Factors associated with Autumn rearing of duck broods in temperate North America

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Dabbling ducks Genus Anas *occasionally nest during mid- and late summer in the Prairie Pothole Region (PPR) of midcontinent North America but little information is available on their Autumn-reared broods or those of other duck genera. Densities, species composition, and wetland habitat use by Autumn reared duck broods (age classes I and II) were determined on randomly distributed transects on a 3,735 km^2 study area in eastern North Dakota. Brood densities (±SE) averaged 0.38±0.08, 0.30±0.08 and 0.23±0.10 broods km^{-2} during 1993-95 with dabbling ducks accounting for 70, 44, and 9%, and diving ducks 30, 54, and 91% of sighted broods. The principal species were Blue-winged Teal* Anas discors, *21%; Gadwall* A. strepera, *11%; Mallard* A. platyrhynchos, *7%; Redhead* Aythya americana, *13%, and Ruddy Duck* Oxyura jamaicensis, *35%. Of Blue-winged Teal and Mallard broods, 67% of each were located on seasonal ponds, and 50, 56, and 59% of Gadwall, Redhead and Ruddy Duck broods were on semi-permanent ponds. Interspecific variation in numbers of Autumn-reared broods resulted, in part, from intrinsic differences among species in capacity to nest during mid- and late summer. Survival of thousands of class I and II dabbling duck broods to mid-September during 1993-94 probably resulted from a combination of factors including an abundance of seasonal ponds, low rainfall, and limited cold weather through mid-September when brood surveys were conducted. Redheads and Ruddy Ducks do not terminate breeding under long daylengths in late spring so summer nesting accounts for a much larger portion of the annual nesting effort than in dabbling ducks except under drought conditions when ducks generally terminate reproduction by mid-spring.*

Key Words: *Anas discors, A. platyrhynchos, A. strepera, Aythya americana,* Autumn, *Oxyura jamaicensis*, Prairie Pothole Region, precipitation, temperature, wetland use.

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Dabbling duck species breeding in temperate regions of the Northern Hemisphere generally terminate nesting by early summer (Murton & Kear 1976). However, recent studies in the Prairie Pothole Region (PPR) in the north-central United States have shown that occasionally some species of dabbling ducks continue to nest during mid- and late summer (Krapu 2000). Summer breeding by ducks results in their broods being reared during the Autumn, a period for which virtually no information has been collected on duck brood ecology. Insight into Autumn brood ecology in dabbling ducks and other waterfowl genera is needed to gain a better understanding of factors influencing reproductive cycles of temperate-breeding waterfowl. Therefore, duck brood surveys were undertaken during mid- to late September of three wet years, 1993-95, to gain a better understanding of Autumn brood ecology. Specifically, our objective was to determine densities of Autumn-reared duck broods, species composition, types of wetland habitats used, and to evaluate factors responsible for the presence of duck broods during the autumn in North Dakota.

Methods

Study Area

The 3,735 km^2 study area was located in Stutsman and Barnes counties of eastern North Dakota (**Figure 1**), within stratum 46 of the U.S. Fish and Wildlife Service breeding waterfowl survey (Smith 1995). The western 25% of the study area was within the Missouri Coteau and the remainder was glaciated drift plain (Bluemle 1977). Land use in the Missouri Coteau was dominated by production of livestock and annual crops with the proportion in cropland varying from about 35 to 85% (Krapu *et al.* 1997). Land use in the drift plain was mostly cropland (>80%), with perennial cover consisting principally of introduced perennial grasses and legumes established under the Conservation Reserve Program (Kantrud 1993). Native grassland on the drift plain was limited primarily to areas too steep, rocky, or wet to cultivate and was used mostly for livestock grazing. The landscapes retain high densities of wetlands (Kantrud *et al.* 1989).

Brood transects

The study area was divided into 30 plots of similar size (**Figure 1**), each encompassing an area of about 13.7 km by 9.4 km and corresponding to a 1:24,000 U.S. Geological Survey 7.5-minute quadrangle map. One plot was dropped when inspection revealed most of the area was covered by a large reservoir. For each plot, a 19.4 x 0.4 km transect (0.2 km on each side of the road) was established within the existing road system. Transects were randomly located as was the order in which transects were surveyed. The following protocol was used to determine transect route: (1) the corner of origin within the plot was determined

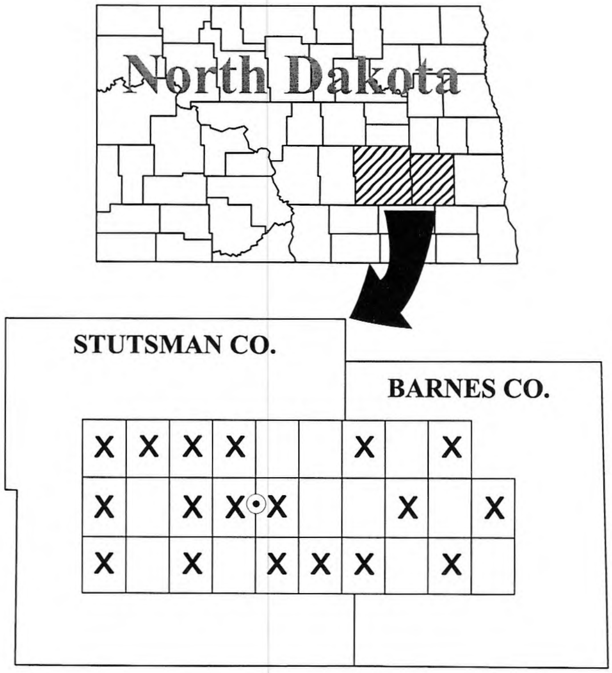

Figure 1. The 3,735 km^2 study area in Stutsman and Barnes counties of eastern North Dakota is located in the north-central United States. Each of the 18 randomly selected plots containing a transect in which flightless duck broods were surveyed during September 1993-95 is identified by an X. The location of Jamestown, North Dakota on the study area is indicated by a circled dot.

by a coin toss. The starting point for each transect was at the milepost starting in the first driveable mile on a route that would allow for 19 continuous km. If a corner did not allow for a 19-km route, the coin was tossed again. (2) At each intersection where alternate choices existed, a coin toss was again employed to determine the route taken. The survey route and area to be surveyed were drawn on National Wetlands Inventory maps to assist brood surveyors in determining transect boundaries. High water levels in ponds and loss of foliage from frost and senescence provided excellent visibility of broods during fall 1993-95. Numbers and areas (ha) of wetland basins on the 18 surveyed transects were as follows: temporary, 1,116 (241); seasonal, 1,265 (746); semipermanent, 228 (421); and lake, 12 (66).

Description of brood surveys

Brood surveys were conducted on the first 18 transects randomly drawn from the 29 available; number of transects surveyed was determined by number of trained personnel available to assist. The area surveyed totalled

Table 1. Estimated number of May and July ponds in stratum 46 of the Annual Breeding Pair and Pond Survey conducted by the U.S. Fish and Wildlife Service (U.S. Fish and Wildlife Service, unpublished data). Estimated sizes of breeding populations of Blue-winged Teal (BWTE), Mallard (MALL), Gadwall (GADW), Northern Pintail (NOPI), Northern Shoveler (NSHO), Redhead (REDH) and Ruddy Duck (RUDU) in stratum 46 during 1992-94 (Smith 1995) and 1995 (U.S. Fish and Wildlife Service, unpublished data).

	Number of ponds		Breeding population size (in thousands)						
Year	May	July[a]	BWTE	MALL	GADW	NOPI	NSHO	REDH	RUDU
1992	47,878 ± 3,327	44,612	88	76	85	24	29	9	7
1993	162,997 ± 16,261	174,442	109	118	115	60	82	53	21
1994	275,532 ±20,381	156,407	437	306	149	137	214	61	31
1995	347,970 ±21,986	260,292	468	321	233	135	162	82	28

[a]Standard errors are not available for July surveys due to lack of error estimates.

140 km^2 with surveys conducted on 20-21 September 1993, 14-15 September 1994, and 13-14 September 1995. Surveys began at about 0800hr and continued until completed. All wetlands and parts of wetlands within transects that were visible from roads were surveyed for broods. For each brood sighted, surveyors recorded species, age, and wetland basin type. Wetland basin classes were temporary, seasonal, semipermanent, or lake (Cowardin *et al.* 1988), which approximate classes II-V of Stewart & Kantrud (1971). Only broods of age classes I and II were considered to be Autumn-reared with class assigned based on stage of down and feather development (Gollop & Marshall 1954). Brood densities, species composition, and wetland use were calculated from results gained from the 18 transects.

Results

Precipitation, ponds, and breeding pairs

This study followed a five-year drought (1988-92), a period when numbers of May and July ponds and breeding waterfowl were much reduced in stratum 46 in North Dakota (**Table 1**). In 1993, precipitation was below average from January through April (**Figure 2**), continuing in the pattern of the 1988-92 drought, but precipitation increased dramatically on the study area from May through July (**Figure 2**) and annual precipitation exceeded the long-term average of 42.9 cm by 33.8 cm or 79%. Pond numbers generally decline from May to July in the PPR (Crissey 1969), but during 1993 across stratum 46, and including the study area, numbers of ponds increased from May to July (**Table 1**) due to high summer rainfall and associated runoff. During the night of 15-16 July, an 18 cm downpour on the study area triggered a major flood that filled most wetland basins with water and inundated existing emergent vegetation in seasonal and semipermanent wetlands. As a result of the flood, most wetland habitat on the study area had standing water in late July 1993 for the first time following the 1988-92 drought. July pond surveys in stratum 46 in 1993 were completed before the flood and several other large rains so number of July ponds in stratum 46 (**Table 1**) does not represent number of ponds present during the period when most mid- and late summer nests were being initiated. The small increase in number of breeding pairs of ducks from 1992 to 1993 reflects most pairs had settled into their breeding locations before high rainfall made ponds abundant in May-July.

In 1994, precipitation remained near or below average through June but increased sharply in July, a pattern that continued in 1995 (**Figure 2**). In 1994 and 1995, annual precipitation on the study area exceeded the long-term average by 16.5 and 12.1 cm, respectively, with July rainfall responsible for most of the increase in all three years. Above average precipitation caused

Table 2. Species composition and number of Class I and II broods on 18 randomly distributed transects in Barnes and Stutsman counties of eastern North Dakota based on surveys conducted during 20-21 September 1993, 14-15 September 1994 and 13-14 September 1995.

	Number of broods by species and age class						
	Class I			Class II			
Species	1993	1994	1995	1993	1994	1995	**Totals**
Perching duck (Genus *Aix*)							
Wood Duck	0	0	0	0	1	0	**1**
Dabbling ducks (Genus *Anas*)							
Blue-winged Teal	3	0	0	15	8	1	**27**
Mallard	0	0	0	4	5	0	**9**
Gadwall	2	0	1	6	4	1	**14**
Northern Pintail	0	0	0	1	0	0	**1**
Northern Shoveler	0	0	0	0	1	0	**1**
Unknown dabbler	0	0	0	1	0	0	**1**
Pochards (Genus *Aythya*)							
Redhead	2	1	0	2	3	8	**16**
Lesser Scaup	0	0	0	3	1	1	**5**
Stiff-tailed ducks (Genus *Oxyura*)							
Ruddy Duck	0	6	1	7	11	19	**44**
Other							
Unknown diver	0	0	0	1	0	0	**1**
Unknown ducks	2	0	0	4	0	0	**6**
Totals	**9**	**7**	**2**	**44**	**34**	**30**	**126**

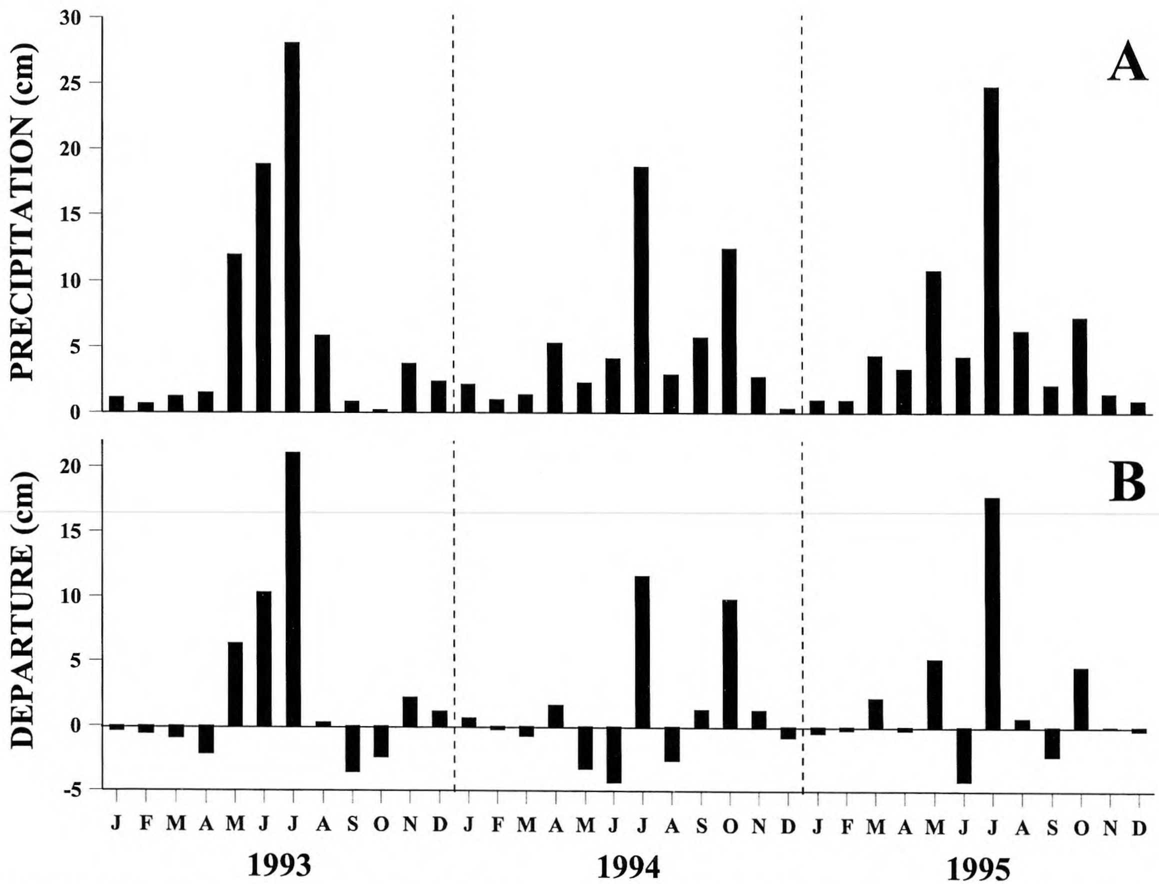

Figure 2. (A) Precipitation (in cm) by month at Jamestown, North Dakota during 1993-95, and (B) Departure of precipitation (in cm) by month from the long-term mean (1940-1992). Precipitation data were collected at the Jamestown Municipal Airport by the Federal Aviation Administration and compiled by the National Oceanic and Atmospheric Administration (1993-95).

many ponds to deepen and enlarge in 1994 and 1995. Numbers of breeding pairs of the principal species of ducks increased in May 1994 from the previous year in stratum 46 but patterns were more variable in 1995 (**Table 1**).

Brood densities

1993: During 20-21 September, 53 broods (age classes I and II) were sighted including 32 of dabbling ducks, 14 of diving ducks (pochards and Ruddy Ducks), and 7 of unidentified species (**Table 2**). Brood density averaged 0.38±0.08 broods km^{-2} (n=18 transects; estimates unadjusted for visibility) or an estimated 1,419 broods for the study area.

1994: During 14-15 September, 41 broods were sighted including 1 of perching ducks (ie a Wood Duck *Aix sponsa*), 18 of dabbling ducks and 22 of diving ducks (pochards and Ruddy Ducks) (**Table 2**). Brood density averaged 0.30±0.08 broods km^{-2} or an estimated 1,121 broods for the study area.

1995: During 13-14 September, 32 broods were sighted including three of dabbling ducks and 29 of diving ducks (pochards and Ruddy Ducks) (**Table 2**). Brood density averaged 0.23±0.10 broods km^{-2} or an estimated 859 broods for the study area.

Species composition of broods

The primary species represented among Autumn-reared broods were Blue-winged Teal (hereafter Teal) (21%), Gadwall (11%), Mallard (7%), Redhead (13%), and Ruddy Duck (35%) (**Table 2**). Dabbling ducks accounted for 70, 44, and 9%, and diving ducks 30, 54, and 91% of duck broods identified to genus during 1993-95, respectively (**Table 2**). Teal, Gadwall, and Mallard accounted for an estimated 51, 26, and 17% of the 53 dabbling duck broods seen on transects in 1993-95 (**Table 2**). Blue-winged Teal accounted for 56, 44, and 33% of the dabbling duck broods sighted in 1993, 1994, and 1995, respectively. Ruddy Ducks, Redheads and Lesser Scaup comprised 68, 25, and 8% of diving duck broods sighted during September surveys in 1993-95 (**Table 2**). Ruddy Ducks accounted for 47, 77, and 69% of diving duck broods during 1993-95.

Species distribution of broods by wetland type

Of the 110 broods of the five principal species sighted on the 18 transects during 1993-95, 47% occurred in seasonal wetlands, 46% were on semi-permanent wetlands, 6% were on temporary wetlands, and 1% were on lakes (**Figure 3**). Teal and Mallards were most often on seasonal ponds and Gadwall, Redhead, and Ruddy Ducks were principally on semipermanent ponds (**Figure 3**).

Discussion

Mid- and late summer nesting by dabbling ducks is limited to years when wetland habitat conditions are excep-

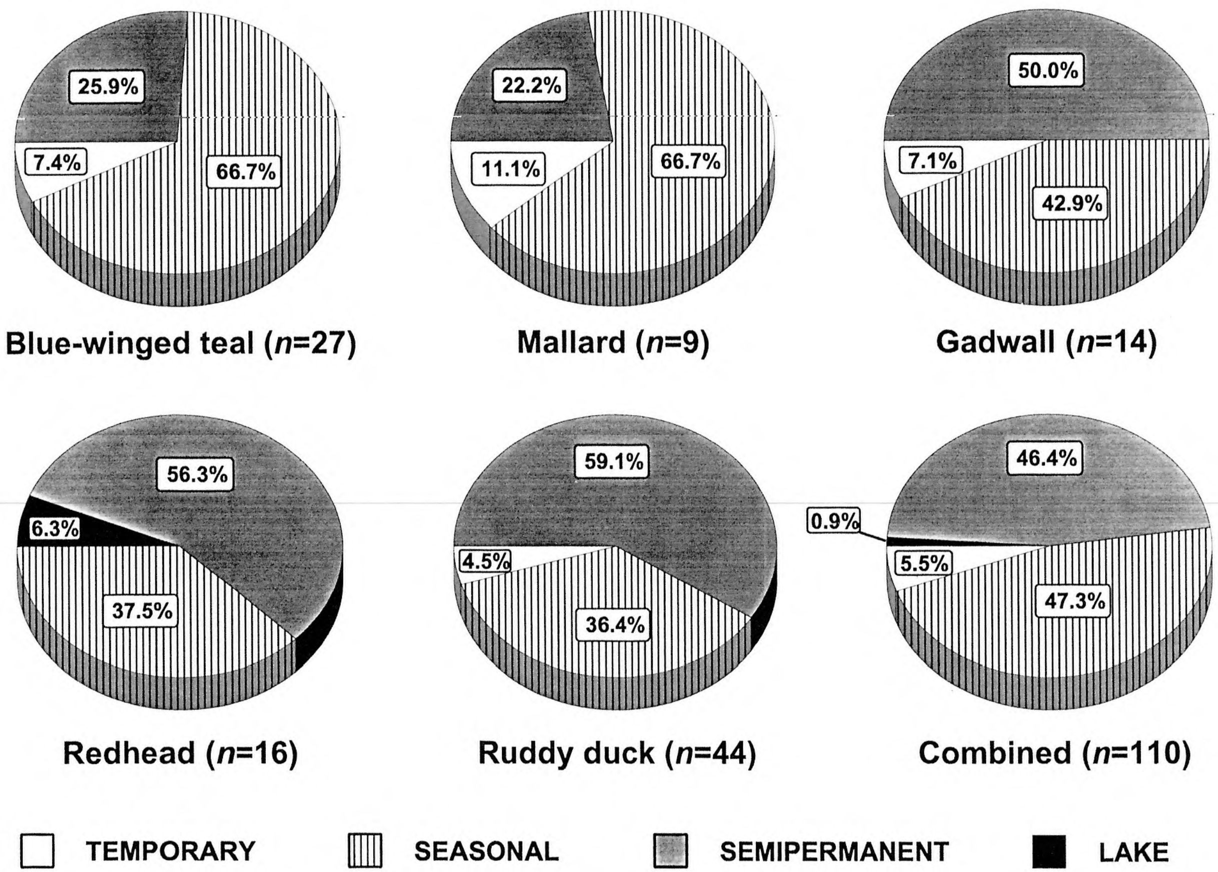

Figure 3. Distribution of Autumn-reared broods of the five principal species of ducks by wetland basin type on 18 randomized transects in Stutsman and Barnes counties of eastern North Dakota during September 1993-95.

tionally favourable for waterfowl breeding. In 1962 and 1993, years when extensive Autumn brood-rearing by dabbling ducks is known to have occurred in North Dakota (Bluhm 1992:343, this study), July floods inundated vast amounts of wetland habitat that had been dry for several years. Inundation of dry basins is conducive to the rapid build-up of detritivorous macroinvertebrates (Euliss *et al.* 1999), which are sought by female dabbling ducks during egg production (Krapu & Reinecke 1992). Clutches laid by several species of dabbling ducks were larger in the late spring and early summer of 1993 than in 1994 and 1995 in North Dakota (G. Krapu, unpublished data) also suggesting high quality food was exceptionally available to female dabbling ducks during late spring and summer in 1993. The low density of breeding dabbling ducks in spring 1993 (**Table 1**) reflects that high precipitation during late May-July (**Figure 2**) came after most settling had occurred and most female dabbling ducks in all three years terminated breeding in late spring (Krapu 2000). As a result, pair densities in summer were low resulting in reduced competition for food and space from spring which may have contributed to exceptional levels of summer nesting by dabbling ducks in 1993.

Species composition of Autumn reared dabbling duck broods resulted, in part, from intrinsic differences among species in capacity to breed through summer. Photic cues are thought to have a major role in controlling timing of refractoriness in dabbling ducks in late spring (Murton & Kear 1976) but their influence might vary among species depending on nutrient constraints faced by females. For example, small Teal body mass reduces maintenance energy requirements which may have contributed to Teal being more flexible physiologically (ie less affected by photo controls than were larger-bodied ducks when wetland conditions were exceptionally favourable in the summer of 1993) resulting in a higher proportion of the Teal population continuing to nest in summer. However, smaller body mass, if contributing to the capacity of a species to breed in summer, does not fully explain relative level of female reproductive effort in summer. Northern Pintails *Anas acuta* and Northern Shovelers *Anas clypeata* (hereafter Shovelers) have smaller body masses than Mallard (Alisauskas & Ankney 1992) but terminate nesting earlier in spring with little apparent nesting in summer (Krapu 2000). Pintails rely on stored lipids for a greater part of their nutrient requirements for reproduction than any other species of temperate-nesting dabbling duck studied (Esler & Grand 1994) and Shovelers have a highly specialised diet (Swanson *et al.* 1979), traits suggesting these species may face greater nutrient constraints when breeding late in the season than Mallards, Gadwalls, and Teals. Further research is needed to more fully examine whether interspecific differences in level of nutrient constraint account for variation in when species of dabbling ducks respond to photic cues by terminating reproduction. Other possible explanations for why numbers of Autumn-reared broods varied among species in patterns encountered include species abundance in spring, timing of onset of nesting, and variation in nest success rates. The number of Teal broods was disproportionately high in 1993 considering the ratio of Teal pairs to Mallard and Gadwall pairs in stratum 46 in May (**Table 1**). This suggests species abundance was not a major influence. Mallards in the PPR begin nesting early at about the same time as Pintails but continue to nest later in spring than Pintails (Krapu 2000), and based on number of Autumn-reared broods seen, nest more during mid- and late summer. As a result, timing of onset of breeding by a species in spring does not appear to influence relative abundance of broods in summer. Last, nest success rates during 1993-95 did not vary in patterns consistent with Teal, Gadwalls, and Mallards commonly nesting in mid- and late summer nor explain why Pintails and Northern Shovelers *Anas clypeata* did not (Krapu 2000).

Survival of thousands of dabbling duck broods to mid-September in eastern North Dakota during 1993-94 probably was due to a combination of factors including abundance of seasonal water, low rainfall during August and September (**Figure 2**), and minimum ambient temperature remaining relatively high during late summer and early Autumn (**Figure 4**). In North Dakota, survival rate of Mallard broods reared during late spring and summer have been shown to vary with percentage of seasonal wetland basins containing water (Krapu *et al.* 2000). Broods disperse when seasonal ponds are plentiful lowering duckling predation by mink *Mustela vison*, the principal predator of ducklings in North Dakota and west-central Minnesota. Low rainfall during August and September (**Figure 2**) when broods were hatching reduced their vulnerability to exposure when still covered with down. Rain has been identified as an important cause of total brood loss in Mallards during spring and summer (Krapu *et al.* 2000). Minimum daily temperatures dropped to near freezing on two days in mid-September 1993 (**Figure 4**) suggesting that if temperature-related losses occurred, mortality from cold weather may have been highest in 1993 when broods were hatching exceptionally late and more age class I broods were present in September (**Table 2**). Low temperatures during brood-rearing have been identified as an important cause of Canvasback *A. affinis* duckling mortality in late spring and early summer (Korschgen *et al.* 1996).

The increase in numbers of Ruddy Duck broods from 1993 to 1995 probably resulted, in part, from increasing numbers of pairs settling on ponds in eastern North Dakota as hydroperiods lengthened increasing amount of semi-

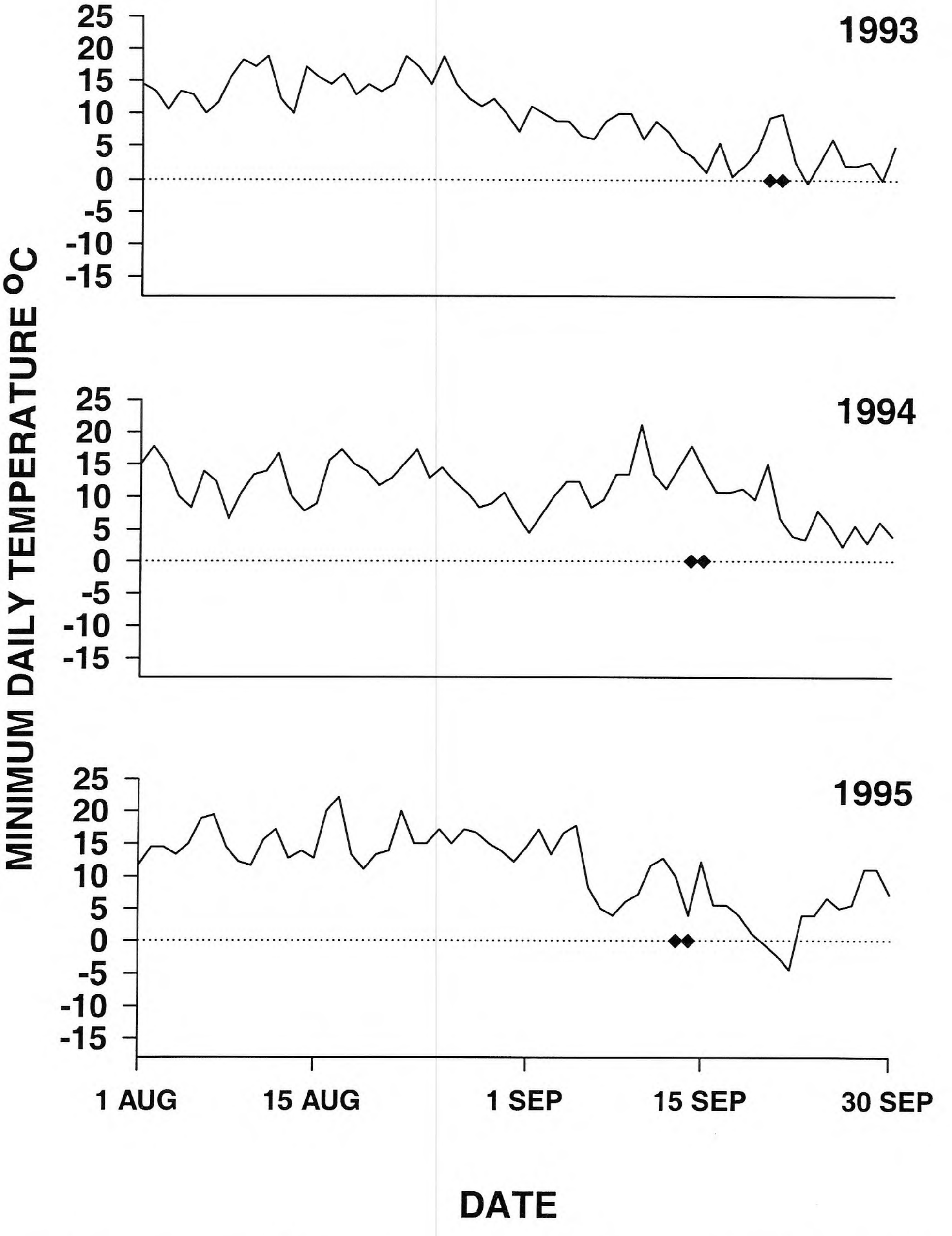

Figure 4. Minimum ambient daily temperatures during 1 August - 30 September, 1993-95 at Jamestown, North Dakota (National Oceanic and Atmospheric Administration 1993-95). Dates that brood surveys were conducted during 1993-95 are indicated by diamond-shaped markers.

permanently flooded wetland habitat. In North Dakota, breeding female Ruddy Ducks typically forage primarily on semi-permanent wetlands while female Redheads forage on both semi-permanent and seasonal ponds (Woodin & Swanson 1989). In years of drought when foraging conditions are poor, Ruddy Ducks terminate nesting in May in the PPR (Alisauskas & Ankney 1994) reflecting that length of breeding varies widely from dry to wet years. The relatively high percentage of Redhead and Ruddy Duck broods using seasonal wetlands during the Autumn of 1993-95 (**Figure 2**) probably reflects, in part, that because of the exceptionally wet summers during 1993-95, many basins classified as having seasonally-flooded water regimes held water throughout the year and developed food resources characteristic of semipermanent ponds.

Mid- and late-summer breeding by dabbling ducks in midcontinent North America involves a small fraction of the annual nesting effort, even in years of peak summer-nesting activity, eg 1993 and 1994, so summer breeding has limited significance to annual production. Among dabbling ducks, summer breeding is probably adaptively significant for Teal because their young only require 35-42 days to fledge, or about 10-20 days less than for Mallards and Gadwall (Bellrose 1980). As a result of Teal requiring less time to fledge, a smaller percentage of their late-hatched young can be expected to remain flightless and die when ponds freeze during the Autumn, than young of species requiring more time to fledge. Redheads and Ruddy Ducks are not responsive to photo cues in late spring as are most dabbling ducks so a higher proportion nest during summer than do dabbling ducks (G. Krapu, unpublished data) except during drought periods when dabbling and diving ducks either terminate breeding early or fail to breed altogether (Bluhm 1992).

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