

FACTORS AFFECTING SURVIVAL OF NORTHERN PINTAIL DUCKLINGS IN ALBERTA¹

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Abstract. We determined brood and duckling survival from 57 radio-marked Northern Pintail (*Anas acuta*) females in southern Alberta during 1994–1996, and related duckling survival to maternal and environmental attributes. Annual brood survival estimates ranged from 72.2% to 88.2%. Brood survival declined with hatch date in all years. Duckling survival was highest in 1994 at 65.2%, but fell to 42.4% and 43.8% in 1995 and 1996, respectively. Duckling mortality was highest during the first 10 days post-hatch in all years. Duckling survival did not vary with female age, or distance from nest to nearest wetland, but did decline throughout the breeding season. Duckling survival was higher for ducklings from larger broods in 1994, but the opposite trend was found in 1995 and 1996.

Key words: *Anas acuta*, brood survival, duckling survival, hatching date, Northern Pintail.

INTRODUCTION

Considerable attention has focused on nesting success of ducks, but much less is known about processes affecting brood-rearing and recruitment (Rotella and Ratti 1992b). Implicit in many studies is the assumption that nesting success is an appropriate measure of reproductive success (Greenwood et al. 1987), but recent evidence reveals much variation in post-hatch survival of ducks (see Grand and Flint 1996 for review). Thus, further work is needed to evaluate sources of variation in duckling survival and to more adequately assess individual reproductive performance. Here, we address this deficiency by looking at brood-rearing success of individually-marked female Northern Pintails (*Anas acuta*; hereafter pintail), and relating duckling survival to maternal and environmental attributes.

Unpredictable habitat conditions or severe weather events (occurring when ducklings are young) may induce substantial annual variation in duckling survival (Makepeace and Patterson 1980, Mendenhall and Milne 1985, Rotella and Ratti 1992b). Survival often declines with hatching date (Dow and Fredga 1984, Rotella and

Ratti 1992b, Dzus and Clark 1998), a pattern which may arise because of seasonal deterioration in food resources, loss of wetlands, or lower maternal investment in brood care (Sedinger and Raveling 1986, Rotella and Ratti 1992b), creating directional selection for early nesting. On the other hand, earlier nesting may be counterbalanced by lower survival in the earliest-hatched broods, producing stabilizing selection on nesting date (Rohwer 1992), a hypothesis which is rarely examined. In some species, older parents are better able to raise offspring, but age-specific analyses are limited in ducks (Hepp and Kennamer 1993, Blums et al. 1997). Although evidence is limited, poorer survival of young in larger than average broods has been found for several waterfowl species (Leblanc 1987, Rockwell et al. 1987, Dzus and Clark 1997a). Finally, some studies report a negative correlation between distance traveled overland and duckling survival (Ball et al. 1975, Rotella and Ratti 1992a), whereas others do not (Talent et al. 1983, Dzus and Clark 1997b). Thus, with respect to purported factors affecting duckling survival, there has been limited investigation and, in some cases, conflicting results have been obtained.

Therefore, our overall objective was to re-evaluate hypothesized sources of variation in duckling survival. Specifically, we tested wheth-

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er survival varied annually and related this to wetland conditions. We also looked for a seasonal decline in survival, assessed whether survival might be related to female age or initial brood size, and then checked for a negative association between distances moved and survival.

METHODS

STUDY AREA

Work was conducted on the Kitsim Ducks Unlimited Project land (hereafter Kitsim) located near Brooks, Alberta, Canada (50°30'N, 112°3'W). Kitsim was constructed during 1980–1983, encompasses approximately 40 km², and contains a main reservoir and 65 managed wetland basins. Basins range in size from 0.5 to 24 ha with some containing small nesting islands measuring 40 x 18 m (Giroux 1981). Water in most basins was less than 1 m deep, except for 1–2 m deep moats around islands. Basins are interconnected through a canal system that allows irrigation water to flow into them through the main reservoir. Depending on water availability, the basins are usually reflooded in mid-spring and late fall, and some become dry by mid-summer. Upland habitat consisted of mixed-grass prairie, of the needlegrass (*Stipa*)-grama (*Bouteloua*) association (Coupland 1961), which was subject to seasonal grazing by cattle. Dispersed clumps of prickly pear (*Opuntia polyacantha*), ball cactus (*Mamillaria vivipara*), and silver sagebush (*Artemisia cana*) were obvious vegetation components. Emergent wetland vegetation is primarily cattail (*Typha latifolia*) and spikerush (*Eleocharis palustris*). Extensive oil development, consisting of existing well sites and active drilling, occurs throughout the eastern half of the Kitsim project.

TRAPPING AND RADIO-TRACKING

Pre-laying, female pintails were trapped during April using decoy traps (Sharp and Lokemoen 1987). Traps were set in wetlands where pintail pairs were frequently seen, but we did not place traps on wetlands with large flocks of birds to avoid capturing migrants. To meet sample size targets for brood-rearing females (20 broods per year), we also trapped females on nests. Nests were located using an 80-m chain dragged between two all-terrain vehicles (Klett et al. 1986). Nesting females were then trapped late in incubation using mist nets (Bacon and Evrard 1990), drop-door traps (Weller 1957), or walk-in traps

(Dietz et al. 1994). Mass (nearest 10 g, measured with a Pesola spring scale), wing chord length (nearest 1 mm, measured with a ruler), and combined length of the head and bill (hereafter head-bill length; nearest 0.1 mm, measured with dial calipers) were obtained for all females. The fifth secondary covert was collected, and a visual inspection of the middle secondary coverts (1995 and 1996 only) was used to classify females as second year (SY) or after second year (ASY), following Duncan (1985). We likely misclassified the age of some females (Esler and Grand 1994). Given that misclassification was likely random, this error would reduce test power and not false conclusions. Females were given a standard leg band, nasal tags (Lokemoen and Sharp 1985), and equipped with an 8-g anchored backpack radio transmitter (Advanced Telemetry Systems, Isanti, Minnesota) attached with a subcutaneous stainless-steel wire (anchor), glue, and three subcutaneous sutures (Mauser and Jarvis 1991). The procedure was performed under local anesthetic, and was approved by the University of Saskatchewan Animal Care Committee on behalf of the Canadian Council of Animal Care. Before being placed back on the nest, nest-trapped females were anesthetized using methoxyflurane to reduce capture-induced abandonment (Rotella and Ratti 1990).

Radio-tagged females captured in decoy traps were located twice daily between 07:00 and 13:00, from the morning following marking until late July. Locations were determined by triangulating from two positions using a vehicle-mounted null-array antennae system (4- or 5-element Yagi antennas; Kenward 1987). If a female's position was triangulated to the same upland location for five consecutive mornings, the area was visited using a hand-held receiving antenna to determine if the female was in nesting cover (i.e., rather than on a nearby wetland). If the female was in cover, she was flushed and the nest, if present, located. When a female's nest was found, she was located daily via telemetry to verify her presence at the nest. After "completed" clutch size was determined, the nest was not revisited while the female was present.

Nesting females (decoy trapped and nest trapped) were monitored daily using telemetry to determine whether the female had left the nest. If a female was absent from her nest for two consecutive telemetry locations (approximately 3 hr), we visited the nest to determine

nest fate. If the eggs hatched, we determined initial brood size by subtracting the number of eggs that did not hatch from the last recorded clutch size. Broods were tracked daily and brood counts were attempted every 7 days until ducklings were 30 days old. If the observer was uncertain that all ducklings had been seen, counts were omitted. We assumed all ducklings were dead if, on two consecutive visits (1–2 days apart), the female was seen either with no ducklings or in an adult flock.

Distances from nest to nearest wetland were measured from air photographs, unless distance estimates were recorded on the original nest map (typically for nests located < 50 m from wetlands). All measurements were recorded as straight line distances. Nests located on islands were assigned a distance of 10 m.

STATISTICAL ANALYSES

We tested whether brood size at hatch varied annually or with hatch date using analysis of covariance (ANCOVA; PROC GLM; SAS Institute 1990). We defined brood survival as the proportion of broods with at least one duckling surviving to 30 days post-hatch. Variance was determined from a binomial distribution (SPSS 1993). Duckling survival was the proportion of hatched ducklings that survived 30 days. Duckling survival was estimated using a modification of the Mayfield method (Flint et al. 1995a). One of the assumptions of the Mayfield method is that survival is constant through the period of observation. Ducklings often experience high mortality early in brood rearing and inspection of survival curves from this study suggested that most pintail duckling mortality occurred prior to 7 days post-hatch. Therefore, we estimated daily survival rates for ducklings < 8 days of age and ducklings 8 to 30 days old. The 30-day survival estimate was the product of the survival estimates for the two periods (Johnson 1979). To address the problem of non-independence of brood mates, variance of the duckling survival rate was based on results for cluster sampling with individual broods treated as clusters (Flint et al. 1995a). Variation associated with this survival estimate was calculated following Goodman (1960) and DeMaso et al. (1997). A chi-square test for independent survival rates was used to compare daily survival rates among years (program CONTRAST; Sauer and Williams 1989). Variation in daily survival rate with

duckling age was determined using conditional probabilities of mortality and exposure (Klett and Johnson 1982), where conditional probability of an observed change was calculated using methods in Grand and Flint (1996). The product of individual daily survival rates produced an estimate of the survival function and cumulative estimates of duckling survival (Klett and Johnson 1982, Flint et al. 1995b).

To correct for date effects on initial brood size at hatch, we used the residuals derived by regressing brood size at hatch against hatching date. Residuals rather than initial brood size were then used in all subsequent analyses. To examine inter-brood variability in survival, a duckling survival estimate also was calculated on a per brood basis (above). Distance from nest to nearest wetland was log transformed to improve normality.

Logistic regression (PROC LOGISTIC; SAS Institute 1990) was used to evaluate brood survival (at least one duckling survived versus none) in relation to the following six attributes: (1) year, (2) female age (SY vs. ASY), (3) hatch date, (4) hatch date squared, (5) distance from nest to nearest wetland, and (6) brood size at hatch (residuals). Variables 1 and 2 were categorical, the remaining were continuous. We limited analyses, *a priori*, to two-way interactions, and further limited interactions to those involving main effects and covariates. We used the Akaike Information Criterion (AIC) (Akaike 1985, Burnham and Anderson 1992) with the small-sample bias adjustment ($AIC_c = AIC + [(2p(p + 1))/(n - p - 1)]$) (Hurvich and Tsai 1995) to choose the models that best fit the data. We started with a set of 25 candidate models and selected the model or family of models with the lowest AIC score(s) as the best model(s). If two or more models had similar AIC values, we chose the model with the fewest parameters, based on the principal of parsimony.

Analysis of covariance was performed to evaluate sources of variation in duckling survival rate (per brood), using the same explanatory variables. For this analysis, we used the same model selection criteria used in the brood survival analysis based on a set of 44 candidate models. AIC scores were derived from sum of squares error (SSE) using the formula $(n)[\ln(SSE/n)] + 2p$ (SAS Institute 1990), where n is the sample size and p is the number of model parameters, including the intercept. AIC_c

TABLE 1. Method of capture and age ratio of brood hens, average (\pm SE) brood sizes at hatch, and hatch dates of Northern Pintails at Kitsim, Alberta, 1994–1996.

Year	Method of capture			SY:ASY	Brood size	Hatch dates		
	decoy	nest	total			first	last	medium
1994	2	15	17	5:11 ^a	7.0 \pm 0.5	11 May	30 June	9 June
1995	5	13	18	7:11	5.9 \pm 0.4	23 May	30 June	10 June
1996	3	19	22	4:18	7.1 \pm 0.4	20 May	25 June	6 June
Total	10	47	57	16:40	6.7 \pm 0.2	11 May	30 June	11 June

^a One female could not be aged.

scores were then calculated. Unless stated otherwise, we report least squares means and standard errors derived from ANCOVA when comparing groups.

All results are reported as mean \pm SE, and we used $P < 0.05$ as our level of accepted significance.

RESULTS

We trapped and radio-tagged a total of 65 females. Because few decoy-trapped females nested successfully, the majority of our sample consisted of nest-trapped females. We excluded eight females where brood counts were not obtained, three females that lost transmitters, and two that experienced nest destruction prior to hatch. We obtained data from 57 brood-rearing females that successfully hatched 383 ducklings (Table 1). Yearlings (SY) comprised 31, 38, and 18% of the sample in 1994, 1995, and 1996, respectively, but this variation was not significant ($\chi^2_2 = 2.2$, $P > 0.3$). Initial brood sizes at hatch did not vary among years (ANCOVA, $F_{2,55}$

$= 2.2$, $P > 0.1$), but did decrease with hatch date ($F_{1,56} = 13.00$, $P < 0.001$, Fig. 1). Hatch dates spanned 50, 38, and 36 days in 1994, 1995, and 1996, respectively, but did not differ among years (Kruskal-Wallis test, $\chi^2_2 = 0.5$, $P > 0.7$). Distance from nest to nearest wetland varied from < 10 m to 1,500 m, but 72% of all nests were located ≤ 100 m from wetlands, with no differences among years (Kruskal-Wallis test, $\chi^2_2 = 1.1$, $P > 0.5$).

Brood survival did not vary among years ($\chi^2_2 = 1.4$, $P > 0.4$), at 0.88 ± 0.08 , 0.72 ± 0.11 , and 0.82 ± 0.08 for 1994, 1995, and 1996, respectively. The model with the lowest AIC_c score (Table 2; AIC_c = 54.0) indicated that brood survival declined with hatch date; successful broods hatched about 10 days earlier than unsuccessful broods (mean hatch dates: June 5 \pm 12 days vs. June 15 \pm 12 days).

Although duckling survival to 30 days appeared to vary annually (1994: 0.65 [CI 0.29–1.00], 1995: 0.42 [CI 0.11–1.00], 1996: 0.44 [CI 0.12–1.00]), being substantially greater in 1994,

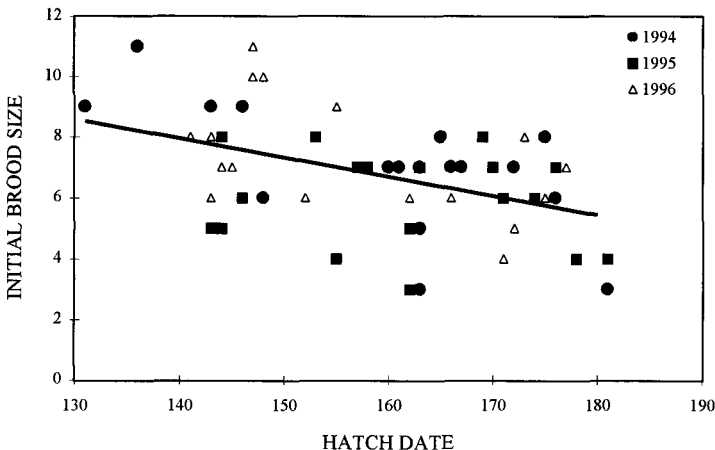


FIGURE 1. Initial brood sizes by hatching date for Northern Pintails at Kitsim, Alberta, 1994–1996. Days since 1 January: day 130 is 9 May and day 180 is 28 June.

TABLE 2. Akaike Information Criterion (AIC_c) values, adjusted for small sample size, for representative models of 30-day survival of Northern Pintail broods near Brooks, Alberta, 1994–1996. Analyses were based on logistic regressions.

Model	NP ^a	AIC_c ^b
Hatch date	2	54.0
Distance to wetland	2	58.6
Age	2	59.7
Initial brood size	2	59.1
Year	2	60.0
Hatch date, hatch date squared	3	54.8
Hatch date, distance to wetland	3	54.8

^a Number of parameters in model.

^b Model with the lowest AIC_c value is optimal and indicated by bold-faced type.

there was no difference among years (Program Contrast; $\chi^2_2 = 0.5$, $P > 0.7$). Daily survival rate did not differ among years in either the ≤ 7 -day-old age category ($\chi^2_2 = 5.0$, $P > 0.08$) or the 8–30-day-old age group ($\chi^2_2 = 0.5$, $P > 0.7$). However, daily survival rate was higher for older (8–30 days) ($\chi^2_1 = 20.2$, $P < 0.001$) than younger (< 8 -day-old) ducklings. Duckling mortality was greatest during the first 7 days post-hatch in all years (Fig. 2), estimated as 60, 76, and 76% of all losses during 1994, 1995, and 1996, respectively.

The model best describing duckling survival included hatch date, year, initial brood size, and an interaction between initial brood size and year (Table 3, $AIC_c = -132.2$). Although the

model which included distance to wetland had a similar AIC_c value (-132.3), we chose the simpler model (i.e., fewer parameters) based on the principle of parsimony. Ducklings which hatched earlier in the season had better survival than those hatched later (Fig. 3). Closer examination of the interaction between initial brood size and year revealed that duckling survival tended to be higher for larger initial broods in 1994 but lower in 1995 and 1996 (Fig. 4).

DISCUSSION

BROOD AND DUCKLING SURVIVAL

Our 1994 duckling survival estimate (65%) for pintails is one of the highest reported for waterfowl, but, in 1995 and 1996, survival fell more than 20% to values often reported for Mallards (*Anas platyrhynchos*) (Rotella and Ratti 1992b, Mauser et al. 1994). Nonetheless, pintail brood and duckling survival estimates for Kitsim were much greater than those recently reported for pintails in Alaska (3.3 to 14.5%; Grand and Flint 1996). These findings indicate that there may be substantial temporal and spatial/geographic variation in survival.

We speculate that water conditions are at least partially responsible for the tendency for higher duckling survival in 1994. In 1994, water from the main reservoir was diverted into wetlands during late April, resulting in relatively stable and high wetland water levels throughout most of the brood-rearing period. This additional wa-

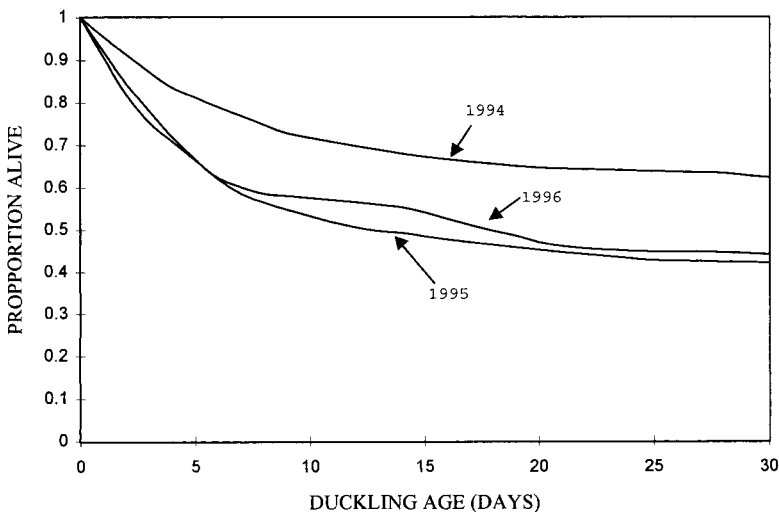


FIGURE 2. Proportion of Northern Pintail ducklings surviving by age at Kitsim, Alberta, 1994–1996.

TABLE 3. Akaike Information Criterion (AIC_c) values, adjusted for small sample size, for a confidence set of models of 30-day survival of Northern Pintail ducklings near Brooks, Alberta, 1994–1996.

Model	NP ^a	AIC ^b
Year, init. brood size, hatch date	5	-130.5
Year, init. brood size, dist. wetland, hatch date	6	-130.1
Year, init. brood size, hatch date, hatch date squared	6	-128.8
Year, init brood size, hatch date, hatch date squared, dist. wetland	7	-129.3
Year, init. brood size, hatch date, init. brood*year	7	-132.2
Year, init. brood, hatch date, hatch date squared, init. brood*year	8	-131.0
Year, init. brood size, hatch date, dist. wetl., init. brood*year	8	-132.3

^a Number of parameters in model.

^b Akaike information criteria were used to evaluate models; the model with the lowest AIC value is optimal and indicated by bold-faced type.

ter, along with favorable precipitation that summer (May/June rainfall; 1994 = 141 mm, 1995 = 89 mm, 1996 = 80 mm; K. Guyn, unpubl. data), kept most wetlands full. Conversely, in 1995 and 1996, many wetlands were drawn down, resulting in several completely dry basins. For example, in 1996, 68% of wetlands in the eastern half of the main study area were either dry or very shallow (i.e., wide mud flats) by early July (K. Guyn, unpubl. data). Finally, Mauser et al. (1994) studied Mallard duckling survival on managed wetlands in California and found that duckling survival was reduced in a year when water was removed from seasonal wetlands prior to peak hatch. In two other years when seasonal wetlands contained water throughout most of the brood-rearing season,

survival was higher. Our study and that of Mauser et al., further illustrate that duckling survival varies with wetland conditions.

FACTORS RELATED TO SURVIVAL

We found that pintail brood and duckling survival decreased with hatching date. In birds, young hatched early in the season often have higher survival to fledging than late hatched offspring (Dow and Fredga 1984, Cooke et al. 1995). In waterfowl, several studies report greater survival to independence for ducklings hatching earlier in the season (Rotella and Ratti 1992b, Grand and Flint 1996, Dzus and Clark 1998), although this pattern is not consistent (Dawson and Clark 1996).

Several hypotheses have been proposed to ex-

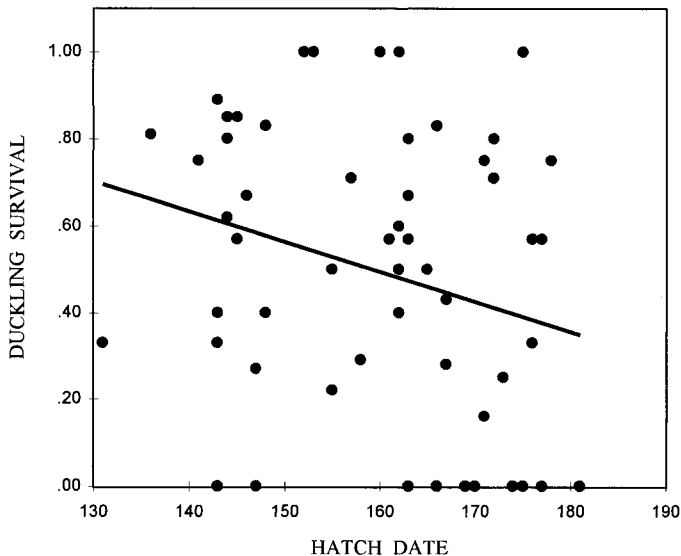


FIGURE 3. Northern Pintail duckling survival, 1994–1996, by hatching date at Kitsim, Alberta. Days since 1 January: day 130 is 9 May and day 180 is 28 June.

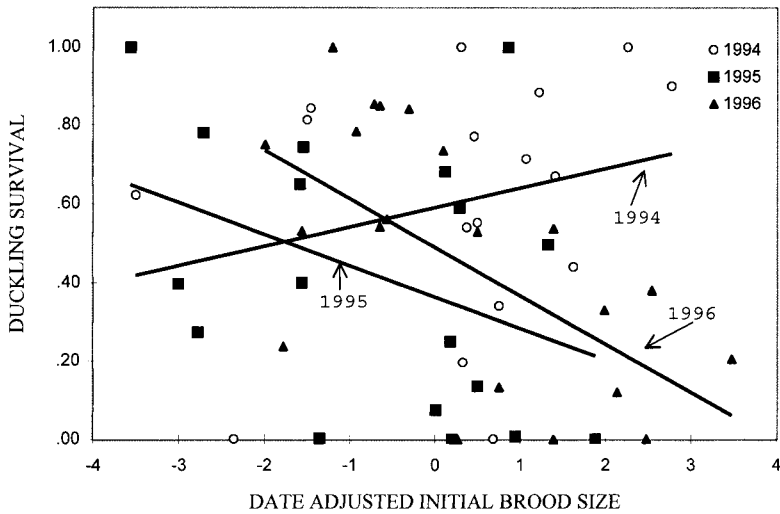


FIGURE 4. Northern Pintail duckling survival in relation to initial brood size at hatch (corrected for hatch date), 1994–1996, at Kitsim, Alberta.

plain a seasonal decline in duckling survival. Grand and Flint (1996) suggested that the late-season decrease in duckling survival of arctic-nesting pintails was related to increased predation on ducklings, mediated by declining availability of alternate prey. In prairie habitats, higher survival of early-hatched ducklings may be related to seasonal declines in wetland quality, as indexed by abundance and depth (Rotella and Ratti 1992a, Dzus and Clark 1998). Although water levels are managed on Kitsim, by mid to late-June many wetlands have reduced water levels, occurring either naturally or due to planned drawdowns. Rotella and Ratti (1992b) found that late-hatched broods in areas of high wetland density also had poor survival, prompting them to suggest that other factors such as reduced invertebrates or increased predator numbers may be responsible. Cox et al. (1998) reported that growth of Mallard ducklings to 17 days was positively related to invertebrate numbers. How invertebrate abundance varied seasonally in Kitsim wetlands and what potential impact this had on pintail duckling survival are unknown. Alternatively, wetlands which are drawn down may increase in salinity and high salinity concentrations have been found to be fatal to young ducklings (Mitcham and Wobeser 1988).

We did not find strong evidence that ducklings which hatched from nests closer to wetlands had higher survival. Several researchers have sug-

gested that young ducklings are most vulnerable to mortality during overland movement (Ball et al. 1975). Rotella and Ratti (1992b) found that Mallard duckling survival was negatively correlated with distance traveled. However, Talent et al. (1983) and Dzus and Clark (1997b) did not detect a relationship between distance moved and offspring survival.

Duckling survival was associated with a year-by-brood size interaction. In 1994, duckling survival was higher for larger initial broods. This trend was reversed in 1995 and 1996, and perhaps these patterns are related to different yearly habitat conditions. In 1994, flooded vegetation was abundant and this may have afforded protection to large broods, whereas in 1995 and 1996, flooded emergent vegetation was less available and large broods may have been more conspicuous to potential predators. Dzus and Clark (1997a) found that experimentally enlarged Mallard broods showed lower survival to 30 days than did control broods, but total brood loss to 14 days did not differ between enlarged and control broods. Among successful Snow Goose (*Chen caerulescens*) broods, Cooke et al. (1995) found that goslings from small broods tended to have a higher probability of survival, although small broods had higher total brood loss than larger ones. In two of three years, we found evidence of a survival advantage for small brood sizes at hatch. Because pintails have one of the smallest clutch sizes of all dabbling duck

species, selection for small brood sizes may at least partially explain this trait. However, experimental manipulation of brood size is required to adequately test this hypothesis.

We found that duckling survival on Kitsim was higher than that reported for pintails in Alaska and similar or higher to estimates for Mallards on the prairies. Early hatched young tended to survive better, and we did not detect any stabilizing selection on timing of nesting. Although Kitsim is a managed wetland project, habitat conditions influenced not only female success (brood survival), but duckling survival, as evidenced by the yearly and annual variation in duckling survival in relation to brood size.

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LITERATURE CITED

- AKAIKE, H. 1985. Prediction and entropy, p. 1–24. *In* A. C. Atkinson and S. E. Fienberg [eds.], *A celebration of statistics: the ISI centenary volume*. Springer-Verlag, New York.
- BACON, B. R., AND J. O. EVRARD. 1990. Horizontal mist nest for capturing upland nesting ducks. *N. Am. Bird Bander* 15:18–19.
- BALL, I. J., D. S. GILMER, L. M. COWARDIN, AND J. H. RIECHMAN. 1975. Survival of Wood Duck and Mallard broods in north-central Minnesota. *J. Wildl. Manage.* 39:776–780.
- BLUMS, P., G. R. HEPP, AND A. MEDNIS. 1997. Age-specific reproduction in three species of European ducks. *Auk* 114:737–747.
- BURNHAM, K. P., AND D. R. ANDERSON. 1992. Data-based selection of an appropriate biological model: the key to modern data analysis, p. 16–30. *In* D. R. McCullough and R. H. Barrett [eds.], *Wildlife 2001: populations*. Elsevier, New York.
- COOKE, F., R. F. ROCKWELL, AND D. B. LANK. 1995. The Snow Geese of La Perouse Bay: natural selection in the wild. Oxford Univ. Press, New York.
- COUPLAND, R. T. 1961. A reconsideration of grassland classification in the northern great plains of North America. *Ecology* 49:135–167.
- COX, R. R., M. A. HANSON, C. C. ROY, N. H. EULISS, D. H. JOHNSON, AND M. G. BUTLER. 1998. Mallard duckling growth and survival in relation to aquatic invertebrates. *J. Wildl. Manage.* 62:124–133.
- DAWSON, R., 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.
- DEMASEO, S. J., A. D. PEOPLES, S. A. COX, AND E. S. PARRY. 1997. Survival of Northern Bobwhite chicks in western Oklahoma. *J. Wildl. Manage.* 61:846–853.
- DIETZ, N. J., P. J. BERGMANN, AND L. D. FLAKE. 1994. A walk-in trap for nesting ducks. *Wildl. Soc. Bull.* 22:19–22.
- DOW, H., AND S. FREDGA. 1984. Factors affecting reproductive output of the Goldeneye Duck *Bucephala clangula*. *J. Anim. Ecol.* 53:679–692.
- DUNCAN, D. C. 1985. Differentiating yearling from adult Northern Pintails by wing-feather characteristics. *J. Wildl. Manage.* 49:576–579.
- DZUS, E. H., AND R. G. CLARK. 1997a. Brood size manipulation in mallard ducks: effects on duckling survival and brooding efficiency. *EcoScience* 4: 437–445.
- DZUS, E. H., AND R. G. CLARK. 1997b. Overland travel, food abundance, and wetland use by Mallards: relationships with offspring survival. *Wilson Bull.* 109:504–515.
- DZUS, E. H., AND R. G. CLARK. 1998. Brood survival and recruitment of Mallards *Anas platyrhynchos* in relation to wetland density and hatching date. *Auk* 115:311–318.
- ESLER, D., AND J. B. GRAND. 1994. Comparison of age determination techniques for female Northern Pintails and American Wigeon in spring. *Wildl. Soc. Bull.* 22:260–264.
- FLINT, P. L., K. H. POLLOCK, D. THOMAS, AND J. S. SEDINGER. 1995a. Estimating pre fledging survival: allowing for brood mixing and dependence among brood mates. *J. Wildl. Manage.* 59:448–455.
- FLINT, P. L., J. S. SEDINGER, AND K. H. POLLOCK. 1995b. Survival of juvenile Black Brant during brood rearing. *J. Wildl. Manage.* 59:455–463.
- GIROUX, J-F. 1981. Use of artificial islands by nesting waterfowl in southeastern Alberta. *J. Wildl. Manage.* 45:669–679.
- GOODMAN, L. A. 1960. On the exact variance of products. *J. Am. Stat. Assoc.* 55:708–713.
- GRAND, J. B., AND P. L. FLINT. 1996. Survival of North-

- ern Pintail ducklings on the Yukon-Kuskokwim Delta, Alaska. *Condor* 98:48-53.
- GREENWOOD, R. J., A. B. SARGEANT, D. H. JOHNSON, L. M. COWARDIN, AND T. L. SHAFFER. 1987. Mallard nest success and recruitment in prairie Canada. *Trans. N. Am. Wildl. Nat. Resour. Conf.* 52:298-309.
- HEPP, G. R., AND R. A. KENNAMER. 1993. Effects of age and experience on reproductive performance of Wood Ducks. *Ecology* 74:2027-2036.
- HURVICH, C. M., AND C. TSAI. 1995. Model selection for extended quasi-likelihood models in small samples. *Biometrics* 51:1077-1084.
- JOHNSON, D. H. 1979. Estimating nest success: the Mayfield method and an alternative. *Auk* 96:651-661.
- KENWARD, R. E. 1987. *Wildlife radio tagging*. Academic Press, London.
- KLETT, A. T., H. F. DUEBBERT, C. A. FAANES, AND K. F. HIGGINS. 1986. Techniques for studying nest success of ducks in upland habitats in the Prairie Pothole Region. U.S. Fish and Wildlife Serv. *Resour. Publ.* 158, Washington, DC.
- KLETT, A. T. AND D. H. JOHNSON. 1982. Variability in nest survival rates and implications to nesting studies. *Auk* 99:77-87.
- LEBLANC, Y. 1987. Egg mass, position in the laying sequence, and brood size in relation to Canada goose reproductive success. *Wilson Bull.* 99:663-672.
- LOKEMOEN, J. T., AND D. E. SHARP. 1985. Assessment of nasal marker materials and designs used on dabbling ducks. *Wildl. Soc. Bull.* 13:53-56.
- MAKEPEACE, M., AND I. J. PATTERSON. 1980. Duckling mortality in the shelduck in relation to density, aggressive interaction and weather. *Wildfowl* 31:57-72.
- MAUSER, D. M., AND R. L. JARVIS. 1991. Attaching radio transmitters to 1-day-old Mallard ducklings. *J. Wildl. Manage.* 55:488-491.
- MAUSER, D. M., R. L. JARVIS, AND D. S. GILMER. 1994. Survival of radio-marked Mallard ducklings in northeastern California. *J. Wildl. Manage.* 58:82-87.
- MENDENHALL, V. M., AND H. MILNE. 1985. Factors affecting duckling survival of eiders *Somateria mollissima* in northeast Scotland. *Ibis* 127:148-158.
- MITCHAM, S. A., AND G. WOBESER. 1988. Toxic effects of natural saline waters on Mallard ducklings. *J. Wildl. Diseases* 24:45-50.
- ROCKWELL, R. F., C. S. FINDLAY AND F. COOKE. 1987. Is there an optimal clutch size in snow geese? *Am. Nat.* 130:839-863.
- ROHWER, F. C. 1992. The evolution of reproductive patterns in waterfowl, p. 486-539. *In* B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu [eds.], *Ecology and management of breeding waterfowl*. Univ. Minnesota Press, Minneapolis, MN.
- ROTELLA, J. J., AND J. T. RATTI. 1990. Use of methoxyflurane to reduce nest abandonment of Mallards. *J. Wildl. Manage.* 54:627-628.
- ROTELLA, J. J., AND J. T. RATTI. 1992a. Mallard brood movements and wetland selection in southwestern Manitoba. *J. Wildl. Manage.* 56:508-515.
- ROTELLA, J. J., AND J. T. RATTI. 1992b. Mallard brood survival and wetland habitat conditions in southwestern Manitoba. *J. Wildl. Manage.* 56:499-507.
- SAS INSTITUTE INC. 1990. *SAS/STAT user's guide*. Version 6. SAS Institute Inc., Cary, NC.
- SAUER, J. R., AND B. K. WILLIAMS. 1989. Generalized procedures for testing hypotheses about survival or recovery rates. *J. Wildl. Manage.* 53:137-142.
- SEDINGER, J. S., AND D. G. RAVELING. 1986. Timing of nesting by Canada Geese in relation to the phenology and availability of their food plants. *J. Anim. Ecol.* 55:1083-1102.
- SHARP, D. E., AND J. T. LOKEMOEN. 1987. A decoy trap for breeding-season Mallards in North Dakota. *J. Wildl. Manage.* 51:711-715.
- SPSS. 1993. *SPSS for windows: basic systems user's guide*, release 6.0. SPSS Inc., Chicago.
- 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. 1957. An automatic nest-trap for waterfowl. *J. Wildl. Manage.* 21:456-458.