

BROOD SURVIVAL AND RECRUITMENT OF MALLARDS IN RELATION TO WETLAND DENSITY AND HATCHING DATE

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ABSTRACT.—Reproductive success in birds often is measured in terms of the proportion of nests that hatch or fledge young. We assessed survival of 35 Mallard (*Anas platyrhynchos*) broods near Yorkton in east-central Saskatchewan, Canada, from 1990 to 1993. Brood survival was higher for offspring that hatched early in the breeding season in three of four years when wetland abundance declined over the summer. Seasonal patterns of wetland abundance were reversed in 1993, and early hatching broods suffered higher mortality. A more accurate measure of reproductive success is the number of young that survive to breed, i.e. recruitment. Ducklings were tagged at Yorkton and on the St. Denis National Wildlife Area (1985 to 1995), enabling us to identify individuals that returned to breed in subsequent years. Female recruits were more likely to originate from early hatched nests at both sites. With respect to recruitment, we also tested for an additional advantage of hatching early, over and above that associated with duckling survival. There was no statistical difference in the seasonal distribution of nests producing recruits compared with broods that successfully fledged at least one young. Thus, the selective advantage to nesting early for Mallards likely is driven by a seasonal decline in duckling survival, which in turn may be associated with decreasing wetland density. Received 3 September 1996, accepted 6 August 1997.

TIMING OF BREEDING is considered an adaptive trait that evolved to maximize reproductive output (Lack 1968). Survival of offspring born later in the breeding season often is lower than that of young born earlier in the season (e.g. mammals, Iason 1989, Virgl and Messier 1997; fish, Schultz 1993). Similarly, among birds, young that hatch early in the breeding season have higher survival to independence than young that hatch late in the season (e.g. Perrins 1965, Murton and Westwood 1977, Dow and Fredga 1984, Newton and Marquiss 1984, Burger et al. 1996). Survival to fledging or independence often is used as an estimate of reproductive success; however, this measure may lead to improper inferences about reproductive fitness (Cooke et al. 1984). Reproductive success is best measured by the number of offspring that enter the breeding population (i.e. recruitment; Howard 1979, Hepp et al. 1989). As with other measures of productivity in birds, survival to recruitment often is highest for early hatching young (Grice and Rogers 1965, Cooke et al. 1984, Poole 1989, Hochachka

1990, Rohwer 1992, Harris et al. 1994; but see Hepp et al. 1989, Dawson and Clark 1996). Additional benefits to hatching early, over and above that documented for survival to fledging, may be related to social dominance (Spear and Nur 1994) and a longer period of time to improve body condition and flight skills before migrating. Although the advantages of hatching early in relation to survival to fledging and recruitment are well documented, the question of an additional advantage to recruitment due to hatching early is largely unexplored.

The annual cycle of the Mallard (*Anas platyrhynchos*) has been the focus of much research, but the brood-rearing stage has been examined in detail only recently. Interrelationships between time of season, wetland condition, and duckling survival have not been clearly established. Poor wetland conditions may have a negative effect on many aspects of the reproductive biology of Mallards, including pre-fledging survival (Reynolds 1987, Rotella and Ratti 1992). Survival of young that hatch early typically is higher than that of late-hatched young (Orthmeyer and Ball 1990, Rotella and Ratti 1992), but recruitment into the breeding population relative to hatching date has not been determined for Mallards.

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In this paper, we focus on two aspects of current reproduction, survival of offspring to fledging and postfledging survival to recruitment. Our objectives were to: (1) determine survival of ducklings from hatching to near independence relative to hatching date and wetland density, (2) evaluate recruitment in relation to hatching date, and (3) test if there is an additional benefit to hatching early (over and above any advantage associated with seasonal variation in duckling survival). Because natal and breeding philopatry in Mallards are strongly biased toward females (Greenwood 1980, Rohwer and Anderson 1988), we focus on recruitment of females only.

METHODS

Study areas.—Work was conducted on two sites in Saskatchewan, Canada. Brood ecology was studied from 1990 to 1993 40 km west of Yorkton in east-central Saskatchewan (51°12'N, 103°07'W). The Yorkton study area consisted of five managed nesting areas (63 ha each). The area is characterized by gently undulating topography interspersed with aspen (*Populus tremuloides*) bluffs and has a moderate wetland density (range in mid-May, 27 to 49 per km²). Recruitment was examined from 1990 to 1993 at Yorkton and from 1985 to 1996 on the St. Denis National Wildlife Area (SDNWA; 52°20'N, 106°10'W) located 40 km east of Saskatoon, Saskatchewan, and 270 km northwest of the Yorkton site. The SDNWA is a 385-ha contiguous block of land that is managed primarily for nesting ducks and has been described by Sugden and Beyersbergen (1985), Clark et al. (1991), and Woo et al. (1993). Both sites lie within the Prairie Pothole Region, and the predominant land uses surrounding the managed nesting areas are agricultural cereal and oilseed production.

Data collection.—Mallard nests were found by searching on foot or using cable-chain drags pulled between two all-terrain vehicles (Klett et al. 1986). Nests (defined as a depression with ≥ 1 egg) were visited every 7 to 10 days, and stage of incubation was determined by candling the eggs (Weller 1956). The proportion of duck nests where at least one egg hatched (i.e. nesting success) is very low in the Prairie Pothole Region (Greenwood et al. 1995). Hence, we elevated nesting success by protecting nests with fences to deter predators (Sargeant et al. 1974, Greenwood et al. 1990). Mallard nests on the Yorkton study area that were not located in one of two 16-ha predator-exclosure fences (see Trottier et al. 1994) were surrounded by wire-mesh fences if they survived to late egg laying or early incubation (Sargeant et al. 1974). Females were captured at about day 20 of incubation using hand-carried mist nests (Bacon

and Evrard 1990) or automatic walk-in nest traps (Weller 1957). All females received leg bands and unique combinations of nylon nasal markers (Lokenmoen and Sharp 1985).

Females used in the brood ecology study also received radio transmitters. Twenty-four females in 1990, nine in 1991, and one in 1992 received a 22-g harness-style transmitter (28 × 18 × 8 mm; model CHP2H, Telonics Inc.) using a crisscross modification (Smith and Gilbert 1981) of the traditional Dwyer (1972) harness. The remaining brood-rearing females in 1991 and 1992, and all individuals in 1993, had 21-g cylindrical transmitters (23 × 53 mm; model IMP150, Telonics Inc.) implanted into their abdominal cavity (Olsen et al. 1992). Females were located one to four times daily using either a truck-mounted or hand-held receiving system. Observations to determine brood size were conducted at least every seven days until the young could fly (ca. 55 days; Bellrose 1976). Survival of ducklings to fledging was not influenced by the type of transmitter carried by the attending female (Dzus and Clark 1996).

To allow an evaluation of brood survival in relation to wetland density, we quantified wetland abundance on the Yorkton managed nesting areas during weekly waterfowl pair counts. Wetland characteristics such as depth and conductivity were measured once per year and are discussed in terms of use by broods in Dzus and Clark (1997a).

Ducklings on both study areas received uniquely coded metal tags on the web of one foot either just before or just after hatching (Alliston 1975). Some juveniles were captured or recaptured later in the season in drive traps; large ducklings were banded and females were fitted with a unique combination of nylon nasal tags. Recruits (i.e. those that produced their first eggs) were identified in years subsequent to hatching primarily by being recaptured on nests or occasionally by resighting females ($n = 5$) with nasal tags. Resighted birds probably attempted to breed because most were seen paired with males, and most female Mallards make at least one nesting attempt even under drought conditions (Cowardin et al. 1995). Recruits were recaptured at Yorkton from 1991 to 1993 and at SDNWA from 1986 to 1996.

Statistical analysis.—Survival analysis for ducklings at Yorkton was conducted on a per-brood basis to avoid complications with the lack of independence of ducklings within a brood (Rotella and Ratti 1992, Winterstein 1992). Most duckling mortality occurs in the first two weeks after hatching, and survival after 30 days old is nearly constant (Ringelman and Longcore 1982, Orthmeyer and Ball 1990). Thus, to maximize the sample of broods, we used survival to 30 days as the measure of reproductive success during brood rearing. Brood survival was defined as one or more ducklings surviving to 30 days; failed broods lost all ducklings by 30 days. Brood size was manipulated to $\pm 50\%$ of control size ($n = 10$ young) in 1991

to 1993 at Yorkton as part of another study (Dzus and Clark 1997b). Relative to control broods (9 of 13 broods surviving), brood survival was lower ($P = 0.04$) for reduced broods (2 of 10 broods surviving) but was virtually identical between control and enlarged brood (5 of 8 broods surviving; Dzus and Clark 1997b). Therefore, we present brood-survival data only for control and enlarged broods combined. Because brood survival follows a binomial distribution, we used logistic regression with maximum-likelihood estimates of the logit function (PROC CATMOD; SAS Institute 1990) to test whether year, hatching date, or wetland density affected brood survival (Haramis et al. 1986, Boyce and Perrins 1987, Hepp et al. 1989). Broods hatching within three days of the weekly wetland count day were assigned a value for wetland density that corresponded to the number of wetlands counted in that week. For broods hatching after Julian date 160 in 1990 and 168 in 1991, wetland density was calculated based on linear extrapolation to a minimum of 23 wetlands (the lowest number of wetlands that held water in the driest year). P -values are presented for individual factors (or interactions); results are only presented if goodness-of-fit tests indicate the model fits the data.

To evaluate recruitment in relation to hatching date, successful nests were divided into two groups: those that produced recruits and those that did not. The date of the first-hatched Mallard nest varied only slightly among years at Yorkton (Julian date: 160 in 1990, 154 in 1991, 154 in 1992, and 150 in 1993). To control for annual differences in breeding chronology, hatching dates were expressed relative to the first-hatched nest of each year (day = 0). Hatching dates of successful nests were included in the analysis only if ducklings were tagged. When siblings were recruited ($n = 9$ occurrences), hatching date was recorded only once.

A bias may exist if the likelihood of detecting female recruits varies with distance from the natal nest to the edge of our study area. To investigate this possibility, we used logistic regression to evaluate recruitment in relation to date and distance (to edge of the SDNWA). Low sample sizes precluded an analysis of the Yorkton data.

Based on independent data from Yorkton and SDNWA, we compared the distributions of hatching dates for nests that produced recruits and those that did not using a one-tailed Kolmogorov-Smirnov (K-S) two-sample test (Siegel and Castellan 1988). To test for differences between brood survival and recruitment, we used a K-S test to compare the distribution of hatching dates for nests that produced recruits with the distribution of hatching dates for broods that successfully fledged ≥ 1 duckling. A one-tailed test was used based on the prediction that there would be a benefit to hatching early, an advantage above and beyond that associated merely with enhanced brood survival.

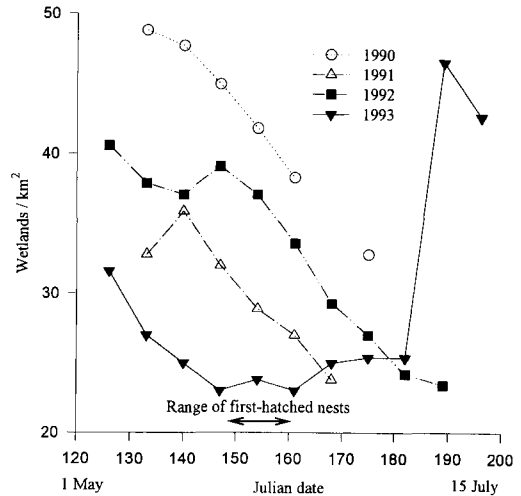


FIG. 1. Wetland density on managed nesting areas near Yorkton, Saskatchewan, Canada.

RESULTS

Wetland conditions.—Wetland abundance on the Yorkton study area decreased over the summer in three of four years (Fig. 1). The number of wetlands holding water when Mallard clutches began hatching in 1993 was the lowest recorded during the four-year period (Fig. 1). Another characteristic of 1993 was that late-summer rains refilled dry wetland basins, resulting in a dramatic increase in the number of wetlands when the clutches of late-nesting females were hatching. Recharging of wetlands did not occur in the other three years on the Yorkton site, and this phenomenon was recorded on the SDNWA in only 2 of 30 years (J. B. Millar pers. comm.).

Effect of hatching date and wetland density on brood survival.—We positively identified fate at 30 days after hatching for 35 broods at Yorkton from 1990 to 1993. In a model containing year and hatching date as independent variables, the interaction of year \times hatching date was significant when all years were included in the analysis (logistic regression, $\chi^2 = 5.93$, $P = 0.05$). Although our sample is small, an examination of the distribution of brood loss in relation to hatching date revealed that more brood loss occurred early in 1993, and young in two broods that hatched late in the season survived to 30 days (Fig. 2). Because the wetland inundation pattern in 1993 was opposite that of the other three years, we removed 1993 and reran the lo-

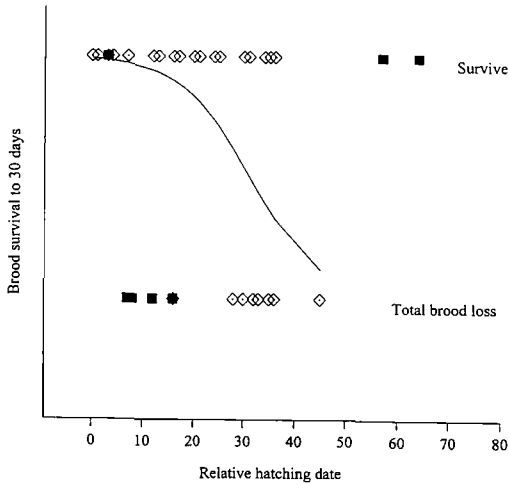


FIG. 2. Survival of Mallard broods in relation to relative hatching date near Yorkton, Saskatchewan, Canada (1990 to 1993). A significant ($P = 0.05$) year by hatching date interaction exists when all four years (1990 to 1993) were analyzed (1990 to 1992 open diamonds; 1993 filled squares). Broods hatching earlier in 1990 to 1992 had higher brood survival than those hatching later ($P = 0.02$).

gistic regression (Fig. 2). For 28 broods observed from 1990 to 1992, those hatching early in the season were more likely to survive to 30 days than those hatching late ($\chi^2 = 5.41$, $P = 0.02$).

To more fully understand the effects of wetland density, date, and year on brood survival, we included all three variables in a logistic regression. With wetland density included in the model, the interaction between year and date was not significant ($\chi^2 = 0.21$, $P = 0.9$), indicating that variation in wetland density probably accounts for much of the variation in brood survival. After dropping the year \times date interaction, and then year ($\chi^2 = 4.26$, $P = 0.12$) from the model, brood survival was negatively related to wetland density ($\chi^2 = 4.36$, $P = 0.04$), and date was not a significant factor ($\chi^2 = 0.66$, $P = 0.41$) when 1993 was included. In years with more typical wetland inundation patterns (1990 to 1992), hatching early was more important ($\chi^2 = 2.93$, $P = 0.09$) than wetland density ($\chi^2 = 0.89$, $P = 0.34$) in terms of brood survival. Thus, in most years, brood survival declined seasonally.

Recruitment in relation to hatching date.—A total of 1,245 ducklings was web-tagged at or near hatching on SDNWA (1985 to 1995), and

343 young received tags at Yorkton (1990 to 1992). The proportion of successful nests at which young were web-tagged at SDNWA increased from 1985 to 1990, then effort remained relatively constant at $>90\%$. Web-tagging effort was high ($\geq 83\%$ of successful nests) in all years at Yorkton. Five recruits were found at Yorkton (three were recaptured on nests and two were resighted). Three of the Yorkton recruits hatched in 1990, and one each hatched in 1991 and 1992. Hatching dates were available for 49 of the 55 recruits recaptured on SDNWA from 1986 to 1996. Nine broods produced two or three recruits, reducing the number of independent hatching dates from SDNWA to 39 (36 were recaptured on nests and 3 were resighted).

For 144 nests on SDNWA whose nest location was >10 m from the edge of the study area, and that produced young, there was no effect on recruitment probability due to distance from the natal nest to the edge of the study area ($\chi^2 = 2.08$, $P = 0.15$). Early hatching nests produced significantly more recruits in the SDNWA sample ($\chi^2 = 9.0$, $P = 0.003$).

The SDNWA and Yorkton samples did not differ in the distributions of successful nests that: (1) produced recruits (K-S test, $D = 0.49$, $n_1 = 5$, $n_2 = 39$, $P > 0.1$), or (2) produced no recruits ($D = 0.21$, $n_1 = 30$, $n_2 = 125$, $P > 0.1$; Table 1). Thus, to use two independent data sets we combined the respective groups of nests that produced recruits and "other successful" nests from SDNWA and Yorkton. Overall, recruits were more likely to be produced from nests that hatched in the first 10 days of the breeding season ($D = 0.23$, $n_1 = 44$, $n_2 = 155$, $P < 0.001$; Fig. 3).

Is there an additional advantage to hatching early?—To test if there is a benefit to hatching early (above that associated with brood survival), we compared the cumulative frequency distribution of hatching dates for surviving broods with the distribution for nests that produced recruits. If there is an additional advantage to hatching early, then the distributions would differ early in the nesting season, with the recruit curve increasing more quickly. Although the recruit distribution did increase more rapidly early in the season, the maximum difference at 6 to 10 days was not significant ($D = 0.23$, $n_1 = 44$, $n_2 = 19$, $P = 0.25$; Fig. 4).

TABLE 1. Number of nests that produced female recruits and successful nests^a for which no female recruits were recaptured at Yorkton (1990 to 1992) and St. Denis National Wildlife Area (SDNWA, 1985 to 1995), Saskatchewan.

| Study area | Relative hatching date ^b | | | | | | | | | |
|---|-------------------------------------|------|-------|-------|-------|-------|-------|-------|-------|-----|
| | 0-5 | 6-10 | 11-15 | 16-20 | 21-25 | 26-30 | 31-35 | 36-40 | 41-45 | ≥46 |
| Recruit-producing^c | | | | | | | | | | |
| Yorkton | 1 | 0 | 0 | 2 | 0 | 0 | 2 | 0 | 0 | 0 |
| SDNWA | 11 | 5 | 2 | 0 | 2 | 0 | 0 | 0 | 3 | 2 |
| Other successful nests^d | | | | | | | | | | |
| Yorkton | 6 | 1 | 2 | 4 | 3 | 4 | 4 | 4 | 0 | 2 |
| SDNWA | 18 | 12 | 9 | 12 | 12 | 5 | 10 | 8 | 9 | 15 |

^a Nests in which >1 egg hatched.

^b Hatching dates set relative to the first-hatched nest of the year (day = 0).

^c Nests from which recruits were either recaptured or resighted. Hatching date is recorded only once for nests where siblings were recruited.

^d Nests from which eggs hatched but no female recruits were recaptured or resighted in subsequent years.

DISCUSSION

Perrins (1966) reported that recruitment declined with hatching date in Manx Shearwaters (*Puffinus puffinus*) and speculated that this pattern was widespread. This prediction has been verified for many species of birds (e.g. Procellariiformes [Harris et al. 1994]; Anseriformes [Cooke et al. 1984]; Falconiformes [Newton and Marquiss 1984, Poole 1989]; Galliformes [Zwickel 1983, Martin and Hannon 1987]; Charadriiformes [Spear and Nur 1994]; Passer-

iformes [Hochachka 1990]). Many of these studies also reported a seasonal decline in survival of young to fledging. In contrast, Hepp et al. (1989) found no evidence that recruitment was higher for early than for late-hatched female Wood Ducks (*Aix sponsa*) in South Carolina, and they suggested that seasonal effects were more pronounced at more northern latitudes where the breeding season is shorter. Reasons underlying the widespread decline in repro-

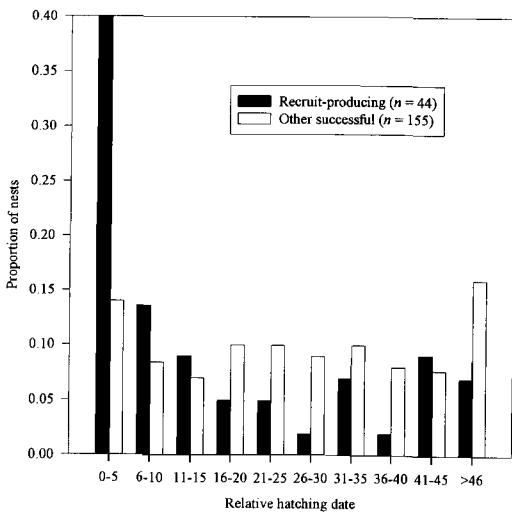


FIG. 3. Distribution of successful Mallard nests (i.e. with ≥1 egg hatched) in relation to relative hatching date (Yorkton [1990 to 1992] and SDNWA [1985 to 1995] combined). Nests that produced recruits hatched earlier ($P = 0.01$) than other successful nests that were not known to produce recruits

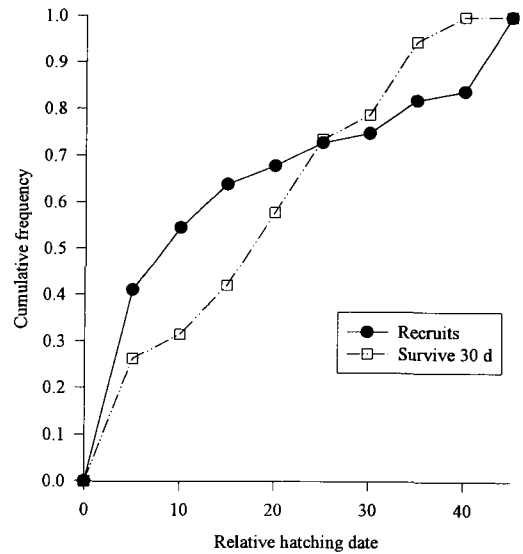


FIG. 4. Cumulative frequency distribution of brood survival at Yorkton (1990 to 1992) and recruit-producing nests (combined data from Yorkton [1990 to 1992] and SDNWA [1985 to 1995]). There is no statistical difference in the curves in relation to relative hatching date ($P = 0.23$).

ductive success relative to timing of breeding are varied. In some species, it may be related to social dominance, with early hatched individuals being more dominant and realizing higher survival (Martin 1987). Related to the issue of dominance is the idea that early hatched young have a longer period of time to complete development before migrating (Cooke et al. 1984). In species that suffer high rates of nest predation (e.g. Willow Ptarmigan [*Lagopus lagopus*] and Mallards), an additional advantage to nesting early may be the increased time available for renesting (Hannon et al. 1988). Higher survival of early hatched ducklings also may be related to a seasonal decline in wetland abundance and water depth, although causal relationships remain unclear (Rotella and Ratti 1992). A seasonal decline in food abundance or availability could influence survival probabilities both before and after independence from parental care (Perrins 1965, Sedinger and Raveling 1986). However, for many species (including Mallards), little is known about seasonal trends in prey availability. Examining the interrelationships between offspring survival, predators, wetland conditions, and food abundance remains one of the most important research needs to enhance our understanding of seasonal variation in reproductive success.

The seasonal decline in clutch size perhaps is the most pervasive and consistent reproductive pattern found in birds (e.g. Klomp 1970, Winkler and Walters 1983). Although the pattern of clutch-size decline is widespread in waterfowl and other birds, its adaptive significance is debated (Rohwer and Eisenhauer 1989, Rohwer 1992). A decrease in lipid or protein reserves may influence the seasonal decline in clutch size (Lack 1967, 1968, Krapu 1981, Ankney et al. 1991), but a seasonal decline in the probability of survival of young to fledging and recruitment may be an important ultimate factor influencing clutch-size decline. Selection should reduce clutch size late in the breeding season when the probability of recruitment is lowest. However, clutch-size decline cannot account for the higher probability of recruitment in early hatched nests.

A variety of measures of annual reproductive success has been reported in the literature. Nesting success has been used as a predictor of reproductive success, but it can be misleading if survival of offspring varies with date or brood

size (see Spear and Nur 1994). Offspring survival to independence often is used as a measure of annual reproductive success (Howard 1979). However, survival to recruitment is a more accurate measure of success because it takes into account differences in survival after fledging (Cooke et al. 1984, Spear and Nur 1994).

One aspect that has received less attention in discussions about reproductive success is whether there is an additional advantage to hatching early over and above the well-documented seasonal decline in survival to independence. Some studies have shown that late-fledged offspring are less likely to be recruited to the breeding population (e.g. Newton and Marquiss 1984, Spear and Nur 1994). Spear and Nur (1994) found no significant difference in the effect of hatching date on survival to independence or recruitment probability in Western Gulls (*Larus occidentalis*). However, due to differences in the shapes of the survival curves, they reported that early hatched chicks were at an advantage in terms of recruitment probability over chicks that hatched after mid-season. Fledging success of early hatching chicks did not differ from those hatching in mid-season, but late-hatched chicks had significantly lower survival relative to those in the earlier periods (Spear and Nur 1994). Recruitment probability for Mallards in our study did not differ from brood survival, suggesting that the relationship with hatching date is driven by changes in survival of young to independence. Few studies have tested for additional benefits of early hatching that may exist beyond survival to fledging. Further evaluation of these relationships will enhance our understanding of the selective pressures influencing initiation of egg laying and the seasonal decline of clutch size.

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LITERATURE CITED

- ALLISTON, W. G. 1975. Web-tagging ducklings in pipped eggs. *Journal of Wildlife Management* 39:625-628.
- ANKNEY, C. D., A. D. AFTON, AND R. T. ALISAUSKAS. 1991. The role of nutrient reserves in limiting waterfowl reproduction. *Condor* 93:1029-1032.
- BACON, B. R., AND J. O. EVRARD. 1990. Horizontal mist net for capturing upland nesting ducks. *North American Bird Bander* 15:18-19.
- BELLROSE, F. C. 1976. Ducks, geese and swans of North America. Stackpole Books, Harrisburg, Pennsylvania.
- BOYCE, M. S., AND C. M. PERRINS. 1987. Optimizing Great Tit clutch size in a fluctuating environment. *Ecology* 68:142-153.
- BURGER, J., I. C. T. NISBET, C. SAFINA, AND M. GOCHFELD. 1996. Temporal patterns in reproductive success in the endangered Roseate Tern (*Sterna dougallii*) nesting on Long Island, New York, and Bird Island, Massachusetts. *Auk* 113:131-142.
- CLARK, R. G., T. D. NUDDS, AND R. O. BAILEY. 1991. Populations and nesting success of upland-nesting ducks in relation to cover establishment. Canadian Wildlife Service Progress Notes No. 193, Saskatoon, Saskatchewan.
- COOKE, F., C. S. FINDLAY, AND R. F. ROCKWELL. 1984. Recruitment and the timing of reproduction in Lesser Snow Geese (*Chen caerulescens caerulescens*). *Auk* 101:451-458.
- 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. U.S. National Biological Service, Biological Science Report No. 2.
- 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.
- DOW, H., AND S. FREDGA. 1984. Factors affecting reproductive output of the Goldeneye Duck *Bucephala clangula*. *Journal of Animal Ecology* 53:679-692.
- DWYER, T. 1972. An adjustable radiopackage for ducks. *Bird-Banding* 43:282-284.
- DZUS, E. H., AND R. G. CLARK. 1996. Effects of harness-style and abdominal transmitters on survival and return rates of Mallards. *Journal of Field Ornithology* 67:549-557.
- DZUS, E. H., AND R. G. CLARK. 1997a. Overland travel, food abundance, and wetland use by Mallards: Relationships with offspring survival. *Wilson Bulletin* 109:504-515.
- DZUS, E. H., AND R. G. CLARK. 1997b. Brood size manipulation in Mallard ducks: Effects on duckling survival and brooding efficiency. *Ecoscience* 4:437-445.
- GREENWOOD, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour* 28:1140-1162.
- GREENWOOD, R. J., P. M. ARNOLD, AND B. G. MCGUIRE. 1990. Protecting duck nests from mammalian predators with fences, traps, and a toxicant. *Wildlife Society Bulletin* 18:75-82.
- GREENWOOD, R. J., A. B. SARGEANT, D. H. JOHNSON, L. M. COWARDIN, AND T. L. SHAFFER. 1995. Factors associated with duck nest success in the Prairie Pothole Region. *Wildlife Monographs* No. 128.
- GRICE, D., AND J. P. ROGERS. 1965. The Wood Duck in Massachusetts. Massachusetts Division of Fish and Game, Boston.
- HANNON, S. J., K. MARTIN, AND J. O. SCHIECK. 1988. Timing and reproduction in two populations of Willow Ptarmigan in northern Canada. *Auk* 105:330-338.
- HARAMIS, G. M., J. D. NICHOLS, K. H. POLLOCK, AND J. E. HINES. 1986. The relationship between body mass and survival of wintering Canvasbacks. *Auk* 103:506-514.
- HARRIS, M. P., S. T. BUCKLAND, S. M. RUSSELL, AND S. WANLESS. 1994. Post fledging survival to breeding age of Shags *Phalacrocorax aristotelis* in relation to year, date of fledging and brood size. *Journal of Avian Biology* 25:268-274.
- HEPP, G. R., R. A. KENNER, AND W. F. HARVEY IV. 1989. Recruitment and natal philopatry of Wood Ducks. *Ecology* 70:897-903.
- HOCHACHKA, W. 1990. Seasonal decline in reproductive performance of Song Sparrows. *Ecology* 71:1279-1288.
- HOWARD, R. D. 1979. Estimating reproductive success in natural populations. *American Naturalist* 114:221-231.
- IASON, G. R. 1989. Growth and mortality in mountain hares: The effect of sex and date of birth. *Oecologia* 81:540-546.
- 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 Service Resource Publication No. 158.
- KLOMP, K. 1970. The determination of clutch size in birds: A review. *Ardea* 58:1-124.
- KRAPU, G. L. 1981. The role of nutrient reserves in Mallard reproduction. *Auk* 98:29-38.
- LACK, D. 1967. The significance of clutch-size in waterfowl. *Wildfowl* 18:125-128.
- LACK, D. 1968. Ecological adaptations for breeding in birds. Methuen, London.
- 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.
- MARTIN, K., AND S. J. HANNON. 1987. Natal philopatry and recruitment of Willow Ptarmigan in north central Canada. *Oecologia* 71:518-524.

- MARTIN, T. E. 1987. Food as a limit on breeding birds: A life-history perspective. *Annual Review of Ecology and Systematics* 18:453-487.
- MURTON, R. K., AND N. J. WESTWOOD. 1977. Energy requirements for egg laying and brood care. Pages 185-214 in *Avian breeding cycles* (R. K. Murton and N. J. Westwood, Eds.). Clarendon Press, Oxford.
- NEWTON, I., AND M. MARQUISS. 1984. Seasonal trend in breeding performance of Sparrowhawks. *Journal of Animal Ecology* 53:809-829.
- OLSEN, G. H., F. J. DEIN, G. M. HARAMIS, AND D. G. JORDE. 1992. Implanting radio transmitters in wintering Canvasbacks. *Journal of Wildlife Management* 56:325-328.
- ORTHMEYER, D. L., AND I. J. BALL. 1990. Survival of Mallard broods on Benton Lake National Wildlife Refuge in north central Montana. *Journal of Wildlife Management* 54:62-66.
- PERRINS, C. M. 1965. Population fluctuations and clutch size in the Great Tit (*Parus major*). *Journal of Animal Ecology* 34:601-647.
- PERRINS, C. M. 1966. Survival of young Manx Shearwaters *Puffinus puffinus* in relation to their presumed date of hatching. *Ibis* 108:132-135.
- POOLE, A. F. 1989. *Ospreys: A natural and unnatural history*. Cambridge University Press, New York.
- REYNOLDS, R. E. 1987. Breeding duck populations, production and habitat surveys, 1979-85. *Transactions of the North American Wildlife and Natural Resources Conference* 52:186-205.
- RINGELMAN, J. K., AND J. R. LONGCORE. 1982. Survival of juvenile Black Ducks during brood rearing. *Journal of Wildlife Management* 46:622-628.
- ROHWER, F. C. 1992. The evolution of reproductive patterns in waterfowl. Pages 486-539 in *Ecology and management of breeding waterfowl* (B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, Eds.). University of Minnesota Press, Minneapolis.
- ROHWER, F. C., AND M. G. ANDERSON. 1988. Female-biased philopatry, monogamy, and the timing of pair formation in migratory waterfowl. *Current Ornithology* 5:187-221.
- ROHWER, F. C., AND D. I. EISENHAEUER. 1989. Egg mass and clutch size relationships in geese, eiders, and swans. *Ornis Scandinavica* 20:43-48.
- ROTELLA, J. J., AND J. T. RATTI. 1992. Mallard brood survival and wetland habitat conditions in southwestern Manitoba. *Journal of Wildlife Management* 56:499-507.
- SARGEANT, A. B., A. D. KRUSE, AND A. D. AFTON. 1974. Use of small fences to protect ground bird nests from mammalian predators. *Prairie Naturalist* 6:60-63.
- SAS INSTITUTE INC. 1990. *SAS/STAT user's guide*, version 6, 4th ed. SAS Institute Inc., Cary, North Carolina.
- SCHULTZ, E. T. 1993. The effect of birth date on fitness of female dwarf perch, *Micrometrus minimus* (Perciformes: Embiotocidae). *Evolution* 47:520-539.
- 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. *Journal of Animal Ecology* 55:1083-1102.
- SIEGEL, S., AND N. J. CASTELLAN, JR. 1988. *Nonparametric statistics for the behavioral sciences*, 2nd ed. McGraw-Hill, New York.
- SMITH, D. G., AND R. GILBERT. 1981. Backpack radio transmitter attachment success in Screech Owls (*Otus asio*). *North American Bird Bander* 6:142-143.
- SPEAR, L., AND N. NUR. 1994. Brood size, hatching order and hatching date: Effects on four life-history stages from hatching to recruitment in Western Gulls. *Journal of Animal Ecology* 63:283-298.
- SUGDEN, L. G., AND G. W. BEYERSBERGEN. 1985. Prediction of duck nest survival in conventional and zero-tilled stubble fields. *Canadian Wildlife Service Progress Notes* No. 156. Saskatoon, Saskatchewan.
- TROTTIER, G. C., D. C. DUNCAN, AND S. C. LEE. 1994. Electric predator fences delay Mallard brood movements to water. *Wildlife Society Bulletin* 22:22-26.
- VIRGL, J. A., AND F. MESSIER. 1997. Habitat suitability in muskrats: A test of the food limitation hypothesis. *Journal of Zoology (London)* 243:237-253.
- WELLER, M. V. 1956. A simple field candler for waterfowl eggs. *Journal of Wildlife Management* 20:111-113.
- WELLER, M. V. 1957. An automatic nest-trap for waterfowl. *Journal of Wildlife Management* 21:456-458.
- WINKLER, D. W., AND J. R. WALTERS. 1983. The determination of clutch size in precocial birds. *Current Ornithology* 1:33-68.
- WINTERSTEIN, S. R. 1992. Chi-square tests for intra-brood independence when using the Mayfield method. *Journal of Wildlife Management* 56:398-402.
- WOO, M., R. D. ROWSELL, AND R. G. CLARK. 1993. Hydrological classification of Canadian prairie wetlands and prediction of wetland inundation in response to climatic variability. *Canadian Wildlife Service Occasional Paper* No. 79, Saskatoon, Saskatchewan.
- ZWICKEL, F. C. 1983. Factors affecting the return of young Blue Grouse to the breeding range. *Canadian Journal of Zoology* 61:1128-1132.

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