

INFLUENCE OF AGE AND TIME ON REPRODUCTIVE PERFORMANCE OF FEMALE LESSER SCAUP

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ABSTRACT.—I examined the influence of age and time on female reproductive performance in a marked population of Lesser Scaup (*Aythya affinis*) breeding in southwestern Manitoba from 1977 to 1980. Arrival date and length of prelaying period varied among years but were not related to female age. Rate of nonbreeding and nest-initiation date varied among years and by female age. Age variation in nonbreeding was due to the failure of yearlings and a few 2-yr-olds to breed. Yearlings began laying an average of 5–8 days later than older females. Clutch size increased with female age but showed no significant annual variation despite extreme changes in water conditions. Reproductive performance generally increased with female age and with improving water conditions.

These results were consistent with theoretical models that predict that reproductive effort (RE) increases with age or with declining residual reproductive value. My data support Williams' (1966) prediction that organisms adapted to living in variable environments adjust their RE in relation to probability of success. Female Lesser Scaup exhibited a temporally dynamic reproductive strategy, and natural selection seemingly has favored "yes-if" genes (Williams 1966) that effect breeding only when conditions are favorable for the individual.

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PARENTAL age and breeding experience influence the reproductive performance of many avian species (Lack 1966, Klomp 1970, Ryder 1980). Among waterfowl, several breeding parameters may vary with age, including spring arrival date, nesting chronology, and clutch size (e.g. Sowls 1955, Finney and Cooke 1978, Krapu and Doty 1979, Baillie and Milne 1982, Rockwell et al. 1983). Reproductive performance of waterfowl also varies annually in response to fluctuating environmental conditions in breeding, wintering, and migration areas (e.g. Crissey 1969, Bengtson 1971, Heitmeyer and Fredrickson 1981, Davies and Cooke 1983, Krapu et al. 1983).

Female age and prairie drought are important factors influencing reproduction of Lesser Scaup (*Aythya affinis*; Rogers 1959, 1964; Trauger 1971). Nonbreeding and age at first breeding in this species have been discussed and speculated upon (see Trauger 1971: 87), but specific factors affecting these breeding parameters re-

main obscure due to insufficient information on known-age individuals. Trauger (1971) reported that productivity, measured by the proportion of returning marked hens that were later observed with broods, increased with female age from 1 to 4 yr. The consistent low productivity of yearling females was attributed to poor nesting success and nonbreeding (Trauger 1971: 78).

I collected reproductive information on a marked population of Lesser Scaup breeding in southwestern Manitoba from 1977 to 1980, a period during which wetland conditions varied dramatically. In this paper, I examine the influence of age and time on the reproductive performance of females. Breeding parameters estimated were: (1) arrival date, (2) rate of nonbreeding, (3) length of prelaying period, (4) nest-initiation date, (5) clutch size, (6) nest success, (7) rate of renesting, and (8) brood survival. Results are discussed in relation to predictions of theoretical models concerning age-specific and temporal variation in reproductive effort.

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STUDY AREA AND METHODS

The 777-ha study area was located 3.3 km southeast of Erickson, Manitoba (50°30'N, 99°55'W) and was de-

TABLE 1. Comparisons of selected environmental parameters and spring arrival dates of Lesser Scaup, 1977-1980.

Parameter	Year			
	1977	1978	1979	1980
Mean maximum April temperature (°C)	14.6	7.4	1.2	14.5
Total April-May precipitation (mm)	107.3	73.4	138.5	10.0
Maximum snowpack before spring thaw (mm H ₂ O)	33.4	47.1	111.1	57.7
Mean April-May total soil moisture (mm) ^a	43.9	66.2	93.0	40.3
Pond ice-free date	17 April	30 April	18 May	22 April
May ponds/km ^{2b}	18.5	32.0	35.1	19.7
First arrival of unmarked Lesser Scaup	14 April	19 April	1 May	16 April
First arrival of marked Lesser Scaup	— ^c	2 May	13 May	21 April

^a Water holding capacity = 177.5 mm.

^b 1962-1981 average = 32.8/km² (Stoudt 1982, J. Serie pers. comm.).

^c A single marked individual returned on 4 May 1977.

scribed in detail by Rogers (1964), Hammell (1973), and Sunde and Barica (1975). Reproductive data were collected from known-age females (banded as ducklings) or those aged by eye color (Trauger 1974, Afton in prep.). Adults were captured in decoy traps (Anderson et al. 1980), nest traps (Weller 1957), and bait traps (Sugden and Poston 1970) modified with a radio-controlled release mechanism. Ducklings and brood hens were captured by drive-trapping (Cowan and Hatter 1952) and night-lighting (Lindmeier and Jessen 1961). Captured birds were banded and individually marked with nasal saddles (Sugden and Poston 1968).

The breeding status of marked females was determined by: (1) intensive behavioral observation, (2) locating nests, and (3) external physical indicators (brood patch, wide pubis spread, egg in oviduct). When estimating the rate of nonbreeding, I also included data from 18 unmarked females that were collected 2-12 km from the study area. The breeding status of these females was determined by ovarian examination (McKnight and Buss 1962).

The breeding status of 5, 1, 4, and 22 marked females could not be accurately determined in years 1977-1980, respectively; consequently, they were excluded from analyses. Sixteen (50%) of these females were probably migrants, because they were captured early in the season and were never observed again in that year or in subsequent years. The remainder (15 yearlings and 1 4-yr-old) were known residents of the study area.

Nests were found by watching females fly or swim to their nests and by flushing hens from cover with a trained dog. One or two assistants and I observed all marked hens on the study area during the nest-initiation period each year. Marked pairs were observed for 265 h, 896 h, and 685 h in years 1977-1979, respectively. Observational effort in 1980 was comparable to previous years, although total hours observed were not recorded.

I used pond counts (Stoudt 1982, J. Serie pers.

comm.) from transects near Minnedosa (23 km south of the study area) and weather data for grid-point 237 (18 km east, Street and Findlay 1981) to index annual changes in wetland conditions. Total soil moisture, considered a prime parameter for expressing meteorological drought, was estimated from a climatic water balance model (Street and Findlay 1981).

Reproductive parameters with categorical responses (nonbreeding, nest success, reneesting) were analyzed with linear models (Grizzle et al. 1969) using the FUNCAT procedure of the Statistical Analysis System (Helwig and Council 1979). Parameters with continuous responses were analyzed with regression techniques (Kleinbaum and Kupper 1978: 362) using the GLM procedure (Freund and Littell 1981). Duncan's multiple range test with Kramer's adjustment was used to detect differences among means of main effects (Duncan 1955, Kramer 1956).

Four female age classes were used: 1-yr, 2-yr, 3-yr, and 4-yr and older. Arrival and nest-initiation dates were coded as Julian dates in analyses. I used pro-

TABLE 2. Probability levels from analyses of the influence of year, female age, and year-by-age interaction on various breeding parameters.

Parameter	Explanatory variables		
	Year	Age	Y by A
Arrival date ^a	0.0005	0.6659	0.8666
Rate of nonbreeding ^b	0.0204	0.0006	0.2551
Prelaying period ^a	0.0001	0.6598	0.1404
Nest-initiation date ^a	0.0001	0.0001	0.0674
Clutch size ^a	0.1374	0.0001	0.4490
Nest success ^b	0.7992	0.0554	0.6343
Rate of reneesting ^b	0.2085	0.6915	0.8090
Brood survival ^a	0.1643	0.4581	0.5778

^a GLM analysis (see text).

^b FUNCAT analysis.

TABLE 3. Summary statistics by year for each breeding parameter. Statistics presented are mean \pm SE (sample size) and range for parameters with continuous responses, and percentages (sample size) for those with categorical responses.

Parameter	Year			
	1977	1978	1979	1980
Arrival date	—	133.5 \pm 2.3 (8) 122-143	136.8 \pm 0.8 (17) 133-145	123.8 \pm 1.9 (45) 111-167
Rate of nonbreeding	28.0% (25)	17.2% (29)	2.3% (43)	15.3% (59)
Prelaying period	—	25.8 \pm 2.6 (5) 21-35	32.2 \pm 0.9 (15) 24-38	43.0 \pm 1.9 (13) 25-56
Nest-initiation date	168.2 \pm 3.8 (6) 154-179	164.7 \pm 1.9 (17) 152-178	169.4 \pm 0.7 (31) 162-179	163.4 \pm 1.2 (24) 152-176
Clutch size	10.4 \pm 0.8 (5) 8-12	10.4 \pm 0.4 (17) 8-14	10.2 \pm 0.2 (31) 8-13	10.3 \pm 0.3 (24) 8-13
Nest success	17.7% (17)	29.2% (24)	40.4% (47)	26.8% (41)
Rate of reneating	0.0% (14)	6.3% (16)	38.9% (18)	16.0% (25)
Brood survival	0.518 \pm 0.134 (3) 0.250-0.667	0.446 \pm 0.101 (7) 0.091-0.846	0.737 \pm 0.076 (19) 0.000-1.000	0.766 \pm 0.067 (10) 0.333-1.000

portions of young in each brood surviving until age class II (>20 days) for analysis of brood survival (Gollop and Marshall 1954). Identification of older broods for counting was frequently impossible because of hens temporarily or permanently leaving their broods. Survival to age class II was considered a good index of fledging success, because most duckling mortality occurs during the first week of life (Hammell 1973, Afton 1983).

RESULTS

Water conditions and spring phenology varied dramatically among years 1977-1980 (Table 1). The springs of 1977 and 1980 were early in comparison to the delayed spring of 1979, as reflected by mean maximum April temperatures and dates on which all study area ponds became ice-free. Wetland numbers were highest in 1979 and lowest during the severe 1977 drought, when wide mud flats were evident on permanent ponds. Water conditions (indexed by pond numbers and soil moisture) improved from 1977 through 1979, due to increasing amounts of winter and spring precipitation, but deteriorated in 1980 because of reduced winter snowfall and almost nonexistent spring rains (Table 1).

First-arrival dates of unmarked Lesser Scaup differed by 17 days among years and were correlated ($r = -0.951$, $df = 2$, $P < 0.05$) with mean maximum April temperatures (Table 1). Marked residents began arriving 1 to 2 weeks later than unmarked birds each year. Arrival dates of res-

idents varied significantly among years 1978-1980 but were not related to female age (Table 2). The mean arrival date in the early spring of 1980 (4 May) was earlier ($P < 0.05$) than the mean arrival dates in the later springs of 1978 (14 May) and 1979 (17 May, Table 3). Annual means and variances of arrival dates were correlated ($r = -0.998$, $df = 1$, $P < 0.05$), suggesting that females arrived more synchronously in late springs.

In 1980, nonbreeding yearlings arrived later ($\bar{x} = 130.6$, $SE = 6.2$ days, $n = 7$), on average, than yearlings that nested ($\bar{x} = 119.7$, $SE = 1.2$, $n = 7$), but the difference was not statistically significant (Mann-Whitney test, $P > 0.05$). Variance in arrival date was greater for nonbreeders than for breeding yearling females (Siegel-Tukey test, $P < 0.01$).

Rate of nonbreeding varied significantly among years 1977-1980 and by female age (Table 2). Age variation in nonbreeding was due to the failure of yearlings and a few 2-yr-olds to breed (Table 4). All 3-yr-old and 4-yr-old and older females nested. Proportions of yearling females that bred ($r = 0.735$) and, to a lesser extent, proportions of 2-yr-olds that bred ($r = 0.201$) generally increased as water conditions (pond numbers) improved, but these relationships were not statistically significant ($df = 2$, $P > 0.05$).

The length of the prelaying period (number of days from arrival until first egg) varied significantly among years 1978-1980 but was not

TABLE 4. Summary statistics by female age for each breeding parameter. Statistics presented are mean \pm SE (sample size) and range for parameters with continuous responses, and percentages (sample size) for those with categorical responses.

Parameter	Female age (yr)			
	1	2	3	≥ 4
Arrival date	129.1 \pm 2.3 (37) 111-167	127.0 \pm 2.9 (12) 116-140	132.2 \pm 3.2 (9) 112-143	122.8 \pm 2.4 (12) 112-134
Rate of nonbreeding	29.3% (58)	9.6% (52)	0.0% (23)	0.0% (23)
Prelaying period	36.6 \pm 3.3 (9) 24-56	39.3 \pm 2.2 (6) 32-44	29.9 \pm 2.7 (9) 21-47	37.4 \pm 2.3 (9) 25-47
Nest-initiation date	171.1 \pm 0.9 (26) 163-178	165.5 \pm 1.3 (22) 157-179	162.8 \pm 1.7 (16) 152-171	163.4 \pm 1.3 (14) 154-169
Clutch size	9.0 \pm 0.1 (26) 8-10	10.0 \pm 0.2 (21) 8-12	10.9 \pm 0.3 (16) 9-12	12.1 \pm 0.2 (14) 11-14
Nest success	26.3% (38)	22.2% (45)	45.5% (22)	41.7% (24)
Rate of renesting	8.7% (23)	17.9% (28)	27.3% (11)	18.2% (11)
Brood survival	0.693 \pm 0.101 (10) 0.111-1.000	0.672 \pm 0.106 (10) 0.000-1.000	0.575 \pm 0.118 (9) 0.000-1.000	0.751 \pm 0.070 (10) 0.250-1.000

related to female age (Table 2). Mean lengths of prelaying periods for years 1978-1980 were all different ($P < 0.05$, Table 3).

The nest-initiation date (first egg date in first nests only) varied significantly among years 1977-1980 and by female age (Table 2). Mean date for yearlings (20 June) was later ($P < 0.05$) than dates for hens of 2-yr (15 June), 3-yr (12 June), and 4-yr and older (12 June, Table 4). Linear regression analysis for years 1978-1980 combined indicated that arrival date explained 26% of the variation in nest-initiation date (Fig. 1). Arrival and nest-initiation dates were not significantly correlated ($P > 0.05$) within any year, although the small 1978 sample suggested a positive relationship ($r = 0.697$, $df = 3$, $P > 0.05$).

Clutch size (first nests only) increased significantly with female age but showed no significant annual variation (Table 2). Covariance analysis, in which the effect of nest-initiation date was removed, gave identical results; age effect was significant ($P < 0.001$) but year and year-by-age interaction were not ($P > 0.05$). The mean clutch sizes of all age classes were different ($P < 0.05$, Table 4).

Multiple regression analysis indicated that age ($P < 0.001$) and nest-initiation date ($P < 0.05$) together explained 71% of the variation in clutch size ($CSIZE = 14.39 + 0.94 (AGE) - 0.04 (NDATE)$, $P < 0.001$, $n = 77$). A comparison of standard partial regression coefficients (see Steel and Torrie 1960: 299) indicated that

female age was 4.3 times more important than nest-initiation date in predicting clutch size.

Nest success (proportion of nests in which at least one egg hatched) tended to vary ($P < 0.06$) with female age but not among years (Table 2). Nest success of 1 and 2-yr-old females combined (24%, $n = 83$) was lower (Chi-square test, $P < 0.05$) than that of older females (43%, $n = 46$). Nest success generally increased as water conditions (pond numbers) improved, but the relationship was not statistically significant ($r = 0.862$, $df = 2$, $P > 0.05$).

Most unsuccessful nests (90%, $n = 89$) resulted from destruction by mink (*Mustela vison*), raccoons (*Procyon lotor*), red fox (*Vulpes vulpes*), or striped skunks (*Mephitis mephitis*); the remainder were caused by farming operations (7%) and investigator disturbance (3%). Seven marked females (3 yearlings, 3 2-yr-olds, 1 4-yr-old) were killed on the nest in 1979 (4 by mink, 2 by red fox) and 1980 (1 by red fox).

Multivariate analysis indicated that the proportion of females renesting, after loss of their first nests, did not vary significantly with age or among years 1977-1980 (Table 2). Univariate analysis, after all ages were combined, however, indicated that proportions varied among years (Chi-square test, $P < 0.02$). Significant variation resulted primarily from lower and higher than expected proportions in 1977 and 1979, respectively. Renesting rates generally increased as water conditions (pond numbers) improved, but the relationship was not statis-

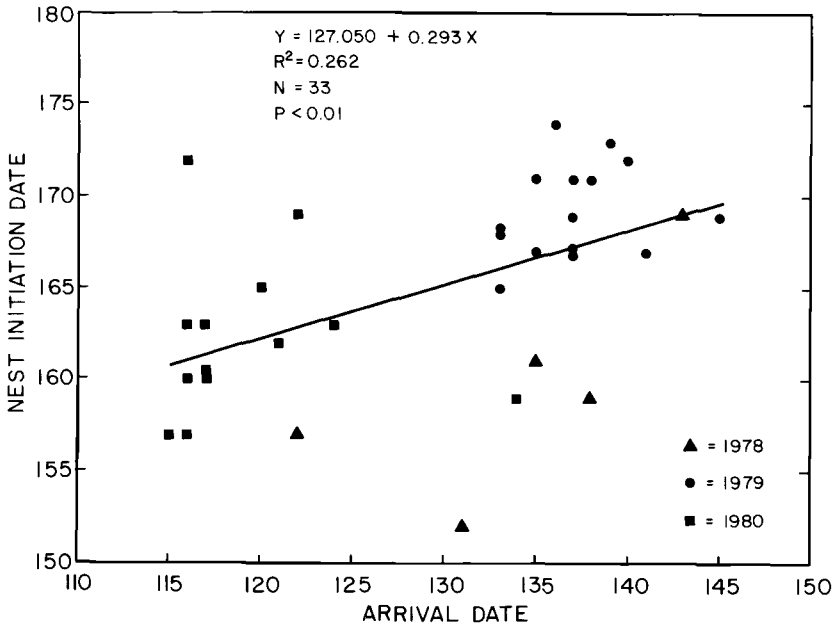


Fig. 1. Relationship of nest-initiation date to spring arrival date for years 1978–1980. Dates are in Julian days.

tically significant ($r = 0.627$, $df = 2$, $P > 0.05$). The renesting rate of 2-yr-old and older females combined (20%, $n = 50$) appeared to be greater than that of yearlings (Table 4), but the difference was not statistically significant (Chi-square test, $P > 0.05$).

Brood survival did not vary significantly with female age or among years 1977–1980 (Table 2). Mean proportion surviving to age class II for all years and age classes combined was 0.675 (SE = 0.049, $n = 39$ broods). Brood survival was not related to water conditions, as indexed by pond numbers ($r = -0.032$, $df = 2$, $P > 0.05$).

DISCUSSION

I found a general relationship between temperature and spring arrival of Lesser Scaup. Similar relationships have been noted for dabbling and diving ducks (*Anas* and *Aythya* spp.) on Delta Marsh, Manitoba (Sowls 1955) and in North Dakota (Hammond and Johnson MS), for Lesser Scaup at Yellowknife, Northwest Territories (Trauger 1971), and for a variety of avian species at other locations (e.g. Saunders 1959, Mikkonen 1981).

The first Lesser Scaup to return in spring were unmarked, and, based on the return of marked

residents in years 1978–1980, these birds were migrants. Gates (1962) noted a similar delay in returns of resident female Gadwall (*Anas strepera*) in Utah. These observations contrast with Sowls's (1955) findings that in a small sample of color-banded Northern Pintails (*Anas acuta*), residents were among the first to arrive in spring. Additional studies of marked birds are needed to determine species differences and whether or not aspects of the breeding strategy (e.g. early nesting versus late nesting) are related to arrival patterns.

I found no age-specific variation in arrival dates, after adjusting for annual differences. This contradicts previous conclusions that adult female residents generally precede yearlings to the breeding grounds, as reported for Lesser Scaup (Trauger 1971), Redheads (*Aythya americana*, Johnson 1978), and Northern Pintails (Sowls 1955). These earlier findings were mostly anecdotal, however, were unsupported by statistical tests, or included direct comparisons of wild adults and hand-reared yearlings.

The tendency of older, more experienced individuals to arrive earlier in the season has been documented in other avian groups, e.g. Arctic Terns (*Sterna paradisaea*, Coulson and Horobin 1976), Prairie Warblers (*Dendroica discolor*, Nolan 1978), and Spotted Sandpipers (*Actitis mac-*

cularia, Oring and Lank 1982). In the latter species, delayed arrival by inexperienced individuals appeared to maximize their success in entering the breeding population, which is consistent with the hypothesis that sexual selection drives arrival times. Sexual selection probably does not directly influence arrival times of ducks, because pairing takes place on wintering and migration areas. It may, however, influence age variation in winter distributions and initiation of spring migration (see Sayler and Afton 1981).

The large variation in arrival dates by nonbreeding yearlings in 1980 suggests that the "decision" not to breed occurs after arrival on breeding areas for some females (some nonbreeders arrive early) but before arrival for other individuals (some arrive late). Three late-arriving yearlings were captured and did not have brood patches, so their late arrival was unlikely to be due to breeding attempts elsewhere. Thus, factors during winter or spring migration may be important in determining an individual's future reproductive performance.

Proportions of 1 and 2-yr-old females that nested tended to increase with improving water conditions. Water levels on the study area in 1980 were much higher than in 1977, contrary to that indexed by soil moisture and pond numbers from transects near Minnedosa (Table 1). Ponds were initially full in 1980 due to carry-over from 1979, and water levels in 1980 were similar to levels in 1978 (based on extent of mud flats). Although Minnedosa is in close proximity to the study area (23 km), there are slight differences in pond size and permanency between the areas (Kiel et al. 1972: 27). Wetlands in the Erickson area are, on average, more permanent, larger in size, and of lower density per unit area. Thus, a statistically significant relationship may have been recorded between rate of nonbreeding and annual water conditions, if water levels had been measured on the study area. Perhaps more important is the fact that the power of this correlation was very low due to my small sample of years ($n = 4$).

Most (94%, $n = 16$) of the known residents whose breeding status was not determined were yearling females. I was unable to determine their status primarily because of their frequent widespread movements and failure to develop small discrete home ranges. Many of these females may have been nonbreeders and thus my

estimate of the rate of nonbreeding by yearlings each year could be slightly low.

Residents spent an average of 4–6 weeks on the study area before nesting. Prelying periods were longest in 1980, when birds arrived an average of 10–13 days earlier than in 1978 and 1979. Arrival dates in 1978 and 1979 were similar, but the mean prelying period in 1979 was longer due to delayed nesting, which correlated with the late date that ponds became ice-free in 1979 (Table 1). Late-nesting dabbling ducks (*Anas* spp.) also spend a lengthy period on breeding areas before laying (Gates 1962, Afton 1979).

Yearlings began laying an average of 5–8 days later than older females. Delayed nesting by first-time breeders has been reported frequently for waterfowl (Mendall 1958, Gates 1962, Bellrose et al. 1964, Brakhage 1965, Dane 1965, Grice and Rogers 1965, Coulter and Miller 1968, Mihelons et al. 1970, Kear 1973, Finney and Cooke 1978, Johnson 1978, Alliston 1979a, Krapu and Doty 1979, Baillie and Milne 1982) and other birds (see Klomp 1970, Perrins 1970, Ryder 1980).

Annual variation in nesting chronology was partially related to variation in arrival dates (Fig. 1). Mean date of nest initiation was earliest in 1980 (12 June), when residents arrived early, and was delayed in 1979 (18 June), when residents arrived, on average, 13 days later than in 1980. Individuals did not show a distinct relationship within years, i.e. the early arrivals in a given year did not initiate nests significantly earlier than later arrivals in the same year.

Although sample size was small, the severe drought in 1977 appeared to delay nesting (even though residents probably arrived as early or earlier than in 1980), based on April temperatures, arrival of unmarked birds, and pond ice-free dates (Table 1). Nesting by Canvasback (*Aythya valisineria*, Stoudt 1982) and Mallards (*Anas platyrhynchos*, Krapu et al. 1983) also is delayed during drought.

Amphipods (Crustacea: Amphipoda) are the most important foods of Lesser Scaup during the breeding season (Rogers and Korschgen 1966, Bartonek and Hickey 1969, Afton in prep.). Egg-laying by Lesser Scaup generally was correlated with June peaks in *Gammarus lacustris* densities in area lakes, although maximum amphipod biomass occurs later in

August (Mathias and Papst 1981, Salki 1981, Mathias et al. 1982, Mathias pers. comm.). Egg-laying by Tufted Ducks (*Aythya fuligula*, Laughlin 1975) and Ruddy Ducks (*Oxyura jamaicensis*, Gray 1980) also is synchronized with peak densities or maximum biomass of their principal foods (chironomid larvae).

Clutch size increased an average of one egg per year of age, from ages 1-yr to 4-yr and older. Small samples prevented me from determining whether or not clutch size continues to increase in the 4-yr and older group, but, because a maximum clutch size of 14 was recorded only once, any average increase must be smaller than that of younger birds. Yearling ducks frequently have been reported to lay smaller clutches than older females (Stotts and Davis 1960, Dane 1965, Coulter and Miller 1968, Morse et al. 1969, Alliston 1979a, Krapu and Doty 1979), but variations in clutch size of older females rarely have been documented (Baillie and Milne 1982), except for geese (Kossack 1950, Brakhage 1965, Kear 1973, Cooper 1978, Finney and Cooke 1978, Rockwell et al. 1983). Clutch size increases with age in many other avian species (see Lack 1966, Klomp 1970, Ryder 1980). Some species, however, show no effect of female age (e.g. Koskimies 1957, Leinonen 1973), and clutch size even declines with age in a few instances (Klomp 1970).

Clutch size did not vary among years 1977-1980 after adjusting for female age, despite marked changes in wetland conditions. Rogers (1962: 56) claimed but did not demonstrate that densities of *Gammarus* spp. were much reduced during low water years. In contrast, J. Mathias (pers. comm.) did not find large variations in *G. lacustris* and *Hyalella azteca* densities among three lakes near the study area or among years 1976-1979, despite marked changes in water levels. Based on stomach analyses of tiger salamanders (*Ambystoma tigrinum*) and stocked rainbow trout (*Salmo gairdneri*), Olenick and Gee (1981) suggested that *Gammarus* spp. were abundant during the severe 1977 drought. These observations suggest that food abundance was not limiting clutch size during the drought for those females that nested.

Variations in abundance, distribution, and quality of food resources, associated with drought and other environmental fluctuations, have been identified as proximate causes of annual variation in clutch size of a variety of wa-

terfowl species (e.g. Bengtson 1971, Davies and Cooke 1983, Krapu et al. 1983). Interestingly, annual mean clutch size increased during drought for some prairie-nesting ducks in two long-term studies (Smith 1971, Stoudt 1971). My results support Bailey's (1981) prediction that this was due to only the oldest females breeding in these years, but, in addition, renesting was probably uncommon, and thus annual means were not reduced by smaller reneest clutches (see Coulter and Miller 1968: 27).

Nest success of 1 and 2-yr-olds was lower than that of older female Lesser Scaup. In contrast, female age does not influence nest success of several other waterfowl species (Brakhage 1965, Johnson 1978, Baillie and Milne 1982). Nest success of Lesser Scaup generally increased with improving water conditions (Rogers 1964, this study). Factors contributing to age-specific and temporal variation in nest success require further study.

The proportion of hens that reneested, after loss of their first clutch, tended to increase with improving water conditions. Renesting rates of yearlings appeared to be lower than that of older birds, but the difference was not statistically significant. A higher rate of reneesting by older females was suggested for Gadwall (Gates 1962), Wood Ducks (*Aix sponsa*, Grice and Rogers 1965), Lesser Scaup (Trauger 1971), Redheads (Alliston 1979b), and Mallards (Krapu and Doty 1979), but was demonstrated only for Blue-winged Teal (*Anas discors*, Strohmeier 1967) and indirectly for Mallards and Black Ducks (*Anas rubripes*, Coulter and Miller 1968).

Brood survival did not vary significantly with female age or among years. These results are tentative because samples were so small in some years, due to nonbreeding and poor nest success, that demonstration of significant differences would be difficult. Lack of annual variation in brood survival was not surprising, because females moved broods to the largest and most permanent ponds (Hammell 1973, Afton in prep.), and amphipod populations, an important duckling food (Bartonek and Hickey 1969, Sugden 1973), did not fluctuate greatly among years.

Several theoretical papers have predicted that reproductive effort (RE) should increase with age, or that RE should vary inversely with residual reproductive value (RRV) (Williams 1966, Gadgil and Bossert 1970, Pianka and Parker

1975, Charlesworth and Leon 1976, Pianka 1976; but see Fagen 1972, Schaffer 1974). Williams (1966) predicted that organisms adapted to living in variable environments should adjust their RE relative to their probability of success.

In general, my data were consistent with predictions that RE increases with age or with declining RRV. Although RE was not measured directly, proportions of females breeding and reneating, and perhaps clutch size, should be positively correlated with RE. My data also support Williams' (1966) prediction that individuals adjust their RE in relation to probability of success. Females exhibited a temporally dynamic reproductive strategy (cf. Nichols et al. 1976), and natural selection seemingly has favored "yes-if" genes (Williams 1966: 173) that effect breeding only when conditions are favorable for the individual. Females 3-yr and older made one nesting attempt regardless of environmental conditions, which probably reflects their higher probability of offspring success (higher nest success) and their relatively small RRV. Changes in RRV with age were probably a function of survivorship, because I found no evidence that fecundity decreased with age.

Nichols et al. (1976) noted that high annual variation in reproductive performance could indicate either variation in RE or variation in food levels with constant RE. Because populations of the predominant food sources of Lesser Scaup did not fluctuate greatly among years (see p. 261), RE apparently did vary among years.

Dynamic reproductive strategists apparently "predict" offspring survival from environmental cues (Cohen 1967, Nichols et al. 1976). Nest success (influenced primarily by predation) decreased with deteriorating water conditions, while brood survival remained relatively constant (Rogers 1964, this study); consequently, nest success was the critical factor affecting variation in offspring survival. Thus, females probably use proximate environmental factors associated with water-level fluctuations (see Rogers 1962, 1964) to predict their probability of success, whereas the primary ultimate factor affecting nonbreeding (and RE) probably is predation upon nests. Because predominant foods did not fluctuate greatly among years, food abundance on breeding areas apparently was not an important proximate factor affecting nonbreeding of Lesser Scaup.

Poor reproductive performance of young female waterfowl has been attributed to less experience in locating, competing for, and exploiting food resources, to less ability to accumulate large endogenous reserves, and to lower efficiency at foraging for specific nutrients needed for egg-formation (e.g. Batt and Prince 1978, Batt 1979, Krapu and Doty 1979, Baillie and Milne 1982). Young birds are less efficient feeders than adults in some species (see citations in Baillie and Milne 1982), but age variation in feeding efficiency has not been documented for waterfowl.

The best evidence that age variation in reproductive performance of ducks is related to feeding comes from the captive experiments of Batt and Prince (1978). They found no age-specific variation in the breeding parameters of Mallards under controlled conditions, in the absence of competition, and when food was provided *ad libitum*, a finding that was inconsistent with the field data of Krapu and Doty (1979). Studies of age variation in feeding efficiency and how such variation relates to reproductive performance are urgently needed.

Batt (1979) suggested that delayed breeding and smaller clutches of yearling Mallards and other waterfowl were consequences of inexperience and competition with older birds rather than part of an evolved reproductive strategy *per se*. I believe that he was implying that the REs of yearlings and older females were similar but that the total amount of resources available to yearlings was less (due to lower feeding efficiency and/or displacement to inferior territories). This seems likely for Mallards, when one considers Batt's experimental results, observations of territorial behavior (e.g. Titman 1983), and Krapu and Doty's (1979) findings that, although the clutch size of wild yearlings averaged one egg less than that of adults, the clutch size of adults (2-yr and older) did not increase further with age.

I believe, however, that clutch-size variation of Lesser Scaup was not due solely to experience or competition but was at least partially related to age variation in RE. Breeding pairs did not defend territories but, instead, had relatively small, highly overlapping home ranges (Hammell 1973, Afton in prep.). Although inexperience in locating and efficiently exploiting food resources on breeding areas could ex-

plain lower reproductive performances of yearlings, such explanations alone seem unlikely to account for subsequent large increases in clutch size of older females (see also Curio 1983). Captive breeding experiments with Lesser Scaup are needed to examine the relative importance of experience and age variation in RE more critically. Comparisons of clutch size of wild first-time breeding females of different ages might provide a strong field test of the hypothesis.

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