters) were 50–99% classified, and 52% (68 clusters) were 100% classified. For each duckling exposure day, we calculated the value of WETSEAS using the aerial videography obtained closest to that exposure day. All values for WETSEAS were either ≤18% or >40%, so we treated this variable as binary, with these values defining dry (1988–1992) and wet (1993–1994) conditions, respectively.

Weather, hatch date, duckling age.—We obtained daily records of precipitation and minimum air temperature for each study area from the nearest National Weather Service observation station (National Oceanic and Atmospheric Administration 1988–1994). For each duckling exposure day, we calculated RAIN ("1" if it had rained [even trace amounts] on the current or 2 previous days, and "0" otherwise) and TMIN (the average of daily minimum temperatures for the current and 2 previous days). HATCHDATE was the annual date on which the first egg of a clutch hatched. We designated duckling age (AGE) as 0–7 or 8–30 days.

Data Analysis

Movements and habitat use.—For measures of travel from nests to wetlands, we excluded broods hatched inside predator exclosures. We tested for variation in the distance broods traveled between wetlands in relation to brood age (in days) and wetland condition (dry period [1988–1992] vs. wet period [1993–1994]) using repeated measures analysis of covariance (PROC MIXED; SAS Institute 1996). The response variable for this analysis was the distance between the centroid of the wetland from which the brood moved to the centroid of the wetland to which the brood moved; it included all inter-wetland moves made by radiomarked broods (i.e., broods with radiomarked hens or ducklings). We also used analysis of covariance (PROC GLM; SAS Institute 1990) to assess variation in maximum distances between nests and subsequent brood locations. We controlled for the number of exposure days for each brood in these analyses by including this variable as a predictor in all models. We estimated the probability that broods would initiate an inter-wetland move as a function of brood age and wetland condition using PROC LOGISTIC (SAS Institute 1990). We estimated the average number of inter-wetland moves that broods would make over 30 days during wet and dry periods by combining the predicted daily probabilities of movement using the Delta Method (Seber 1982). We tested for variation in habitat use (with habitats defined as wetland types) by broods in relation to wetland condition using compositional data analysis (Aebischer et al. 1993).

Duckling survival.—We used only data from radiomarked ducklings for our main analysis of duckling survival. We excluded data collected before ducklings reached their initial wetland to eliminate a potential bias in survival for ducklings that hatched inside predator exclosures. Because survival of ducklings in the same brood may not be independent, we used an extension of Cox (1972) proportional hazards regression (coxph function; Mathsoft 1997) to account for intrabrood correlation when evaluating whether duckling survival to 30 days was related to our explanatory variables. Parameter estimates produced by this model are the same as those produced if one considered brood-mates as independent, but standard error estimates increase in relation to the magnitude of intrabrood correlation.

Following the philosophy of Burnham and Anderson (1998), we constructed a set of 26 candidate models (see Appendix) using carefully selected combinations of WETSEAS, TMIN, RAIN, HATCHDATE, and AGE and evaluated the fit of these models using Akaike's Information Criterion adjusted for small sample sizes (AIC_c). We listed all models considered, regardless of their weight of evidence, in the Appendix to assist development of candidate model sets in the future. A priori, based on existing evidence that mallard brood survival is positively correlated with wetland habitat conditions (Rotella and Ratti 1992*b*, Dzus and Clark 1998), and specifically with seasonal ponds (Krapu et al. 2000), we expected WETSEAS to be an important predictor of duckling survival and we included this variable in all candidate models. We designed our candidate models primarily to assess the relative importance of HATCHDATE and interactions among AGE, TMIN, and RAIN. We also evaluated our decision to include WETSEAS in all models by excluding this variable from our best model and examining the resulting ΔAIC_c score. We calculated model-averaged parameter estimates and their standard errors to account for uncertainty in model selection (Burnham and Anderson 1998). We assessed fit and proportional hazards assumptions of all models by comparing predicted survival

functions to actual survival functions, and by examining plots of Schoenfeld residuals (SAS Institute 1996).

We evaluated effects of radiotransmitters on duckling survival in a separate analysis. We first used proportional hazards regression to compare mortalities among radio-marked and unmarked ducklings to test for an overall effect of transmitters on duckling survival (R. R. Cox, United States Geological Survey, unpublished data; PROC PHREG; SAS Institute 1996). We then tested whether transmitter effects interacted with terms that we found to influence mallard duckling survival in our analysis of radiomarked ducklings only. For any interaction between a survival predictor and transmitters, we reported the risk ratio (e^B) for the survival predictor separately for radiomarked and unmarked ducklings. We accounted for intrabrood correlation when calculating 95% confidence intervals for duckling survival rates (PROC PHREG; SAS Institute 1996) by using a jackknife procedure in a SAS macro (T. M. Therneau, Mayo Clinic College of Medicine, M. R. Riggs, Research Triangle Institute, personal communication).

Results

Brood Movements

Timing of nest exodus determined for 69 radiomarked broods varied from 0535 hours to about 2130 hours but primarily occurred in the morning (Fig. 1). About 36% of broods left their nests by 0800 hours, 57% left by 1000 hours, and 74% left by noon. During the 1988–1992 drought, broods averaged 3.3 hours (range 1.3–5.2 hr; $n = 3$) from nest departure until arrival at a pond. In 1993–1994, when wetland conditions were much improved, broods averaged 1.0 hour (range = 0.03–4.8 hr; $n = 18$) when traveling from nests to water.

Lengths of inter-wetland moves by broods were 3.5 times greater ($F_{1, 52} = 10.1$, $P < 0.003$) during the dry ($\bar{x} = 1,681$
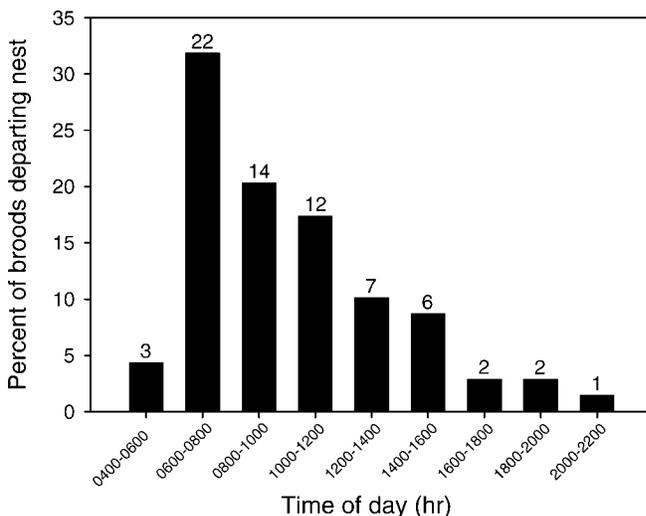

Figure 1. Timing of nest exodus by 69 radiomarked mallard broods in eastern North Dakota, USA, 1988–1994. Bars depict percentages of broods departing from their nests during each 2-hour interval. We listed number of broods leaving during each interval above the bars.

± 216 [SE] m) than during the wet period ($\bar{x} = 488 \pm 107$ m). We did not find evidence of a relation between length of inter-wetland moves and AGE or of an interaction between period and AGE ($P \geq 0.23$ for both tests). Maximum linear distances broods traveled from nest sites over the brood-rearing period (30 d) were 1.5 times greater ($F_{1, 86} = 5.2$, $P < 0.03$) during the dry ($\bar{x}_{max} = 2,183 \pm 209$ m) than during the wet period ($\bar{x}_{max} = 1,484 \pm 196$ m). The likelihood that broods would make inter-wetland moves decreased as broods got older, especially during the dry period (Fig. 2; AGE × period interaction, Wald $\chi^2_1 = 8.8$, $P < 0.003$). Broods of all ages were more likely to make inter-wetland moves during wet than dry periods (Fig. 2). The predicted number of inter-wetland moves made by broods over the entire 30-day interval was 7.3 ± 0.4 (SE) during the wet period and 2.0 ± 0.3 during the dry period. The model predicting daily movement probability by broods 0–30 days of age was

$$\text{Pr(Move)} =$$
$$\{\exp[-0.9811 - 0.359(\text{Wet/dry})$$
$$-0.00972(\text{Age}) - 0.0933(\text{Wet/dry} \times \text{Age})]\}$$
$$\div\{1 + \exp[-0.9811 - 0.359(\text{Wet/dry}) - 0.00972(\text{Age})$$
$$-0.0933(\text{Wet/dry} \times \text{Age})]\}$$

where Wet/dry = 1 if WETSEAS >40% and 0 otherwise, and Age = brood age in days.

Wetland Habitat Use

Broods used fewer ($F_{1, 86} = 7.7$, $P < 0.007$) ponds during the dry period ($\bar{x} = 2.2 \pm 0.4$) than during the wet period ($\bar{x} = 3.6 \pm 0.3$). Habitat use by broods differed (Wilks' $\lambda = 0.80$, $F_{3, 75} = 6.2$, $P = 0.0008$) between dry and wet periods. Semi-permanent ponds accounted for 73% and 50% of wetland use by broods during the dry and wet periods, respectively (Table 1). Use of seasonal ponds nearly doubled from 22% to 43% from the dry to the wet period.

Duckling Survival

Eighty-one of 150 radiomarked mallard ducklings from 59 broods died during 1,604 exposure days. The overall survival rate to 30 days was 0.32 for radiomarked ducklings. Seven of the 26 candidate models had ΔAIC_c scores ≤ 2, indicating considerable model-selection uncertainty (Appendix). However, the AGE × TMIN × RAIN interaction did not appear in any models with ΔAIC_c scores ≤ 4, and HATCHDATE, which we included in half the candidate models, appeared only once among the 7 top models. Hence, there was little evidence that these variables were important compared to other predictors in our analysis.

The AGE × TMIN interaction was in 3 of the top 7 models, but all the top models included AGE and TMIN as main effects. Examination of predicted survivor functions at various temperatures, holding other variables constant, indicated that temperature effects were generally consistent across duckling ages (Fig. 3). Hence, we interpret these findings as strong evidence that low temperatures decreased
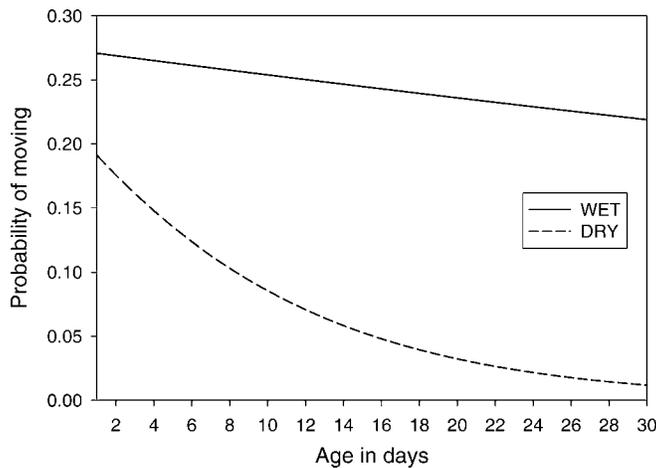
Figure 2. Probability of a mallard brood moving to a new wetland relative to brood age during a dry period (1988–1992) and the following wet period (1993–1994) in prairie pothole landscapes in eastern North Dakota, USA.

Table 1. Wetland habitat use by 79 radiomarked mallard broods during the dry period (1988–1992; $n = 33$ broods, 672 locations) and the following wet period (1993–1994; $n = 46$ broods, 1,852 locations) in prairie pothole landscapes of eastern North Dakota, USA.

Status	Wetland type[a]	No. of locations	Use (%)[b]	SE
Dry	Lake	21	3.8	2.1
	Semi-permanent	498	73.2	6.5
	Seasonal	152	22.4	6.4
	Temporary	1	0.6	0.6
Wet	Lake	58	2.9	2.1
	Semi-permanent	888	50.0	5.7
	Seasonal	805	42.5	5.5
	Temporary	101	4.6	2.0

[a] Wetland types follow Cowardin et al. (1979).
[b] Percentages obtained by calculating the percent use of each wetland type for each brood, and then averaging over broods. We conducted statistical analyses on transformed data (see Methods).

duckling survival, and weak evidence that temperature effects varied with age. The AGE × RAIN interaction was contained in 2 of the top 7 models. In contrast to the AGE × TMIN interaction, examination of predicted survivor functions under constant levels of RAIN = 0 and RAIN = 1 indicated that RAIN had a strong effect on survival of ducklings 0–7 days old but did not affect ducklings 8–30 days old (Fig. 4). Finally, the TMIN × RAIN interaction appeared in 3 of the top 7 models. Examination of predicted survivor functions at various levels of RAIN and TMIN indicated that 1) main effects of TMIN, and particularly RAIN, had a strong influence on duckling survival, and 2) the interaction of TMIN and RAIN was weak because constant conditions of RAIN = 1
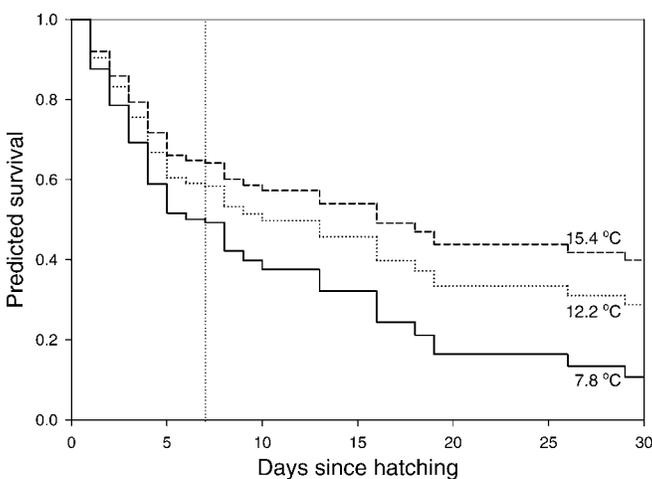
resulted in low survival across the entire range of temperatures (Fig. 5).

To assess further our interpretations that TMIN acted primarily as a main effect, we constructed a model that contained WETSEAS, TMIN, AGE, RAIN, and AGE × RAIN. This model was not one of our original candidate models and we evaluated this model on an exploratory basis. This model was 0.4 AIC_c units lower than our previously best model. While this model was not convincingly better than the top models in our candidate set, it is relatively simple compared to many others and allowed interpretable effects of TMIN without complications from interactions. The risk ratio from this model indicated that the risk of duckling death increased 9.3% (95% CI = 1.7–16.3%) for each 1°C decrease in TMIN.

Model-averaged risk ratios indicated that radiomarked mallard ducklings were 1.5 (95% CI = 0.82–2.76) times more likely to die on any given day when WETSEAS was ≤18% compared to when WETSEAS was >40% (Fig. 6). To evaluate our decision to include WETSEAS in all candidate models, we compared the AIC_c score of the best model (WETSEAS, AGE, TMIN) to that of the best model without the WETSEAS term. The AIC_c score for the model without WETSEAS was 0.56 units higher. Taken alone, this finding does not provide strong evidence that WETSEAS was an important predictor of mallard duckling survival. However, we found strong evidence that the effect of WETSEAS differed ($\chi_1^2 = 6.74$; $P = 0.009$) between radiomarked ($\beta = -0.01 \pm 0.58$) and unmarked ($\beta = 2.02 \pm 0.53$) ducklings. Conversion of these parameter estimates to risk ratios indicates that the effect of WETSEAS was negligible ($e^B = 0.99$; 95% CI = 0.32–3.1) on radiomarked ducklings, but unmarked ducklings were 7.6 (95% CI = 2.7–21.3) times more likely to die on any given day when WETSEAS was ≤18% than when WETSEAS was >40%. The presence of radiotransmitters on mallard ducklings dampened the positive effect of WETSEAS on duckling survival and reduced their 30-day survival by 0.227 ($\chi_1^2 = 5.05$; $P = 0.02$). We did not detect a difference in parameter estimates for the AGE × TMIN

Figure 3. Survival rates of radiomarked mallard ducklings in relation to duckling age (AGE) and minimum daily ambient temperature (TMIN), predicted from a proportional-hazards regression model in prairie pothole landscapes in eastern North Dakota, USA, 1988–1994. The vertical line separates duckling AGE categories (0–7 d and 8–30 d old) used in analyses. Levels of TMIN represents 10th, 50th, and 90th percentiles based on exposure days of ducklings in our study.
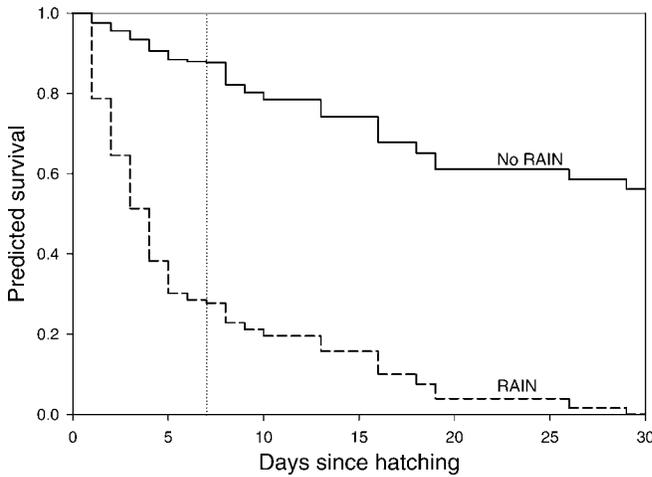
Figure 4. Survival of radiomarked mallard ducklings in relation to duckling age (AGE), and presence or absence of rain during the present or 2 previous days (RAIN or No RAIN), as predicted from a proportional-hazards regression model for prairie pothole landscapes in eastern North Dakota, USA, 1988–1994. The vertical line separates the duckling AGE categories (0–7 d and 8–30 d old) used in analyses.

Figure 5. Survival of radiomarked mallard ducklings 0–30 days in relation to minimum daily ambient temperature (TMIN) and presence or absence of rain during the present and/or 2 previous days (RAIN or No RAIN), predicted from a proportional-hazards regression model for prairie pothole landscapes in eastern North Dakota, USA, 1988–1994. Levels of TMIN represent 10th and 90th percentiles based on exposure days of ducklings in our study.

effect ($\chi_1^2 = 0.55$; $P = 0.46$) between radiomarked ($\beta = 0.05 \pm 0.18$ [SE]) and unmarked ($\beta = 0.23 \pm 0.15$) ducklings. We could not compare parameter estimates between radiomarked and unmarked ducklings for the AGE × RAIN effect because of small samples (missing cells), or for the TMIN × RAIN effect because of fixed variance in one cell.

Discussion

Differences in mallard brood movements between wet and dry years may help explain why brood and duckling survival were higher during the wet period. The higher frequency of moves when seasonal water was readily available suggests that broods shift their locations as foraging conditions and predation pressures warrant. Relocation options are limited when few seasonal ponds exist in prairie pothole landscapes because of drought or wetland drainage. Broods that do move overland during drought must travel farther between wetlands, thereby increasing their exposure to predators that forage in the uplands. When broods reach a new pond, they are more likely to encounter mink, which also are concentrated by drought (Krapu et al. 2004a). Broods in landscapes with an abundance of seasonal ponds can avoid or escape from permanent (lake) or semi-permanent wetland habitats preferred by mink (Krapu et al. 2004a); thus, ducklings are less likely to be depredated. Most moves occurred before broods reached 1 week of age, when ducklings are particularly vulnerable to food shortages and less capable of escaping predators. High use of seasonal ponds when available probably resulted, in part, because re-flooding of shallow wetland habitat after prolonged drought leads to increased production of aquatic macro-invertebrates (Euliss et al. 1999), the primary food of young mallard ducklings in prairie potholes (Perret 1962), and an abundance of seeds and other plant material eaten by older broods (Chura 1961). Semi-permanent wetlands continued
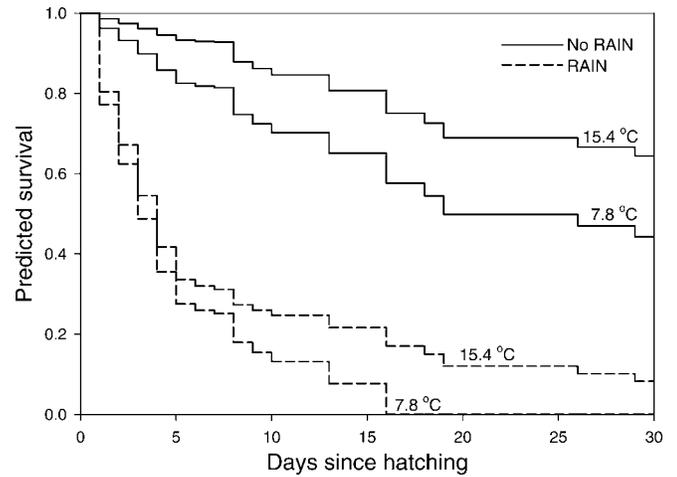
to receive high brood use during the wet period probably, in part, because many semi-permanent basins had extensive shallow marsh and wet meadow zones (Stewart and Kantrud 1971) that re-flooded in 1993–1994 (Krapu et al. 2004b).

Using data from our radiomarked ducklings, we did not find strong support for WETSEAS as a predictor of mallard duckling survival because the presence of radiotransmitters dampened the positive effect of WETSEAS on survival. However, when we considered unmarked ducklings, we found a much stronger positive relationship between duckling survival and WETSEAS. We also found WETSEAS to be an important predictor of mallard brood survival (Krapu et al. 2000). Variables generally must strongly affect duckling mortality in order to show an
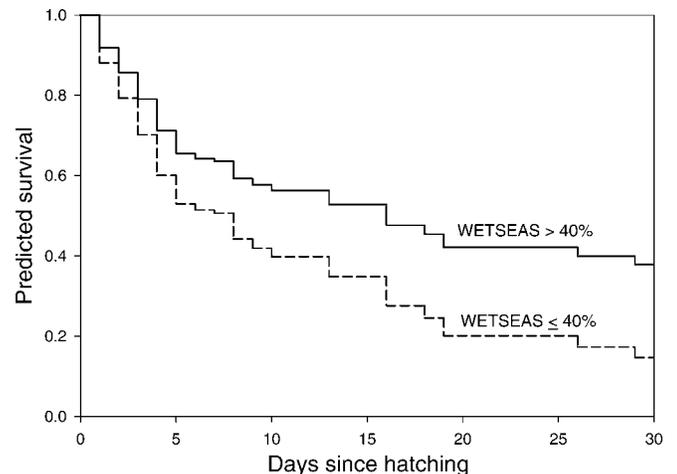

Figure 6. Survival rates of radiomarked mallard ducklings (0–30 d old) relative to percent of seasonal basins with water (WETSEAS), predicted from a proportional-hazards regression model for prairie pothole landscapes in eastern North Dakota, USA, 1988–1994.

important effect on total brood loss. Consequently, we conclude that WETSEAS is an important predictor of mallard duckling survival.

Previous analyses documented that RAIN was an important predictor of mallard brood survival (Krapu et al. 2000); thus, it is not surprising that we found it to be an important predictor of mallard duckling survival as well. Krapu et al. (2000) noted several reasons why rainy weather may result in higher mortality, especially among young ducklings. For example, young ducklings must be brooded more during rain and, thus, have less time to feed. Rain also reduces availability of invertebrates on vegetation and at the water surface (Chura 1961, Nelson 1989), where young ducklings forage. Reduced feeding time, and less food being available, results in more rapid depletion of energy reserves, potentially leading to duckling hypothermia, starvation, and increased susceptibility to predators while foraging. Endogenous reserves are sufficient to meet energy needs of young mallards for only about 3 days posthatch (Marcström 1966). These factors may help explain the disproportionate percentage of duckling deaths we recorded during the first week of life, a pattern reported in several studies (Talent et al. 1983, Orthmeyer and Ball 1990, Mauser et al. 1994, Cox et al. 1998, Hoekman et al. 2004), and the interaction we detected between AGE and RAIN. Other researchers have reported an apparent interaction between duckling age and wet weather for canvasbacks (*Aythya valisineria*) on impoundments at Agassiz National Wildlife Refuge in northwestern Minnesota (Korschgen et al. 1996).

We found clear evidence that cold temperatures decreased mallard duckling survival. Cold temperatures increase maintenance energy requirements (Kendeigh et al. 1977), which causes ducklings to become more susceptible to starvation and increases the risk of predation if more time must be spent searching for food to meet higher energy costs. Our analyses failed to demonstrate an interaction between minimum daily temperature and rainy conditions on duckling survival. Minimum temperatures are lower on clear nights than during overcast, rainy weather; thus, our ability to detect an interaction between RAIN and TMIN may be limited because temperature extremes are less likely during extensive periods of rain.

Several studies have reported a decrease in duckling survival with hatch date (Orthmeyer and Ball 1990, Rotella and Ratti 1992*b*, Guyn and Clark 1999, Hoekman et al. 2004), but other studies have reported no, increasing, or variable relationships between duckling survival and hatch date (Dawson and Clark 1996, Leonard et al. 1996, Dzus and Clark 1998, Gendron and Clark 2002). Despite our large sample size, we found no evidence of an effect of HATCHDATE on mallard duckling survival. This may reflect the atypical pattern of WETSEAS we documented in 1993. Seasonal water increased from late spring through summer that year (Krapu et al. 2004*b*), the reverse of the usual pattern (see Kantrud et al. 1989). Similarly, in studies conducted in Saskatchewan, Dzus and Clark (1998) found

that pond density and mallard brood survival increased with date during 1993; both measures had decreased with date during each of the previous 3 years.

Management Implications

Seasonal and semi-permanent wetlands accounted for ≥90% of wetland habitat use by mallard broods during our study, reflecting the importance of these habitats to mallard production in the PPR. Greater availability of seasonal ponds probably enhanced brood (Krapu et al. 2000) and duckling survival by allowing broods to make more frequent inter-wetland moves. Efforts to enhance mallard recruitment in the PPR are likely to be more effective where seasonally flooded wetland habitat is abundant or can be restored. Few options exist to reduce risk to mallard ducklings from the adverse effects of cold temperatures and rainy weather, important causes of duckling mortality. However, any steps managers take to enhance food production (e.g., restoration of drained seasonally flooded wetlands, managed draw-downs) are likely to increase survival by improving foraging conditions so young can acquire nutrients more rapidly, thus reducing feeding time and exposure to mink, other predators, and adverse weather. Failure to include minimum ambient temperature in models used to predict annual mallard production from the PPR almost certainly will result in under-estimation of variation in duckling survival and, correspondingly, annual recruitment.

Acknowledgments

Literature Cited

Aebischer, N. J., P. A. Robertson, and R. E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. Ecology 74:1313–1325.

American Ornithologists' Union. 1988. Report of committee on use of wild birds in research. Auk 105(1, Supplement).

Anderson, D. R., and C. J. Henny. 1972. Population ecology of the mallard. I. A review of previous studies and distribution and migration from breeding areas. U.S. Fish and Wildlife Service Resource Publication 105, Washington, D.C., USA.

Bluemle, J. P. 1977. The face of North Dakota: the geologic story. North Dakota Geological Survey Education Series 11, Washburn, USA.

Burnham, K. P., and D. R. Anderson. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.

Chura, N. J. 1961. Food availability and preferences of juvenile mallards. Transactions of the North American Wildlife Conference 26:121–134.

Cowardin, L. M. 1982. Some conceptual and semantic problems in wetland classification and inventory. Wildlife Society Bulletin 10:58–60.

Cowardin, L. M., P. M. Arnold, T. L. Shaffer, H. R. Pywell, and L. D. Miller. 1988. Duck numbers estimated from ground counts, MOSS map data, and aerial video. Pages 205–219 in J. D. Scurry, editor. Proceedings: fifth national MOSS users workshop. Louisiana Sea Grant College Program, Baton Rouge, and U.S. Fish and Wildlife Service, Slidell, Louisiana, USA.

Cowardin, L. M., V. Carter, F. C. Golet, and E. T. LaRoe. 1979. Classification of wetlands and deep water habitats of the United States. U.S. Fish and Wildlife Service Biological Services Program FWS/OBS-79/31, Washington, D.C., USA.

Cowardin, L. M., P. J. Pietz, J. T. Lokemoen, H. T. Sklebar, and G. A. Sargeant. 1998. Response of nesting ducks to predator exclosures and water conditions during drought. Journal of Wildlife Management 62:152–163.

Cowardin, L. M., T. L. Shaffer, and P. M. Arnold. 1995. Evaluations of duck habitat and estimation of duck population sizes with a remote-sensing based system. National Biological Service Biological Science Report 2, Washington, D.C., USA.

Cox, D. R. 1972. Regression models and life-tables. Journal of the Royal Statistical Society Series B 34:187–220.

Cox, R. R., Jr., M. A. Hanson, C. C. Roy, N. H. Euliss Jr., D. H. Johnson, and M. G. Butler. 1998. Mallard duckling growth and survival in relation to aquatic invertebrates. Journal of Wildlife Management 62:124–133.

Dawson, R. D., and R. G. Clark. 1996. Effects of variation in egg size and hatching date on survival of lesser scaup (Aythya affinis) ducklings. Ibis 138:693–699.

Dietz, N. J., P. J. Bergmann, and L. D. Flake. 1994. A walk-in trap for nesting ducks. Wildlife Society Bulletin 22:19–22.

Dwyer, T. J. 1972. An adjustable radio-package for ducks. Journal of Wildlife Management 44:282–284.

Dzus, E. H., and R. G. Clark. 1998. Brood survival and recruitment of mallards in relation to wetland density and hatching date. Auk 115:311–318.

Euliss, N. H., Jr., D. A. Wrubleski, and D. M. Mushet. 1999. Wetlands of the Prairie Pothole Region: invertebrate species composition, ecology, and management. Pages 471–514 in D. P. Batzer, R. B. Rader, and S. A. Wissinger, editors. Invertebrates in freshwater wetlands of North America: ecology and management. John Wiley and Sons, New York, New York, USA.

Gendron, M., and R. G. Clark. 2002. Survival of gadwall and mallard ducklings in southcentral Saskatchewan. Journal of Wildlife Management 66:170–180.

Gilmer, D. S., L. M. Cowardin, R. L. Duval, L. M. Mechlin, C. W. Shaiffer, and V. B. Kuechle. 1981. Procedures for the use of aircraft in wildlife biotelemetry studies. U.S. Fish and Wildlife Service Resource Publication 140, Washington, D.C., USA.

Guyn, K. L., and R. G. Clark. 1999. Factors affecting survival of northern pintail ducklings in Alberta. Condor 101:369–377.

Haramis, G. M., and A. D. Nice. 1980. An improved web-tagging technique for waterfowl. Journal of Wildlife Management 44:898–899.

Higgins, K. F., L. M. Kirsch, and I. J. Ball Jr. 1969. A cable-chain device for locating duck nests. Journal of Wildlife Management 33:1009–1011.

Hoekman, S. T., T. S. Gabor, R. Maher, H. R. Murkin, and L. M. Armstrong. 2004. Factors affecting survival of mallard ducklings in southern Ontario. Condor 106:485–495.

Johnson, D. H., J. D. Nichols, and M. D. Schwartz. 1992. Population dynamics of breeding waterfowl. Pages 446–485 in B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, editors. Ecology and management of breeding waterfowl. University of Minnesota, Minneapolis, USA.

Kantrud, H. A., G. L. Krapu, and G. A. Swanson. 1989. Prairie basin wetlands of the Dakotas: a community profile. U.S. Fish and Wildlife Service Biological Report 85, Washington, D.C., USA.

Kendeigh, S. C., V. R. Dol'nik, and V. M. Gavrilov. 1977. Avian energetics. Pages 127–207 in J. Pinkowski, and S. Kendeigh, editors. Granivorous birds in ecosystems. Cambridge University, United Kingdom.

Korschgen, C. E., K. P. Kenow, W. L. Green, D. H. Johnson, M. D. Samuel, and L. Sileo. 1996. Survival of radiomarked canvasback ducklings in northwestern Minnesota. Journal of Wildlife Management 60:120–132.

Krapu, G. L., R. J. Greenwood, C. P. Dwyer, K. M. Kraft, and L. M. Cowardin. 1997. Wetland use, settling patterns, and recruitment in mallards. Journal of Wildlife Management 61:736–746.

Krapu, G. L., A. T. Klett, and D. G. Jorde. 1983. The effect of variable spring water conditions on mallard reproduction. Auk 100:689–698.

Krapu, G. L., P. J. Pietz, D. A. Brandt, and R. R. Cox Jr. 2000. Factors limiting mallard brood survival in prairie pothole landscapes. Journal of Wildlife Management 64:553–561.

Krapu, G. L., P. J. Pietz, D. A. Brandt, and R. R. Cox Jr. 2004a. Does presence of permanent fresh water affect recruitment in prairie-nesting dabbling ducks? Journal of Wildlife Management 68:332–341.

Krapu, G. L., R. E. Reynolds, G. A. Sargeant, and R. W. Renner. 2004b. Patterns of variation in clutch sizes in a guild of temperate-nesting dabbling ducks. Auk 121:695–706.

Leonard, J. P., M. G. Anderson, H. H. Prince, and R. B. Emery. 1996. Survival and movements of canvasback ducklings. Journal of Wildlife Management 60:863–874.

Lokemoen, J. T., and D. E. Sharp. 1985. Assessment of nasal marker materials and designs used on dabbling ducks. Wildlife Society Bulletin 13:53–56.

Marcström, V. 1966. Mallard ducklings (Anas platyrhynchos L.) during the first days after hatching. Viltrevy 4:343–368.

Mathsoft. 1997. S-Plus 4 user's guide. Data Analysis Products Division, Mathsoft, Seattle, Washington, USA.

Mauser, D. M., and R. L. Jarvis. 1991. Attaching radio-transmitters to 1-day-old mallard ducklings. Journal of Wildlife Management 55:488–491.

Mauser, D. M., R. L. Jarvis, and D. S. Gilmer. 1994. Survival of radio-marked mallard ducklings in northeastern California. Journal of Wildlife Management 58:82–87.

Mech, L. D. 1983. Handbook of animal radio-tracking. University of Minnesota, Minneapolis, USA.

Miller, L. D., M. Unverferth, K. Ghormely, and M. Skrdla. 1990. A guide to MIPS, Map and Image Processing System. MicroImages, Lincoln, Nebraska, USA.

National Oceanic and Atmospheric Administration. 1988–1994. Climatological data: North Dakota and Minnesota, monthly summaries. National Climatic Data Center, Asheville, North Carolina, USA.

Nelson, R. D. 1989. Seasonal abundance and life cycles of chironomids (Diptera:Chironomidae) in four prairie wetlands. Dissertation, North Dakota State University, Fargo, USA.

Orthmeyer, D. L., and I. J. Ball. 1990. Survival of mallard broods on Benton Lake National Wildlife Refuge in northcentral Montana. Journal of Wildlife Management 54:62–66.

Perret, N. G. 1962. The spring and summer foods of the common

mallard (*Anas platyrhynchos platyrhynchos* L.) in south central Manitoba. Thesis, University of British Columbia, Vancouver, Canada.

Pietz, P. J., D. A. Brandt, G. L. Krapu, and D. A. Buhl. 1995. Modified transmitter attachment method for adult ducks. Journal of Field Ornithology 66:408–417.

Pietz, P. J., G. L. Krapu, D. A. Brandt, and R. R. Cox Jr. 2003. Factors affecting gadwall brood and duckling survival in prairie pothole landscapes. Journal of Wildlife Management 67:564–575.

Reynolds, R. E., T. L. Shaffer, R. W. Renner, W. E. Newton, and B. D. J. Batt. 2001. Impact of the Conservation Reserve Program on duck recruitment in the U.S. Prairie Pothole Region. Journal of Wildlife Management 65:765–780.

Rotella, J. J., and J. T. Ratti. 1990. Use of methoxyflurane to reduce nest abandonment of mallards. Journal of Wildlife Management 54:627–628.

Rotella, J. J., and J. T. Ratti. 1992*a*. Mallard brood movements and wetland selection in southwestern Manitoba. Journal of Wildlife Management 56:508–515.

Rotella, J. J., and J. T. Ratti. 1992*b*. Mallard brood survival and wetland habitat conditions in southwestern Manitoba. Journal of Wildlife Management 56:499–507.

Salyer, J. W. 1962. A bow-net trap for ducks. Journal of Wildlife Management 26:219–221.

SAS Institute, Inc. 1990. SAS/STAT user's guide. Version 6. Fourth edition. SAS Institute, Cary, North Carolina, USA.

SAS Institute, Inc. 1996. SAS/STAT software: changes and enhancements through release 6.11. SAS Institute, Cary, North Carolina, USA.

Seber, G. A. F. 1982. The estimation of animal abundance and related parameters. Second edition. Macmillan, New York, New York, USA.

Sharp, D. E., and J. T. Lokemoen. 1987. A decoy trap for breeding-season mallards in North Dakota. Journal of Wildlife Management 51:711–715.

Stewart, R. E., and H. A. Kantrud. 1971. Classification of natural ponds and lakes in the glaciated prairie region. U.S. Fish and Wildlife Resource Publication 92, Washington, D.C., USA.

Talent, L. G., R. L. Jarvis, and G. L. Krapu. 1983. Survival of mallard broods in south-central North Dakota. Condor 85:74–78.

Weller, M. W. 1956. A simple field candler for waterfowl eggs. Journal of Wildlife Management 20:111–113.

Will, G. F. 1946. Tree-ring studies in North Dakota. North Dakota Agricultural Experiment Station Bulletin 338, North Dakota Agricultural College, Fargo, USA.

Associate Editor: Barker.

Appendix. Candidate models and associated Akaike's Information Criterion adjusted for small sample size (AIC$_c$) information for mallard duckling survival in prairie pothole landscapes of eastern North Dakota, USA. An X under the term indicates it was included in the candidate model.

| Model rank | Model terms[a] | | | | | | | | | ΔAIC$_c$ | ω_i |
	WETSEAS	HATCH	AGE	TMIN	RAIN	AGE×TMIN	AGE×RAIN	TMIN×RAIN	3-way		
1	X		X	X						0.0	0.1523
2	X		X	X	X	X	X			0.47	0.1202
3	X		X	X	X			X		0.71	0.1067
4	X		X	X		X				1.28	0.0805
5	X	X	X	X						1.30	0.0796
6	X		X	X	X		X	X		1.60	0.0686
7	X		X	X	X	X		X		1.93	0.0581
8	X	X	X	X	X	X	X			2.05	0.0546
9	X	X	X	X	X			X		2.13	0.0526
10	X		X	X	X	X	X	X		2.60	0.0415
11	X	X	X	X		X				2.83	0.0369
12	X	X	X	X	X		X	X		2.90	0.0358
13	X	X	X	X	X	X		X		3.62	0.0250
14	X		X	X	X	X	X	X	X	4.15	0.0192
15	X	X	X	X	X	X	X	X		4.20	0.0187
16	X	X	X							4.51	0.0160
17	X	X	X		X		X			4.98	0.0126
18	X	X	X	X	X	X	X	X	X	5.65	0.0090
19	X		X							6.75	0.0052
20	X		X		X		X			7.58	0.0034
21	X			X						9.38	0.0014
22	X	X		X						10.26	0.0009
23	X		X	X				X		10.38	0.0009
24	X	X		X	X			X		11.44	0.0005
25	X	X								17.16	0.0000
26	X									21.14	0.0000

[a] Model terms: WETSEAS = percent of seasonal wetland basins containing water ($\leq$18% vs. >40%); HATCH = annual date on which first egg hatched; AGE = 0–7 days or 8–30 days; TMIN = average minimum temperature for the current and 2 previous days; RAIN = "1" if it rained (including trace amounts) on the current or 2 previous days, "0" otherwise. Three-way interaction = AGE × TMIN × RAIN.