FACTORS LIMITING MALLARD BROOD SURVIVAL IN PRAIRIE POTHOLE LANDSCAPES

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Abstract: In order to estimate mallard (*Anas platyrhynchos*) production from managed and unmanaged lands, waterfowl biologists need measurable predictors of brood survival. We evaluated effects of percent of seasonal basins holding water (WETSEAS), percent of upland landscape in perennial cover (PERNCOVER), rainfall (RAIN), daily minimum ambient temperature (TMIN), hatch date (HATCHDATE), brood age (BA; 0–7 or 8–30 days), age of brood females, and brood size on mallard brood survival in prairie pothole landscapes, and developed a predictive model using factors found to have significant effects. Sixteen of 56 radiomarked broods experienced total loss during 1,250 exposure days. Our final fitted model of brood survival contained only main effects of WETSEAS, HATCHDATE, and RAIN. Total brood loss during the first 30 days of exposure was 11.2 times more likely for broods hatched on areas with <17% WETSEAS than those on areas with >59% WETSEAS. Total brood loss was 5.2 times more likely during rainy conditions than during dry periods, and the hazard of total brood loss increased by 5% for each 1-day delay in hatching between 17 May and 12 August. High survival of mallard broods in landscapes where most seasonal basins contain water underscores the importance of maintaining seasonal wetlands as a major component of wetland complexes managed for mallard production. Because early hatched broods have higher survival, we also suggest that waterfowl managers focus their efforts on enhancing nest success of early laid clutches, especially in wet years.

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Waterfowl managers need effective and economical means of estimating annual duck production on managed and unmanaged lands in public and private ownership. For mallards, brood survival (measured here by total brood loss) is one of the most critical but least understood components of recruitment (i.e., production of fledged young [Johnson et al. 1992]). We sought to identify key factors influencing brood survival and to develop a model that could serve to predict brood survival rates. We focused our research on sites in the Prairie Pothole Region (PPR), the principal breeding grounds of mallards in North America (Anderson and Henny 1972).

We selected environmental factors to study using clues or questions raised by previous research and taking into consideration ease of measurement. Past studies indicate that the ratio of immature:adult mallards in the harvest is positively correlated with number of ponds in the PPR (Crissey 1969), and that brood survival is related to wetland density (Rotella and Ratti 1992). Fragmentation of perennial cover is known to be a major cause of low nest success in mallards and other dabbling ducks (Greenwood et al. 1995), but little is known about its possible effects on brood survival. Percent of upland landscape in perennial cover varies spatially across the PPR due to topography, soils, conservation programs, and other factors.

Although there is little information on the influence of weather on total brood loss in mallards, inclement weather has been shown to lower survival of canvasback (*Aythya valisineria*) ducklings (Korschgen et al. 1996) and probably affects duckling survival of many other species, either directly or indirectly (Johnson et al. 1992). Mallard mortality is greater in younger ducklings (Ball et al. 1975, Talent et al. 1983, Orthmeyer and Ball 1990, Rotella and Ratti 1992) and increases with hatch date (Orthmeyer

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and Ball 1990, Rotella and Ratti 1992, Dzus and Clark 1998). Older, more experienced females may be more attentive to broods, thus improving their chances of survival. Brood size also might affect brood survival rates if larger broods are less likely to suffer total loss through attrition.

In short, several biotic and abiotic factors may influence survival of mallard broods. Our objective was to identify factors affecting survival of mallard broods in prairie pothole landscapes that managers could easily measure and use to predict brood survival rates. We developed a model that included such factors but also included other less-easily measured variables in order to control for their effects. Specifically, we evaluated effects of water conditions, upland cover, ambient temperature, rainfall, hatch date, brood age, age of brood female, and brood size on mallard brood survival.

STUDY AREAS

We monitored radio-equipped female mallards and their broods on 7 51-km^2 circular plots located in 3 glacial landforms in the PPR (Table 1). Study areas 1 and 2 were located in dead-ice moraine in the Missouri Coteau near Kulm in south-central North Dakota (1988–91, 1993–94), and study areas 3 and 4 were on the glaciated drift plain near Jamestown in eastern North Dakota (1988, 1990–92, 1994; Bluemle 1977); study areas 5–7 were in terminal and ground moraine in west-central Minnesota near Detroit Lakes (1988–91; Leverett 1932).

Most land in the study areas was privately owned; public land was limited primarily to scattered Waterfowl Production Areas (WPAs) owned and managed by the U.S. Fish and Wildlife Service. Uplands on study areas were used largely for production of cereal grains, row crops, hay, and livestock grazing. Proportions of landscapes in cropland and grassland varied widely among sites (Table 1). Wetland basins included temporary, seasonal, semipermanent, and lake classes (Cowardin et al. 1988), which are nearly equivalent to classes II–V of Stewart and Kantrud (1971). Number and area of wetland basins varied among study areas, both within and among classes (Table 1).

METHODS

Field Procedures

In 1988–91, we captured female mallards from mid-April through early May with decoy-hen traps (Sharp and Lokemoen 1987). We fitted each female with a 23-g harness transmitter (Dwyer 1972) and a uniquely identifiable combination of nylon nasal markers (Lokemoen and Sharp 1985). We monitored females daily to assess nesting activity (Krapu et al. 1997). At nest sites of marked females, we captured all ducklings in the brood when possible, attached web tags following a procedure modified from Haramis and Nice (1980), and attached 2-g radiotransmitters using sutures and glue to 1–4 randomly selected ducklings per brood.

In 1992–94, we located nests by systematic searching on privately owned Conservation Reserve Program (CRP) fields and WPAs. Nest searching was conducted by dragging a chain between vehicles to flush females 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 females. We fitted each captured female with a 4-g anchor transmitter (Pietz et al. 1995) and a unique combination of nasal markers. After marking, we anesthesized females with methoxyflurane to reduce the risk of nest abandonment (Rotella and Ratti 1990). We web-tagged all ducklings and marked 1–4 (usually 2) ducklings per brood with 1.5–1.8-g anchor transmitters modified from Mauser and Jarvis (1991). All capture and marking procedures were approved by the Animal Care and Use Committee at Northern Prairie Wildlife Research Center and conformed to recommendations of the American Ornithologists' Union (1988).

Maximum ranges of female and duckling transmitters to ground-tracking vehicles were 2–3 km and 1.5 km, respectively. Radios were equipped with mortality sensors (mercury switches or thermistors); we attempted to retrieve carcasses as soon as possible after mortality signals were detected.

We tracked each brood from nest to wetland, then attempted to visually check broods daily to detect losses of unmarked ducklings and radio failures. If no visual sightings were obtained, we recorded the brood location and radio status using standard telemetry methods (Mech 1983). We aerially searched for missing broods (Gilmer et al. 1981) weekly.

Explanatory Variables

Landscape Variables.—The National Wetland Inventory (NWI) delineated upland and wetland habitats on our study areas from high-altitude color-infrared photographs prior to our study. Land cover on each study area was documented using aerial videography beginning in May 1988 and status was updated in the database annually. We calculated percent of upland in perennial cover (PERNCOVER: native grasslands, planted cover, alfalfa hayland, woodlands, shrub lands, odd areas, and road right-of-ways) on each study area. We classified each wetland basin by the most permanent water regime assigned to part or all of that basin (temporary, seasonal, semipermanent, and lake) by the NWI (Cowardin et al. 1979, 1982). Using aerial videography (Cowardin et al. 1988), we estimated water conditions on each study area at monthly intervals from May to September. Ponds were defined as basins that contained water (Cowardin 1982) and were categorized according to basin class (e.g., water within a basin with a seasonally flooded water regime was termed a seasonal pond). We delineated inundated portions of wetland basins (i.e., pond size) using the feature–mapping process from Map and Imaging Processing System software (MIPS; Miller et al. 1990).

We evaluated the relation between water conditions and brood survival using relative abundance of seasonal ponds. We chose percent of seasonal basins with water as an explanatory variable because (1) seasonal ponds account for most annual variation in number of ponds in prairie pothole habitats (Krapu et al. 1997), (2) seasonal ponds are a preferred habitat of brood-rearing females (Talent et al. 1982), and (3) seasonal ponds can be readily monitored by managers over large areas. We calculated percent of seasonal basins containing ponds (WETSEAS) and used it to assign values to the WETSEAS variable (0 = <17%, 1 = >59%). These WETSEAS categories were used because percent of seasonal basins with ponds did not exceed 17% on study areas in 1988–90 and 1992, but was never lower than 59% on study areas in 1993 and 1994.

Unlike loss of individual ducklings, brood loss (i.e., death of all ducklings in a brood) can occur either in a single catastrophic event (Sargeant et al. 1973) or through attrition over a protracted time span and area. Consequently, we calculated landscape variables over the entire study area, and assigned a value of WETSEAS from the wetland survey date nearest to the hatch date of each brood.

Weather, Hatch Date, Brood Age, Brood Female Age, and Brood Size Variables.—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 1988–94). For each brood exposure day, we calculated (1) RAIN ("1" if it had rained [including values recorded as "trace"] on the current or 2 previous days and "0" otherwise); and (2) TMIN (the average of daily minimum temperatures for the current and the 2 previous days). We included any rainfall events that had occurred in the 2 previous days to allow for some lag time between rainfall and mortality (Korschgen et al. 1996) and a possible delay of ≤1 day in detecting a brood loss. The HATCHDATE was the Julian date on which the first egg of a clutch hatched. Brood age (BA) was designated as 0–7 or 8–30 days. We determined age (second-year [SY] or after-second-year [ASY]) of brood females using the greater secondary covert (Krapu et al. 1979). Brood size was the number of ducklings that hatched in each brood.

Data Analysis

To evaluate brood survival, we used data from broods with radiomarked adult females. We used Cox (1972) proportional hazards regression (PROC PHREG; SAS Institute 1996) to test for differences in brood survival to 30 days of age in relation to TMIN (time-dependent, continuous), RAIN (time-dependent, binary), HATCHDATE (continuous), BA (time-dependent, binary), PERNCOVER (continous), WETSEAS (binary), female age (binary), and brood size (continuous). Prior to performing this analysis, we tested for colinearity between HATCHDATE and brood size (PROC CORR; SAS Institute 1990) and found none ($r = -0.06$, $P = 0.66$). We specified BA as a time-dependent variable by resetting the time origin for each brood to 0 at day 8 of life. Our fully specified model included all main effects and 2-way interactions, except WETSEAS-by-BA, WETSEAS-by-RAIN, and all interactions with brood size. We did not include those interactions with WETSEAS because of missing cells. We used backward elimination to delete non-significant

Table 1. Characteristics of 7 51-km² study areas located in eastern North Dakota (ND; MC = Missouri Coteau, DP = Drift Plain) and west-central Minnesota (MN) where radio-equipped mallard broods were monitored during late spring and summer 1988–94. Percentages of study areas in cropland, grassland, and wetland are based on status in May 1988. Number and area of wetland basins on each study area are listed by basin class. Number of radiomarked females hatching broods and number of broods experiencing total loss are identified for each study area.

	Habitat class (%)			No. wetland basins by class[b]				Basin area (ha) by class				Radiomarked females	Total brood loss
Study area[a]	Crop	Grass	Wet	T	S	SP	L	T	S	SP	L	(*n*)	(*n*)
ND-MC													
1	34	34	19	531	689	130	2	98	275	562	17	22	4
2	55	17	13	169	203	111	2	116	181	337	18	1	1
ND-DP													
3	64	5	13	513	371	35	1	115	201	339	1	22	4
4	58	10	18	768	258	99	1	149	170	463	123	1	0
Krap MN													
5	62	5	17	270	292	133	9	55	110	272	451	2	2
6	64	5	11	205	321	137	31	64	225	190	252	1	0
7	49	10	14	218	315	156	38	45	78	207	354	7	5

[a] Study area locations: 1 (46°27′N, 98°56′W); 2 (46°11′N, 98°53′W); 3 (47°11′N, 98°40′W); 4 (46°43′N, 98°06′W); 5 (46°59′N, 96°12′W); 6 (46°55′N, 96°02′W); 7 (46°51′N, 96°13′W).

[b] Wetland basin classes: temporary (T), seasonal (S), semipermanent (SP), and lake (L) after Cowardin et al. (1988). Class of each wetland basin was obtained from digitized maps of study areas prepared by the U.S. Fish and Wildlife Service National Wetland Inventory (NWI) with wetland classification based on water regime (Cowardin et al. 1979). Basin class is named after the most permanent water regime present within the basin and neither class nor area changed among years.

($P > 0.05$) terms, beginning with the interactions. We considered all ducklings in a brood dead when no ducklings remained with the female, as determined by observations, or when erratic female movements indicated no affinity to any wetland. When the exact date of brood loss was unknown, we assigned loss at the midpoint of the interval between the last time the female was seen with a brood and the first time she was seen without a brood or exhibited erratic movements. We censored surviving broods on the date they were last observed alive or day 30 of life. To test for possible effects of duckling radiotransmitters on brood survival, we included a binary explanatory variable identifying whether or not broods contained ≥1 radiomarked ducklings in our final model.

RESULTS

Across study areas and years, seasonal ponds accounted for 91% of the variation in total pond numbers during May ($F_{1,26} = 239.0$, $P < 0.0001$), 97% during June ($F_{1,30} = 831.5$, $P < 0.0001$), and 94% during July ($F_{1,29} = 446.6$, $P < 0.0001$). All ducklings in 16 of 56 broods died during 1,250 exposure days (Table 1). We did not detect effects of TMIN, BA, PERNCOVER, age of brood female, brood size, or any interactions on survival ($P > 0.05$). Further, we did not detect an effect of radiotransmitters on brood survival ($P = 0.68$). Our final fitted model of brood survival contained main effects of WETSEAS (Wald $\chi^2_1 = 13.16$, $P = 0.0003$), HATCHDATE (Wald $\chi^2_1 = 7.40$, $P = 0.007$), and RAIN (Wald $\chi^2_1 = 5.79$, $P = 0.02$). Total brood loss during the first 30 days of exposure was 11.2 (95% CI = 3.0–41.4) times more likely for broods hatched on areas with <17% WETSEAS than those on areas with >59% WETSEAS (Fig. 1A). Total brood loss was 5.2 times (95% CI = 1.4–19.6) more likely during rainy conditions than during dry periods (Fig. 1B) and the hazard of total brood loss increased by 5.0% (95% CI = 1.4–8.7) for each 1-day delay in hatching between 17 May and 12 August (Fig. 1C).

DISCUSSION

We did not include study area or year as explanatory variables in our survival analysis because (1) we wanted our predictive model to generalize beyond the particular areas and years of our study; and (2) effects of certain landscape variables, primarily PERNCOVER and WETSEAS, were partially or totally confounded with effects of study area and year. For example, WETSEAS represents a contrast between dry years (1988–92) and wet years (1993–94). We caution readers that other factors may have contributed to (or worked against) the WETSEAS effect that we observed. However, we feel confident that explanatory variables included in our analyses captured the most important differences among study areas and years with respect to mallard brood survival.

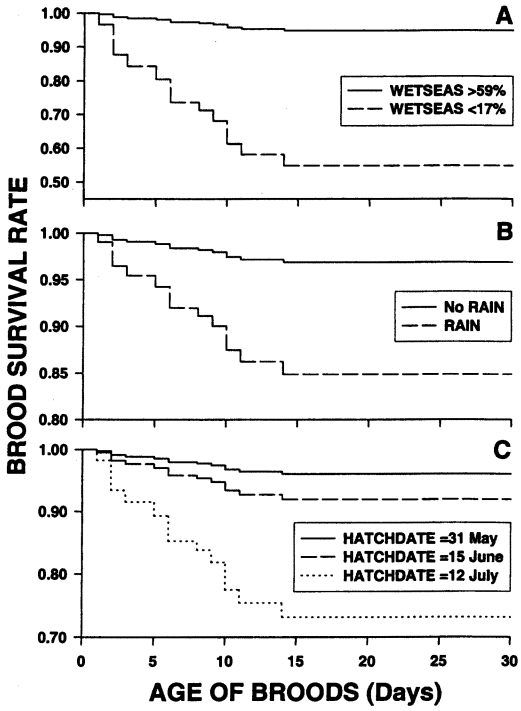

Fig. 1. Predicted 30-day survival rates of mallard broods from proportional hazards regression model in relation to variation in (A) percent seasonal basins with ponds (WETSEAS), (B) rainfall (RAIN), and (C) hatch date (HATCHDATE) in prairie pothole landscapes in North Dakota and west-central Minnesota, 1988–94. For each variable shown, we held remaining explanatory variables constant at their mean values. Levels of HATCHDATE represent 10th percentile, median, and 90th percentile based on exposure days of mallard broods in our sample.

Effect of Seasonal Ponds

Female mallards prefer seasonal ponds during nesting (Krapu et al. 1997), which concentrates pairs (Johnson and Grier 1988) and nests (Greenwood et al. 1995) where spring pond densities are highest in the species' primary range in the PPR. In areas where nest success rates or renesting efforts also are high, broods will be more numerous and, based on our findings, survive at higher rates when seasonal ponds are plentiful in late spring and summer. Percent of landscape in perennial cover did not affect brood survival. However, because nest success rate varies with percent of landscape in perennial cover (Greenwood et al. 1995), brood density would be expected to vary with percent of perennial cover, if other factors are equal.

Several factors probably contribute to higher survival of mallard broods when seasonal ponds are abundant. Ducklings, when in seasonal ponds, are less vulnerable to aquatic predators that prefer permanent water. Mink (*Mustela vison*), the most effective predator of ducklings and other neonatal waterbirds (Sargeant et al. 1973, Talent et al. 1983, Eberhardt and Sargeant 1977, Arnold and Fritzell 1990, Korschgen et al. 1996) and the most frequently identified cause of mortality among radiomarked ducklings in our study (G. Krapu, unpublished data), are dependent on wetland-derived prey for survival (Eberhardt 1974). Mink avoid temporary and seasonal ponds and dry basins (Arnold and Fritzell 1990), reproduce poorly during drought (Eberhardt 1974), and rely on permanent water to survive severe drought (Sargeant et al. 1993). As a result, in landscapes lacking permanent water, few mink remain at the end of severe droughts, and mink populations presumably require several years to recover and become a major cause of duckling mortality. Our study was conducted during and immediately following a major drought and brood survival was exceptionally high in the wet years (>90%). It is not known for how many years high brood survival can be maintained under continued wet conditions in areas where mink are present. Current knowledge of habits of mink and mallard broods would suggest that brood survival would remain relatively high until the first summer that broods are confined largely to semipermanent and permanent water. However, further investigation is warranted to determine the extent to which mink might expand into habitats classified as seasonal that take on more permanent water regimes during extended wet periods. Because wet conditions occurred following an extreme drought on our study areas, our model might over predict brood survival when high levels of WETSEAS are present during prolonged wet periods.

Water conditions also affect food availability for mallard broods. Duckling growth and survival varies with macroinvertebrate availability (Cox et al. 1998), which increases (on a landscape scale) as seasonally flooded pond habitat becomes more abundant (Neckles et al. 1990). During the first 2 weeks after hatch, mallard ducklings feed primarily on macroinvertebrates (Chura 1961, Perret 1962). When invertebrates are scarce, ducklings spend more time feeding, move more, and have lower rates of food intake (Hunter et al. 1984, Hill et al. 1987). As a result, starvation and predation probably increase, lowering duckling and brood survival.

Effect of Rainfall

Higher mortality of mallard broods during rainy periods may result, in part, because young must be brooded more or risk dying from exposure. Reduced feeding time may result in more rapid depletion of energy reserves, and could lead to duckling hypothermia, starvation, or greater susceptibility to predation. Also, availability of invertebrates at the water surface where young mallard ducklings feed, and in particular, emerging chironomid larvae, a key food (Chura 1961), may be depressed during periods of adverse weather (Nelson 1989). Canvasback ducklings in northwestern Minnesota were particularly susceptible to rain during cold periods (Korschgen et al. 1996). Energy required to maintain homeothermy by ducklings during cold conditions is influenced by ambient temperature, wind velocity, and humidity among other factors (Bartholomew 1982). Rainfall may influence the relative importance of these factors, and the amount of energy required for homeothermy, if ducklings become wet. Further research is needed to understand how environmental factors interact to influence homeothermic costs to ducklings, particularly in natural situations where ducklings are brooded.

Effect of Hatch Date

Higher survival of early hatched mallard broods probably results, in part, from greater availability of seasonal ponds during late spring and early summer. However, Rotella and Ratti (1992), Dzus and Clark (1998), and this study documented an effect of hatch date after controlling for temporal declines in ponds during the breeding season. The cause of a residual effect of hatch date on brood survival is unknown but might be caused, in part, by growing dependence on local food resources by females to meet energetic needs as fat reserves are depleted (Krapu 1981), leading to these females being less responsive to the needs of young. When water conditions are poor early in the season but much better late, mallard duckling survival is higher late in the season (Dzus and Clark 1998), presumably linked to lower predation rate and better nutrition.

Despite higher survival of early hatched mallard broods, poor success of early nests (Greenwood et al. 1995) results in disproportionately fewer early than late hatched mallard broods in the PPR. As a result, a tradeoff exists between nesting early (low nest success, high brood survival) versus late (high nest success, low brood survival). This tradeoff probably has intensified over the past 60 years as mallard nest success has declined in the PPR (Beauchamp et al. 1996) with increasing habitat fragmentation from agricultural development (Bethke and Nudds 1995, Krapu et al. 1997). Higher survival to fledging of early hatched broods probably explains, in part, why early nesting has remained adaptive in the mallard despite a lower success rate of early laid clutches.

MANAGEMENT IMPLICATIONS

Waterfowl managers can use our final fitted model as a tool for predicting mallard brood survival in the PPR. Using tables available from the authors or at http://www.npwrc.usgs.gov/resource/broodsrv/broodsrv.htm, managers can obtain predicted brood survival rates and associated standard errors for various levels of WETSEAS, HATCHDATE, and RAIN. The WETSEAS can be estimated or indexed through use of satellite imagery, videography taken from aircraft (Strong and Cowardin 1995), or ground surveys. Brood survival predictors identified in this paper also are being incorporated into a mallard productivity model (Johnson et al. 1987) to improve reliability of mallard recruitment estimates.

The positive relation between WETSEAS and mallard brood survival underscores the need to conserve seasonal wetlands, or where drained, restore seasonally flooded water regimes as a major component of wetland complexes managed for dabbling duck production. Higher survival of early hatched broods suggests management efforts be directed toward improving success of early nests where feasible. Managers may achieve higher nest success by maintaining a high proportion of landscape in perennial cover (Greenwood et al. 1995) through permanent grassland easements, CRP, and other methods. Where adequate perennial cover cannot be maintained, managers may improve nest success by reducing predator numbers (Duebbert and Kantrud 1974), using artificial nesting structures (Doty 1979), or constructing fences (Cowardin et al. 1998) or nesting islands (Giroux 1981) to exclude predators from nesting areas. Management actions that have short-term effects on nesting cover (e.g., spring burning, summer haying) and nest success (e.g., predator removal, maintenance of exclosures) impact recruitment on an absolute basis much more in years when seasonal ponds are plentiful and brood survival

is high. We therefore recommend that managers attempt to schedule activities with potentially deleterious, short-term effects on nesting success, such as burning and haying, until after nesting is completed in years when a high proportion of seasonal wetlands contain water.

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MODELING ANNUAL MALLARD PRODUCTION IN THE PRAIRIE–PARKLAND REGION

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Abstract: Biologists have proposed several environmental factors that might influence production of mallards (*Anas platyrhynchos*) nesting in the prairie–parkland region of the United States and Canada. These factors include precipitation, cold spring temperatures, wetland abundance, and upland breeding habitat. I used long-term historical data sets of climate, wetland numbers, agricultural land use, and size of breeding mallard populations in multiple regression analyses to model annual indices of mallard production. Models were constructed at 2 scales: a continental scale that encompassed most of the mid-continental breeding range of mallards and a stratum-level scale that included 23 portions of that same breeding range. The production index at the continental scale was the estimated age ratio of mid-continental mallards in early fall; at the stratum scale my production index was the estimated number of broods of all duck species within an aerial survey stratum. Size of breeding mallard populations in May, and pond numbers in May and July, best modeled production at the continental scale. Variables that best modeled production at the stratum scale differed by region. Crop variables tended to appear more in models for western Canadian strata; pond variables predominated in models for United States strata; and spring temperature and pond variables dominated models for eastern Canadian strata. An index of cold spring temperatures appeared in 4 of 6 models for aspen parkland strata, and in only 1 of 11 models for strata dominated by prairie. Stratum-level models suggest that regional factors influencing mallard production are not evident at a larger scale. Testing these potential factors in a manipulative fashion would improve our understanding of mallard population dynamics, improving our ability to manage the mid-continental mallard population.

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Biologists have long known that wetland conditions on the breeding grounds may influence mallard populations. Crissey (1969) suggested that territorial behavior of male ducks on spring wetlands may limit nesting sites, leading to a positive correlation between size or production of mallard populations and the abundance of spring wetlands. Duckling survival may also be higher in areas with high wetland density, if

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