Age-related aspects of Mallard reproduction

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Wild dabbling duck females are known to breed as yearlings (Sowls 1955), but their contribution to annual recruitment in comparison to older breeders (adults) is poorly understood for most species including the Mallard *Anas platyrhynchos*. Dzubin (1969) postulated that adult Mallard females may come into breeding condition first and occupy the best habitat, forcing yearlings into less suitable areas thereby contributing to lower productivity among the yearling cohort. It has also been suggested by Smith (1969) that yearling Mallard may be less prone to breed than adults under drought conditions.

The present paper considers whether certain variables potentially important to recruitment in Mallard are influenced by age.

Study area

Research was conducted in that portion of eastern and south central North Dakota shown in Figure 1, a part of the glaciated prairie region of North America. The climate is marked by wide variation in annual temperature and mean annual precipitation ranges from 41–48 cm (Jensen 1972). The Drift Prairie of eastern North Dakota, a part of the Central Lowland, typically is gently rolling ground moraine drained by several intermittent and permanent water courses. The Missouri Coteau, which lies at the eastern edge of the Great Plains, is characterized by a knob and kettle topography with limited natural drainage and numerous wetland basins. Detailed descriptions of the wetland types occurring in this Region are presented by Stewart and Kantrud (1971). Cultivated crops with grassland occur primarily in corridors along water courses in the Drift Prairie and in steeply rolling areas of the Missouri Coteau. Mallard nest at varying densities throughout the Drift Prairie and Missouri Coteau; the highest numbers are in localities where wetlands are numerous and land use is least intensive. The study area is principally in private ownership, but numerous tracts containing wetlands are owned and managed for waterfowl production by the US Fish and Wildlife Service.

Methods

Mallard females were captured at nest sites

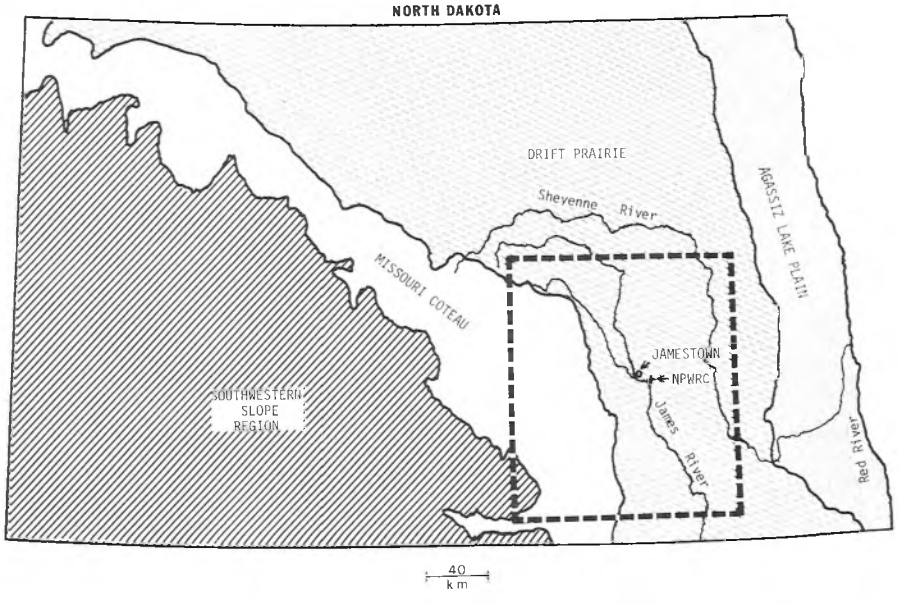

Figure 1. Map of North Dakota with the study area boundaries indicated by dashed lines.

and marked during 1968–1971 as described by Doty & Lee (1974) and during 1975–1976 by the senior author using the capture techniques described by Shaiffer & Krapu (1978). Age of wild females captured during 1975–1976 was determined by a technique developed by Krapu *et al.* (1979). Each was marked with a serially numbered nasal saddle of the design described by Doty & Greenwood (1974).

Nest initiation dates were estimated by back-dating clutches to onset of egg laying by field candling (Weller 1956). Nest initiation dates and clutch sizes of marked females were monitored for 2–7 years.

The age of collected females was determined during 1974–1976 using the technique described by Krapu *et al.* (1979). They were considered to exhibit follicular development when the ovary was enlarged (> 3·0 g) but ovulation had not occurred, and in the laying phase when one or more follicles had ruptured and at least one enlarged follicle remained to be ovulated or an egg was present in the oviduct.

Physical condition was evaluated from body weight, measured on a Pennsylvania scale to the nearest gram (g), and lipid content, determined by the Soxhlet extraction process (Horwitz 1975).

Results

Nest initiation patterns

Clutches were initiated from 4 April to 17 July, with a median date for 265 nests of 3 May. Twenty-four per cent of the adults initiated laying before 20 April (median date 28 April for 45 nests) whereas all nests of known yearlings were initiated after that date (median 5 May for 10 nests).

Nest initiation dates for 21 individually marked females recorded in 2 or more years are shown in Table 1. Analysis of variance indicated the date of nest initiation is significantly different between years ($F = 2{\cdot}71$, 6 DF, $P < 0{\cdot}05$). A substantial part of this effect can be attributed to annual variations in weather during April (Figure 2). Onset of nesting was earliest during 1971 and 1976 when snow cover was absent throughout April and temperatures had climbed above 10°C during the first week. Nesting was delayed when snow cover was present early in April 1 and the maximum daily temperature rose only slightly above 0°C in mid-April. Nest initiation dates of the six marked adult females for which data were available in 1975 and 1976 (Table 1) underscores the pronounced effect of

Table 1. Nesting chronology and clutch size (in parentheses) of marked Mallard females during a 7-year period in eastern North Dakota. Females were 1+ years old during first year.

	Estimated day from 14 April first egg laid (and clutch size)						
Female no.	1968	1969	1970	1971	1972	1975	1976
1	18(11)	7(11)	9(11)				
2	19(11)	13(8)	14(11)				
3	31(9)	17(10)	24(9)	10(11)			
4	47(9)	16(8)	25(9)	10(10)	18(10)	20(11)	5(11)
5		6(11)	12(11)	5(11)	10(11)		
6		6(11)	14(9)	2(12)	6(11)	17(10)	5(11)
7		8(11)	13(14)*	27(9)	26(11)		
8		8(10)	32(10)	19(10)			
9		9(8)	10(11)				
10		15(10)	27(9)		19(10)		
11		36(11)	14(11)	32(9)			
12		37(10)	28(14)*	17(8)	17(10)		
13		61(8)	9(10)	1(10)	20(9)		
14			22(10)	18(9)	12(10)		
15			26(10)	28(9)	17(10)	20(11)	
16			27(9)	17(10)			
17				9(10)	6(11)		17(9)
18						13(12)	4(11)
19						15(11)	6(13)
20						24(10)	5(11)
21						25(10)	4(12)

* Probable multiple clutch.

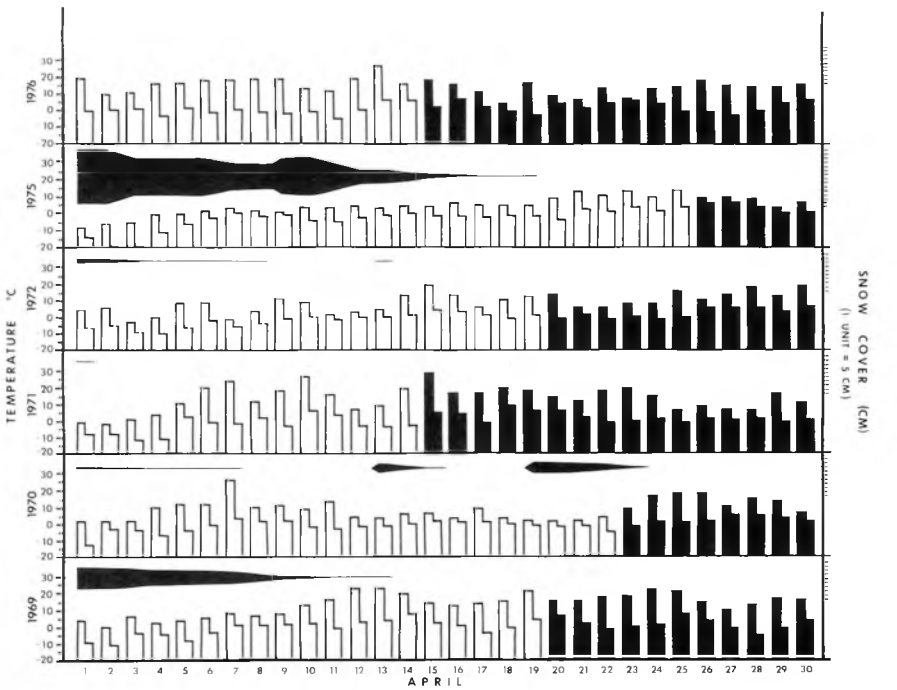

Figure 2. The relationship of daily maximum and minimum temperatures and depth of snow cover at Jamestown, North Dakota, during April to timing of laying by Mallard females. Climatological statistics are from the US Department of Commerce (1969–1972, 1975–1976).

weather. The mean date averaged 14 days earlier in 1976 (19 April). The relationship of temperature to onset of nesting may be caused, in part, by the effect on access to food resources. Invertebrates from shallow prairie wetland basins form a major part of the diet of female Mallard during the laying period (Swanson *et al.* 1979). Analysis of variance of data on nest initiation by marked females during the entire study period did not indicate significant individual differences ($F = 1{\cdot}22$, 20 DF, $P > 0{\cdot}1$).

Nesting activity

Examination of the reproductive tracts of 57 known-age female (17 yearlings, 40 adults) collected during 1974–1976 indicated that most mated females made at least one nesting attempt. Those showing lack of follicle development generally were taken before 20 April. Adults did exhibit a higher frequency (80%) of ovarian follicle development and laying activity than yearlings (67%). Twenty-two per cent of the yearlings were in the laying phase when collected whereas 50% of the adults had ovulated. However, these differences were not significant $P > 0{\cdot}10$, chi-square).

Female condition

The physical condition of Mallard during the breeding period varied with age. Mean weights of 105 adult and 44 yearlings sampled during the breeding seasons were 1,121·2 ± 121·5 g and 1,070·2 ± 121·3 g respectively (Mean ± SD). In April, adults averaged 60 g heavier than did yearlings; the older birds maintained a higher average body weight during May and June (Table 2).

Lipid content in carcasses of adults averaged 24% higher than among yearlings (72·4 ± 44·2 g vs. 55·0 ± 39·7 g). Mean lipid levels of adults exceeded those of the yearling cohort throughout the breeding season (Table 2). Lipid reserves of both age cohorts fell sharply from April to May during the peak of nesting activity. The difference in lipid content between age groups remained consistent during May and June when most females had made one or more nesting attempts.

Table 2. Body weights and lipid reserves (mean and S.D.) of yearling and adult Mallard females at monthly intervals during the nesting season (1974–1976). Sample sizes are shown in parentheses.

Age of female	April	May	June
		Body weight (g)	
Yearling	1,137 ± 106·9(21)	1,028 ± 96·5(20)	889 ± 13·6(3)
Adult	1,197 ± 104·9(41)	1,079 ± 104·5(60)	1,012 ± 134·1(4)
		Total Lipids (g)	
Yearling	81·8 ± 36·6(8)	39·5 ± 16·3(5)	9·6 ± 8·3(3)
Adult	105·9 ± 34·3(19)	49·4 ± 29·8(19)	22·2 ± 21·9(4)

Clutch size

Initial completed clutches laid by yearlings (7 nests) and adults (46 nests) averaged 9·3 ± 1·7 eggs and 10·3 ± 1·1 eggs, respectively. This difference was significant ($P < 0·05$). The yearlings tended to initiate nesting later than did adults. Examination of reproductive tracts suggested that most hens initiate their first nesting attempt by mid-May and clutches laid after that date were mostly renests. Clutch size did not increase consistently with age beyond the yearling age class (Table 1). However, female no. 4, during 7 years, laid clutches of 9, 8, 9, 10, 10, 11, and 11 eggs. Repeatability in clutch size among certain females was high (nos. 1, 5, and 8; Table 1). Weather patterns that influenced timing of the onset of nesting can markedly affect clutch sizes. For example, during 1975 when temperatures were unusually low during April (Figure 2), initial clutch sizes of 6 adult marked females averaged 10·7 ± 0·8 eggs, whereas in 1976, with more favourable temperatures and earlier dates of nest initiation, clutch size averaged 11·5 ± 0·8 eggs (Table 1).

Discussion

Nest initiation by yearlings tends to lag behind the adult cohort. This agreed with indirect evidence in New England of Coulter and Miller (1968). Earlier nesting by adults has been reported previously by Dane (1965) for Blue-winged Teal *Anas discors*, Grice & Rogers (1965) for Wood Ducks *Aix sponsa*, Trauger (1971) for Lesser Scaup *Aythya affinis*, and Johnson (1978) for Redhead *Aythya americana*. Spurr & Milne (1976) reported that young (2- and 3-year old) Common Eider *Somateria molissima* females tended to lay late in the season. All this tends to support the hypothesis of Dzubin (1969) that adults come into breeding condition first and select the most suitable habitat. Because of low densities of Mallard pairs on the study area and throughout eastern North Dakota (Steward and Kantrud 1975), it is uncertain if significant competition existed for resources necessary for breeding. However, past experience and homing would nevertheless favour the adult cohort, less so during years of favourable water conditions.

Because of reduced nutrient reserves, and less experience in locating and exploiting food resources, yearling females presumably are less prone to renest. Our findings suggest that breeding intensity (i.e. the proportion of females actively nesting) may be higher among the adult cohort. Batt (1976) found that where food is fed *ad libitum* in the absence of competition, yearling Mallard females are capable of a similar reproductive effort as adults although weighing less at the onset of breeding. Under field conditions, however, fewer eggs typically are laid by yearlings because they are less efficient at foraging for the nutrients required for egg formation. Krapu (1979) reported that the number of eggs produced by captive Mallard females was directly related to the quality and quantity of food available during the laying period.

Our studies suggest that most yearlings nested at least once during each year in North Dakota. However, this may reflect the favourable habitat conditions existing during that period. Dementiev and Gladkov (1952) state that some yearling Mallard do not breed in the Soviet Union but rather wander through southern parts of the range. Nonbreeding in North America presumably is more prevalent among yearlings than adults under conditions where food is scarce. A more definite interpretation of the effect of age on Mallard recruitment can be achieved through long term studies that actually measure the number of offspring reared to flight stage by females of known age, a difficult but important research need.

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Summary

Several variables potentially important to recruitment in Mallard *Anas platyrhynchos* populations were compared in North Dakota during 1968–1976. Median date of nest initiation by adults was 7 days earlier than for yearlings. Temperature and snow cover during April varied widely and caused significant annual variation the onset of laying.

Weights of adults and yearlings averaged 1,121 g and 1,070 g, respectively, during the breeding season, and carcass lipid content 72 g and 55 g. Age-related differences in body weight and lipid content were maintained throughout the nesting season. Initial clutches of adults averaged 1·0 egg larger. Recruitment among the yearling cohort is more susceptible to deterioration of habit or to intraspecific competition because of less experience in securing the dietary needs for reproduction.

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