INHERITANCE OF EGG PRODUCTION AND JUVENILE GROWTH IN MALLARDS

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ALTHOUGH many studies have been made on the ecology of the Mallard (*Anas platyrhynchos*), little is known about the inheritance of its quantitative traits. This paper reports on the inheritance of egg production and juvenile growth in two strains of Mallards.

MATERIALS AND METHODS

Stocks.—We studied two pedigreed lines (Delta and wild) of Mallards. The base population for the Delta line was ducklings from eggs of free-winged Mallards of uncertain origin collected from nest boxes about the Delta Station. The uncertainty of origin arose from a year-around artificial feeding program, a limited harvest, and a population that included "game farm" Mallards from the McGraw Wildlife Foundation (introduced about 7 years earlier) and "wild" birds attracted to the area. The base population for the wild line was formed in 1966 by collecting eggs from nests 5 to 100 miles from the Delta Station. The Delta and wild lines were reciprocally crossed in 1967.

Management 1965.—We checked 90 nest boxes used by resident free-winged Mallards each afternoon and marked the fresh eggs. Eggs were collected the day after the last egg in a clutch was laid and incubated at 37.5°C and 70 to 80 per cent humidity. Ducklings were removed at about 18 hours posthatching, tagged according to the egg numbers, and placed in small rearing pens with an infrared heat source.

Management 1966.—One male and three females pedigreed from the F_1 generation of the Delta line were randomly assigned (excluding full and half-sib matings) in April to seven 4 × 8 m breeding pens with a 1 × 1 m tank in the center and piles of straw and other vegetation available for nest sites. Pens were checked each afternoon and eggs and ducklings were treated similarly to 1965. Excess birds were maintained as flock matings in two pens (12 × 44 m and 15 × 30 m). Although eggs from wild dams were at varying stages of development when collected, hatching and rearing procedures were the same as those used for the Delta line.

Management 1967.—Within each line, one male and two females from the 1966 pedigreed progeny were randomly assigned (excluding full and half-sib matings) to breeding pens. Fourteen 2 × 4 m pens were used for the Delta line and twelve 3 × 5 m pens were used for the wild line. Reciprocal crosses were made by a random assignment of 8 males and 8 females from each line to breeding pens. There were 4 such pens obtained by subdividing a 14 × 30 m enclosed area with a 10 × 21 m pond in the center. All pens were checked each afternoon. Eggs and ducklings were treated similarly to 1965 and 1966 except that eggs were collected on the 6th afternoon after the clutch was completed. Excess birds were maintained by lines as flock matings in two flight pens (12 × 44 m and 15 × 30 m).

Traits.—Measurements were obtained on an individual bird basis for number of eggs laid; percentage fertility; egg weight in g; time to hatching in hours; body weight in g at 18 hours; 2, 4, 6, and 8 weeks of age, and adults (52 to 60 weeks of age).

Analyses.—Standard statistical procedures are used (Snedecor, 1956). The 0.05 and 0.01 probability levels are used in all tests of significance and the term significance

applies to the 0.01 level unless otherwise specified. Standard deviations are used to denote variation about the mean. Heritability estimates, the regression of genotype on phenotype, are calculated by intra-sire regressions of offspring on dam (Lush, 1940) using the repeated parent technique (Bohren et al., 1961). These estimates were obtained for the Delta line, but not for the wild line because of sample size.

Results and Discussion

Egg production.—Each year the Delta line was overwintered in a 12 × 44 m flight pen. On 18 April the birds for the pedigree matings were removed from this flock and placed in breeding pens. Seasonal egg production started on 27 March 1966 and 30 March 1967, and continued until 6 July 1966 and 3 July 1967, about 14 weeks each year. As the movement of birds may influence egg production, the data presented start on 18 April. Mean egg production for all females is 22.0 ± 4.7 for F_1 females with 85 per cent laying eggs and 22.9 ± 4.8 eggs for F_2 females with 93 per cent laying eggs with no significant difference between means. Egg production peaked each year during the week ending 16 May (Table 1).

The wild line was overwintered in the Delta hatchery and removed to the breeding pens on 19 April. No eggs were laid prior to this date. Egg production lasted about 5 weeks, from 8 May to 11 June, and peaked during the week ending 30 May. The mean number of eggs laid for all females is 4.1 ± 2.0 eggs with 46 per cent laying eggs. Although there is no significant difference for mean egg production between F_1 and F_2 Delta females, production in the Delta line is significantly higher than in the wild line. Also, the production period in the Delta line is about 9 weeks longer than in the wild line.

The difference in egg production between lines is also reflected by the mean number of clutches per female. Wild line females laid 0.6 ± 0.8 clutches and none was observed to lay more than two clutches. The mean number of clutches for F_1 and F_2 Delta line ducks was 2.1 ± 1.4 and 1.9 ± 1.4, respectively. Frequency distributions of numbers of clutches within lines and generations are given in Table 2. Although means between the F_1 and F_2 females are comparable, the percentage of the F_1 females laying more than two clutches is 46 in contrast to only 14 for the F_2 females. The reduction in the F_2 generation may have been caused by the longer time that these females were allowed to incubate their eggs and the significantly larger clutch size (Table 3). Thus, the completion of two clutches in the F_2 generation required an additional 12 days over the F_1 generation which may have been long enough for environmental factors such as photoperiod to suppress additional renesting.

The rate of laying within clutches for the Delta line is essentially an egg a day (Table 3). Laying rates, although high in the wild line, are

TABLE 1

TOTAL WEEKLY EGG PRODUCTION BY LINES AND GENERATIONS

Week ending		No. of eggs		
Day	Month	F_1 Delta	F_2 Delta	F_1 Wild
25	April	17	10	0
2	May	25	32	0
9		59	82	1
16		97	111	12
23		83	95	27
30		63	87	36
6	June	70	70	29
13		68	75	7
20		51	49	0
27		30	21	0
4	July	9	9	0
11		2	0	0
TOTAL		574	641	112
No. Females		26	28	24

significantly lower than in the Delta line. It is interesting that Delta line females had significantly larger clutches in the F_2 than in P_1 and F_1 generations. The average clutch size for the females that laid eggs in the P_1 and F_1 generations for the Delta line and for the wild line is similar to the 9.8 eggs reported by Sowls (1955) for Mallards nesting in the Delta area. His value and those obtained by us are higher than the 8.8 eggs reported for Mallards nesting in southeastern Alberta (Keith, 1961).

Heritability estimates in the F_2 generation are 0.26 for total eggs laid, 0.46 for the number of eggs in the first clutch, and 0.55 for egg weight (Table 4). These values are consistent with those reported by Stasko (1966b) whose estimates range from 0.29 to 0.46 for annual egg production and 0.46 to 0.49 for egg weight in Pekin ducks. These estimates of egg production and egg weight are in agreement with those summarized for chickens and turkeys (Spector, 1956). Lack (1967) demonstrated that average clutch size of different waterfowl species varied inversely

TABLE 2

FREQUENCY DISTRIBUTIONS OF NUMBER OF CLUTCHES WITHIN LINES AND GENERATIONS

		No. of clutches per female					Total no. females
Line	Gen.	0	1	2	3	4	
Delta	F_1	4	5	5	9	3	26
	F_2	2	4	18	4	0	28
Wild	F_1	13	8	3	0	0	24

TABLE 3

CLUTCH SIZE AND RATE OF LAY BY LINES AND GENERATIONS

Line	Gen.	Total no. of clutches	Clutch ($\bar{x} \pm$ SD no. of eggs) First	Second	Third	Total	Rate of lay (% of eggs laid at 1-day intervals)
Delta	Base Pop.	28	–	–	–	9.5 ± 1.6[1]	96
	F_1	40	10.3 ± 2.1	9.6 ± 1.6	9.0 ± 1.5	9.7 ± 1.8	98
	F_2	52	12.8 ± 3.0	11.4 ± 3.3	10.8 ± 1.0	12.1 ± 3.1	97
Wild	F_1	9	–	–	–	9.3 ± 1.6[2]	89

[1] Could not determine if clutch was first, second, or third.
[2] Eight of the nine clutches were first clutches.

with the relative egg size and postulated that heredity was the primary influence on specific differences in clutch size.

Egg production of the wild line is low when compared to field studies (e.g. Sowls, 1955; Keith, 1961) where under natural conditions the majority of females would be expected to lay one or more clutches of eggs. Although clutch size in the wild line is similar to that observed in field studies, only 46 per cent of the females laid eggs suggesting that the captive environment placed restrictions on reproductive success that are not evident under natural conditions. The low egg production for the wild line is not consistent with the higher production noted for the Delta line. As both lines originated from free-winged females, the response in a captive environment is suggestive of different environmental histories and genotype-environment interactions.

Renesting interval.—Two renesting records were obtained for the F_1 wild line and the interval was 6 days in both instances. Renesting was

TABLE 4

HERITABILITY ESTIMATES (h^2) FOR DELTA MALLARDS BASED ON INTRA-SIRE REGRESSIONS OF OFFSPRING ON DAM[1]

Trait		$h^2 \pm$ SE
Total eggs laid[2]		0.26 ± 0.39
No. eggs in first clutch[2]		0.46 ± 0.57
Egg weight[2]		0.55 ± 0.11
Body weight[3]		
4-week	males	0.52 ± 0.16
	females	0.30 ± 0.13
8-week	males	0.64 ± 0.13
	females	0.21 ± 0.17

[1] $h^2 = 2(b)$.
[2] F_2 generation.
[3] F_3 generation.

TABLE 5

FREQUENCY DISTRIBUTIONS OF THE RENESTING INTERVAL FOR THE DELTA LINE[1]

Gen.		No. of days between nests after eggs collected									
		2	3	4	5	6	7	8	9	10 and over	Total
F_1	No.	4	1	6	2	6	4	1	1	3	28
	%	14.3	3.6	21.4	7.1	21.4	14.3	3.6	3.6	10.7	100
F_2	No.	0	0	0	3	12	7	2	1	0	25
	%				12.0	48.0	28.0	8.0	4.0		100

[1] Eggs collected on second afternoon after last egg in F_1 and on sixth afternoon after last egg in F_2.

frequently observed in the Delta line and frequency distributions of the renesting intervals for the F_1 and F_2 generations are given in Table 5. The mean renesting interval, in days, is 6.0 ± 3.6 for the F_1 and 6.4 ± 1.0 for the F_2 females. Although the difference in the renesting intervals for the 2-day and 6-day egg collection methods (F_1 and F_2) is not significant, the variance for the renesting interval is reduced when eggs are collected on the 6th day of incubation. Seubert (1952) reports a positive linear relationship of renesting interval to stage of incubation. Sowls (1955) obtained a similar regression with ducks, but based on the error term it does not appear to be significant.

Fertility.—Fertility was high in both base populations and then it declined in the filial generations (Table 6). Although percentage fertility showed a significant increase in the F_2 over the F_1 Delta line, there was no significant increase in the percentage of clutches with fertile eggs.

In the pens used for reciprocal matings between lines, the Delta males tended to court Delta females on the other side of the fence. Such behavior was not so pronounced in the wild line. This continued until burlap was placed on the fence to restrict vision. On three occasions holes in the fence allowed birds from both sexes of a line to be in the same pens for about 24 hours. This resulted in increased fertility. After these occurrences no ducklings were considered as cross progeny for a period

TABLE 6

FERTILITY OF EGGS AND PERCENTAGE OF CLUTCHES CONTAINING FERTILE EGGS FROM MATINGS BY LINES AND GENERATIONS

Line	Gen.	Per cent fertile eggs	Per cent clutches with fertile eggs
Delta	Base pop.	100	100
	F_1	57	70
	F_2	75	83
Wild	Base pop.	96	100
	F_1	39	50

of 2 weeks (Elder and Weller, 1954; Ash, 1962). Percentage fertility for the season was 28 for matings of wild males with Delta females and 20 for Delta males with wild females. This low fertility suggests that Delta and wild lines did not cross readily.

Emergence time.—Emergence time is the period of time from the onset of hatching within a clutch for the other eggs to hatch. Maximum emergence time (time interval between the hatching of the first and last ducklings) does not exceed 30 hours for the base populations, with 75 and 80 per cent of the ducklings hatching within the first 10 hours for wild and Delta lines, respectively (Table 7). Mean emergence time for the Delta line base population is 6.1 hours. It increases to 8.2 and 16.1 hours for the F_1 and F_2 generations, respectively. Variance among years are heterogeneous and means and variances increase with each filial generation. Under natural conditions one would expect selection against long emergence times. If artificial incubation does not impose such stabilizing selection, then variability should increase. In chickens the heritability for length of incubation period is 0.50 (Siegel et al., 1968) showing considerable genetic variation for this trait. Sowls (1955) observed eggs hatching at four Pintail (*Anas acuta*) and two Blue-winged Teal (*Anas discors*) nests and noted that maximum emergence time under natural incubation was not greater than 1 hour. Although the emergence period is short in the wild there probably has not been gene fixation for this trait.

Body weight.—Juvenile body weight data for the F_2 and F_3 generations Delta line are pooled in Table 8 because there are no differences between generations. For adults, F_2 birds weighed approximately 140 g more than F_1 birds, and Table 8 includes only data for the former.

Body weight data are analyzed by two procedures: (1) between lines and sexes excluding reciprocal crosses by the statistical model:

$$X_{ijk} = \mu + L_i + S_j + (LS)_{ij} + e_{ijk}$$

where X_{ijk} is the weight of the k^{th} progeny in the i^{th} line and the j^{th} sex, μ is the population mean, and e_{ijk} is the variance inherent in the population; and (2) within sexes among pure and cross lines by the statistical model:

$$X_{ij} = \mu + L_i + e_{ij}$$

where X_{ij} is the weight of the j^{th} progeny in the i^{th} line, μ is the population mean, and e_{ij} is the variance inherent in the population (Snedecor, 1956).

At 18-hours posthatching, duckling weight averages 60 to 63 per cent of the fresh egg weight. Pooled fresh egg weight in the F_1 and F_2 Delta line generations is 56.4 $\pm$ 5.3 g. The mean weight in the F_1 generation

TABLE 7

FREQUENCY DISTRIBUTIONS AND MEANS OF EMERGENCE TIME (HRS.) BY LINES AND GENERATIONS[1]

Line	Gen.	No. clutches	Per cent of eggs hatching during time intervals after the first emerged[2]								Mean time	
			0–10	11–20	21–30	31–40	41–50	51–60	61–70	71 and over	n	$\bar{x}$
Delta	Base pop.	7	79.7	17.2	3.1	–	–	–	–	–	61	6.1
	F_1	10	67.7	19.4	7.2	5.7	–	–	–	–	82	8.2
	F_2	29	52.4	22.2	13.1	4.0	2.7	1.3	1.6	2.7	269	16.1
Wild	Base pop.	15	74.8	16.5	8.7	–	–	–	–	–	125	7.9

[1] Clutches in which 7 or more eggs hatched were used.

[2] Percentages were calculated within each clutch and averaged for each generation.

TABLE 8

WEIGHTS OF MALLARD JUVENILES AND ADULTS BY SEX AND LINE[1]

Sex	Line		Body weight (g ± SD)					
			18 hours	2 weeks	4 weeks	6 weeks	8 weeks	Adult
Male	Delta (D)	n	210	185	176	165	134	53
		x̄	35.0 ± 2.9^{c}	225 ± 24^{c}	610 ± 52^{b}	945 ± 96^{b}	1121 ± 131^{b}	1332 ± 110^{b}
	W♂ × D♀	n	19	19	19	19	17	–
		x̄	38.0 ± 3.1^{d}	234 ± 30^{bc}	605 ± 70^{b}	903 ± 85^{ab}	1040 ± 94^{ab}	–
	D♂ × W♀	n	9	8	8	8	6	–
		x̄	29.6 ± 2.4^{a}	204 ± 38^{ab}	589 ± 80^{b}	896 ± 97^{ab}	1072 ± 108^{ab}	–
	Wild (W)	n	83	70	85	77	70	71
		x̄	33.8 ± 2.7^{b}	207 ± 38^{a}	515 ± 66^{a}	844 ± 121^{a}	960 ± 89^{a}	1118 ± 97^{a}
Female	Delta (D)	n	216	188	175	170	132	59
		x̄	35.0 ± 4.0^{c}	214 ± 19^{b}	569 ± 49^{b}	871 ± 82^{b}	986 ± 105^{b}	1166 ± 115^{b}
	W♂ × D♀	n	23	23	23	23	19	–
		x̄	39.5 ± 3.5^{d}	228 ± 40^{b}	567 ± 83^{b}	817 ± 106^{a}	927 ± 105^{b}	–
	D♂ × W♀	n	8	4	4	4	–	–
		x̄	30.3 ± 1.6^{a}	215 ± 23^{ab}	582 ± 49^{b}	809 ± 38^{ab}	–	–
	Wild (W)	n	88	79	92	87	80	81
		x̄	32.8 ± 3.1^{b}	194 ± 41^{a}	474 ± 66^{a}	767 ± 107^{a}	837 ± 83^{a}	954 ± 89^{a}

[1] Any two means in a column within sex having the same superscript are not significantly different ($P < 0.05$).

wild line is 49.0 ± 4.3 g. The 18-hour duckling weights are comparable to those reported by Smart (1965) in Minnesota and Kear (1965) in England, but are less than those Marcstrom (1966) reported in Sweden.

Results from analysis 1 show that at 18-hours posthatching Delta line ducklings are heavier than wild line ducklings with these differences remaining consistent at subsequent ages. Sexual dimorphism in body weight is apparent at 2 weeks of age and culminates with a difference of approximately 200 g for adult weights. Line-sex interactions are not significant showing the growth curves for males and females are comparable across lines.

Results from analysis 2 show a significant difference between lines for 18-hour body weight corresponding to the significant differences in fresh egg weight. From 2 to 8 weeks of age mean weights of ducklings from the reciprocal cross tend to be intermediate to those for the parental lines. These results are similar to those of Phillips (1914). Progeny from Delta line females tend to be heavier than those from wild females although none of these differences is significant after 18-hours posthatching.

Heritability estimates of 4- and 8-week body weight are 0.52 and 0.64 for males and 0.30 and 0.21 for females, respectively (Table 4). These estimates are consistent with those of Stasko (1966a) for 4-week body weight in Pekins. His estimates are 0.58 and 0.64 for males and 0.34 and 0.43 for females. The consistently higher heritability estimates for males than for females suggest additive sex-linked effects for growth, a situation similar to that found in chickens (Siegel, 1962). The intermediate weights of the reciprocal crosses between the Delta and wild lines and the heritability estimates for 4- and 8-week body weight suggest that additive genetic variation is important in the inheritance of body weights in Mallards.

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SUMMARY

The inheritance of egg production and juvenile growth was studied in two lines of Mallards that were maintained in captivity. The lines consisted of semidomestic "game farm" Mallards (Delta line) and wild birds obtained from native populations. The Delta line had a longer breeding season, higher egg production, and higher fertility than the wild line.

Heritability estimates in the Delta line were 0.26 for total eggs laid, 0.46 for the number of eggs in the first clutch, and 0.55 for egg weight. Although the renesting interval is about 6 days when eggs were collected on either the 2nd or 6th day of incubation, the variance is less for the 6-day collection method than for the 2-day method. The mean and variance of emergence time increased over three generations when eggs were artificially incubated which suggests that stabilizing selection influences synchronized hatching under natural conditions.

Birds in the Delta line are heavier than those in the wild line at all ages. Sexual dimorphism for body weight is significant at 2 weeks of age and thereafter. Heritability estimates in the Delta line for 4- and 8-week body weights are 0.52 and 0.64 for males and 0.30 and 0.21 for females, respectively. Body weights of progeny from reciprocal crosses of the Delta and wild lines are intermediate to those of the parental lines and provided further evidence for additive influences in the inheritance of body weight. The higher heritability estimates for males than females suggest additive sex-linked effects for growth.

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