REPRODUCTIVE PARAMETERS OF MALLARDS IN RELATION TO AGE, CAPTIVITY AND GEOGRAPHIC ORIGIN

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ABSTRACT

REPRODUCTIVE PARAMETERS OF MALLARDS IN RELATION TO AGE, CAPTIVITY AND GEOGRAPHIC ORIGIN

By

Bruce Duncan John Batt

A three-year study was conducted on captive mallards (*Anas platyrhynchos*) at the Delta Waterfowl Research Station and at the Michigan State University Wildlife Research Facility. The objectives of the study were to test the effects of age, captivity and geographic origin on several fundamental reproductive parameters of mallards. All base stock used in this study were reared from eggs taken from wild nests.

After one generation in captivity, the F1 generation had a more extended breeding effort and had a higher egg fertility than did the adult P1 generation. First year breeders were found to be lighter in weight at the onset of the breeding season indicating that they may have been physiologically less prepared to breed than older birds. However, significant differences were not detected between the adult and novice groups suggesting that, in an environment of abundant food supply and in the absence of competition with other birds, first year breeders are capable of a reproductive effort similar to that of older birds.

Comparison of nest initiation dates of mallards from Michigan and Manitoba showed that the Michigan birds nested almost four days earlier than did the Manitoba birds in both locations. This result provides evidence to support the hypothesis that regional variation can occur in species with mating systems such as the mallard.

Egg weight appears to be under effective genetic control and was not related to the weight of the female. Significant differences were found between the egg weights of individual females and a high degree of repeatability was determined for this trait. Initiation of first nests extended over 58, 50 and 43 days for the three years of the study. Estimates of repeatability of nesting dates suggest good fidelity of individual birds to particular initiation dates. The repeatability of clutch size suggests that this trait is also significantly related to individual phenotypic response.

Clutch size declined within each nesting attempt and showed a consistent rate of decline from the beginning to the end of the nesting period. Most previous hypotheses involving the influence of proximate factors on clutch size do not apply to the findings of this study. Although these factors may emphasize clutch size decline in the wild, this study indicates that control of mallard clutch size is by underlying genetic influences regardless of seasonal variations.

Mean egg weight was greater in large clutches than in small ones for all nesting attempts. Mean egg weight was shown to be significantly higher in renest clutches. This suggests that mallards may make up for some of the lost reproductive potential of smaller renest clutches by producing larger ducklings which may have a greater chance of survival.

All nests were collected on the fifth day of incubation. Renesting intervals were not significantly different between first, second or third renests and averaged 9.6 days. The interval appears to be fixed by a physiological time limit of how long it takes for ovaries to reactivate and ova to mature. Second, third and fourth

nests showed significantly later first down deposition than did first nests. Down deposition was significantly related to the eventual clutch size in all nesting attempts.

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INTRODUCTION

Numerous field studies of avian breeding biology have suggested causal relationships between reproductive characteristics and various environmental parameters. This work has led to considerable speculation on how endogenous and exogenous mechanisms control reproductive output as a result of interactions between the bird and its' environment. Since most environmental parameters are correlated and since each species demonstrates a unique adaptive strategy, these issues are best clarified using methods of experimental control.

This study examined the roles of three fundamental characteristics that affect the breeding success of the mallard (*Anas platyrhynchos*). Specifically, I examined the effects of one generation in captivity; age and; geographic variation. Further descriptive analyses of several genetically controlled reproductive parameters were possible, due to the nature of the data collected to examine the main effects. The experimental approach throughout involved working with captive mallards of known age and origin.

The mallard is a relevant species for this work as it is the easiest waterfowl species to manage in captivity and it has been the subject of a wide variety of research. Most work of this nature has been done with members of the Order Passeriformes. This study provided an opportunity to study a member of the Order Anseriformes and to thereby contrast species that are products of different evolutionary origins.

Captivity and Reproduction

Fundamental selection theory states that the fitness of all individuals is not the same in any given environment (Falconer 1960: 26). Parents of different genotypes thus pass on their genes unequally to the next generation. It should be expected that succeeding generations will demonstrate better over-all adaptation as selection proceeds in a particular environment such as captivity.

Measurable change in traits should occur rather quickly in the mallard because it is a highly adaptable species. It has holarctic distribution and there are many mallard-derived species in both the northern and southern hemispheres. It is the progenitor of all 17 breeds of domestic duck except the muscovy (*Cairina moschata*) (Delacour 1964:161-165). In North America there are six subspecies of mallards that have evolved from the original parental stock (Johnsgard 1961). Prince *et al.* (1970) demonstrated significant changes in several reproductive traits between F1 and F2 generations within a flock of semi-domesticated mallards. This part of the present study dealt with a comparison of P1 and F1 generations of mallards.

Age and Reproduction

Recent reviews of the effect of age on waterfowl productivity indicate that many species may have reduced breeding potential during the first years of life (Weller 1964, Lack 1966, 1968a, and Trauger 1971). Although geese, swans and some sea ducks are known to be non-breeders in the first 2 to 4 potential breeding seasons, ducks of the Tribe Anatini (dabbling ducks) breed in the first year. However, an increasing amount of information on dabbling ducks suggests that younger breeders may not be as successful as older birds. Some species of waterfowl may breed successfully at a younger age in captivity (Weller 1964:40, and Lack 1968a:237). This suggests that the captive environment is probably free of many of the environmental restraints that affect success in the wild. Analysis of age-related reproductive characteristics of captive birds should thus provide insight into whether or not effects observed in the field are due to environmental factors, or whether they are due to the breeding strategy of the species (*i.e.*, genetic). The reproductive parameters of two age categories of mallards were compared in this study; first year breeders and a mixed age group of older birds.

Geographic Variation and Reproduction

Current understanding of the genetic characteristics of wild duck populations indicates that there is no regional variation in most species due to the high rate of gene flow within continental populations (Hochbaum 1960:239, Johnsgard 1968:72). Mayr (1963:189) considered most migratory waterfowl to have an essentially panmictic mating system thereby negating the opportunity for regional differentiation of gene frequencies. Within the dabbling ducks only the blue-winged teal (*Anas discors*) exhibits sub-specific differences between maritime and prairie populations (Stewart and Aldrich 1956).

Cooke *et al.* (1975) have argued that, in the snow goose (*Chen c. caerulescens*), a 50% gene flow is sufficient to prevent subspeciation or significant regional variation. Most other migratory waterfowl, including the mallard, have a similar mating system to the snow goose. That is, pairing takes place on the wintering grounds or during migration. Both sexes are essentially monogamous within a given season but new pairs are usually formed each year (although snow geese form pairs that last several years). The female is known to home to her natal area (*e.g.*, Sowls 1955, Doty and Lee 1974). The male may theoretically originate from any part of the continental range of the species. Female homing thus accounts for at least 50% restriction in gene flow.

There are, however, several other factors of unknown effect that may restrict gene flow. Population and migration data presented by Lensink (1964) and Bellrose and Crompton (1970) for the mallard, indicate that males may be tied to at least broad regions as a result of their association with females from proximate natal areas on traditional wintering grounds. Restrictions to gene flow may also occur because unmated males may home to their natal area and thus be available for mating with renesting females (Blohm 1976).

This portion of the study was designed to test the hypothesis that there is no regional variation in dabbling duck populations because of the high rate of gene flow. The method of study here was to analyze the breeding response of mallards from different parts of the range while the respective groups were confined at the same locality. Gould and Johnston (1972:474) have pointed out that this procedure is most useful in assigning cause in studies of geographic variation and Miller (1958) inferred the same for studies of breeding schedule adaptation.

Fundamental Reproductive Parameters

Data were also obtained that allowed the description of several parameters of mallard breeding biology. These were; nest initiation dates, clutch size variation within and between clutch sequences, egg size variation within and between clutch sequences, renesting intervals and the schedule of down deposition. I obtained repeat measurements for three consecutive years on the same birds. This added a new level of resolution to the analysis and interpretation of several existing hypotheses, and helped to clarify the genotype-environment interaction of birds during the breeding season.

METHODS AND MATERIALS

Breeding stock were reared from eggs collected from the wild in either of two locations; the southern lower penninsula of Michigan and south central Manitoba. The eggs were hatched, and birds reared and maintained using standard procedures (Ward and Batt 1972). Most of the experimental work was done at the Delta Waterfowl Research Station in Manitoba. Birds used in the study were reared at Delta and at the Michigan State University Wildlife Research Facility. In August of 1972 approximately 20 male and 20 female, 4-5 week old ducklings were exchanged by air transport between the two research locations. In Manitoba the birds were over-wintered indoors while in Michigan they were kept outdoors. In each case they were kept as a flock and were exposed only to natural daylight. At Delta two additional groups of birds were available for study: 1) a group of adult birds that had been reared and held during previous years and; 2) adult progeny of these birds.

The birds were randomly paired in April 1973 and these same pairs were placed back together out of the winter flock each April in 1974 and 1975. Groups of different ages or origins were not mixed. Body weights were taken on the day the birds were placed outside in 1973 and 1975. All birds were kept flightless during the breeding season. In the latter two years, males that had died were replaced with new ones but females were not. The sample sizes for each group were thus changed in relation to the number of females that were available for study. In 1973 approximately 20 pairs of each of four groups were formed. These groups were: 1) adult Manitoba Pl; 2) adult Manitoba Fl; 3) novice Manitoba Pl, and; 4) novice Michigan Pl. In 1974 and 1975 all groups were considered to be experienced but, for consistency, the names "adult" and "novice" were kept. In Michigan only the two novice groups were represented.

Breeding pens were approximately 7 m^2. In Manitoba, the pen area was one-half water and one-half dry concrete base. Each contained a nest box and a feed dish. In Michigan, the pen base was grass and in 1973 only drinking water was available from a waterer and only straw was available for nesting. This proved to be inadequate and an adjustment in the pen environment was required in the last two years of the experiment in Michigan. In 1974 and 1975 water for swimming and a nest box were provided. In both areas pairs were visually but not audibly isolated.

Daily visits were made to each compartment. Food was provided *ad libitum*. Each day, the occurrence of new eggs, egg weight and nest down was recorded. New eggs were numbered and returned to the nest and left until the hen had completed her clutch and incubated it for five days. Deserted nests were also left until laying had not occurred for five consecutive days. After five days the eggs were collected and the nesting material was replaced. This daily routine continued until all hens ceased nesting and had entered their pre-basic molt.

Eggs were artifically incubated. Unhatched eggs were opened to determine fertility. Eggs in which no embryonic tissue could be discerned were designated as infertile. In 1975 ducklings from all hatched eggs were weighed 12-16 hours after hatching.

In Michigan the birds were maintained primarily to give data on first nest initiation dates. Analysis of this trait was done on the 1974 and 1975 data for both novice groups held in both areas. The 1973 data were not considered to be adequate due to problems encountered with husbandry. The remainder of the analyses and related discussions in this paper refers to all four groups of birds held in Manitoba.

Early in the study, it became evident that some hens were "good" nesters in that they deposited eggs in a normal sequence, tended their nests and eggs, and incubated until the five days had passed. Other hens were "poor" nesters and usually deserted their nests at some stage during laying. The data reported in this paper have been analyzed in relation to "good" or "poor" nests.

Data analysis follows Nie *et al.* (1975), Sokal and Rohlf (1969) or Kempthorne (1969). Reference to statistical significance throughout this report is at $p < 0.05$ unless otherwise stated. Where central tendency results are given the format is: mean ± S.E. (n = sample size).

RESULTS AND DISCUSSION

The Effects of Captivity, Age and Geographic Variation

Three comparisons were designated *a priori* as being meaningful between the four groups of birds in Manitoba. These were: 1) adult Manitoba P1 vs. novice Manitoba P1 (age effect); 2) adult Manitoba P1 vs. adult Manitoba F1 (the effect of one generation of captivity) and; 3) novice Manitoba P1 vs. novice Michigan P1 (geographic origin effect). Six parameters were chosen for comparison: first egg day; last egg day; first clutch size; total number of eggs; total number of nesting attempts; and mean egg weight. In 1973 only the age comparison was made (Table 1). None of the reproductive parameters differed between groups.

The insignificant age effect allowed pooling all three year's data for further analysis. The data for each parameter were thus submitted to split-plot analysis of variance to account for the repeat measurements on individual hens (Gill and Hafs 1971). For this latter analysis the meaningful comparisons were between adult Manitoba P1 vs. adult Manitoba F1 and novice Manitoba P1 vs. novice Michigan P1 (Table 2).

The only statistically significant result for group effects was found for last egg day which was significantly later in adult Manitoba F1's than all other groups. This finding is consistent with the concept of increased reproductive effort resulting from one generation

Table 1. Comparison of reproductive parameters of first year breeders and older birds for 1973.

	Group	
Parameter	Adult Manitoba Pl	Novice Manitoba Pl
Day of first egg	May 5.1±2.6(16)[1]	May 5.0±2.9(17)
Day of last egg	June 8.6±3.8(16)	June 1.2±2.9(17)
First clutch size[2]	10.2±0.8(11)	10.2±0.4(10)
Number of eggs/hen	13.6±2.6(20)	12.2±1.9(22)
Number of nests/hen	1.7±0.3(20)	1.2±0.8(22)
Mean egg weight (gms)[3]	50.0±0.9(15)	51.3±0.6(17)

[1] The format of mean ± standard error (sample size) is used on this table and all tables to follow.

[2] Includes first good clutches only.

[3] All nesting attempts included.

Table 2. Results of the split-plot analyses of variance on reproductive parameters for 1973 through 1975 data.

Parameter	Group Adult Manitoba Pl	 Adult Manitoba Fl	 Novice Manitoba Pl[1]	 Novice Michigan Pl[1]
Day of first egg	May 3.4±1.3(42)	May 4.1±1.7(42)	May 3.9±1.5(42)	April 28.7±1.2(42)
Day of last egg	June 17.4±2.4(36)a[2]	June 26.5±1.7(36)b	June 9.4±2.1(36)a	June 14.2±2.6(36)a
First clutch size[3]	10.3±0.3(18)	9.8±0.4(18)	9.7±0.5(18)	11.4±0.6(18)
Number of eggs/hen	16.8±1.4(48)	18.4±1.7(48)	17.5±1.4(48)	20.7±1.8(48)
Number of nests/hen	2.0±0.2(48)	2.2±0.2(48)	1.8±0.1(48)	2.1±0.2(48)
Mean egg weight (gms)	50.8±0.5(40)	51.1±0.4(42)	52.2±0.5(42)	51.4±0.4(42)

[1] In 1974 and 1975 these birds were considered to be adults.

[2] Means not followed by the same letter are significantly different.

[3] Includes good first clutches only.

[4] All nesting attempts included.

in captivity. Prince *et al.* (1970) demonstrated marked increases in reproductive performance between wild line and semi-domestic type mallards. Lack of significance for all other parameters indicate that the rate of adaptation may be slower than suggested at the onset of this study.

The analysis of all three years' data yielded significant results in year effects for four of the six parameters (Table 3). Reproductive effort as measured by date of first egg, date of last egg, total number of nests and total number of eggs was significantly higher in 1974 than 1973. In 1975 there was a decline in all of these parameters although it was not statistically significant. Since husbandry was identical each year, the only explanation for the increase may lie in the fact that in 1974 the birds were returned to an environment in which they had been the year before including their same mates. This familiarity may have allowed them to "settle" better in the last two years of the study and thereby make a greater reproductive effort. In the field, experienced kittewake (*Rissa tridactyla*) pairs breed earlier than others that were newly paired (Coulson 1966).

Perhaps the most significant result obtained from this experiment is the lack of differences found in any of the other comparisons. Breeding bird weights taken just prior to the 1973 season indicated that the novice breeders had significantly lower body weights than the adults (Table 4). This supported the concept of first-year breeders being physically less capable of making the same reproductive effort as adults. Although the trends in the data indicate that the first year birds started later and quit a little sooner (thereby laying fewer eggs in fewer nests), the differences were more subtle than expected.

Table 3. The significant year effects found in the split-plot analyses of variance on reproductive parameters for 1973 through 1975 data.

	Year		
Parameter	1973	1974	1975
Day of first egg	May 4.6±1.5(56)a[1]	May 2.1±1.0(56)ab	April 30.9±1.2(56)b
Day of last egg	June 9.4±2.4(48)a	June 23.6±1.8(48)b	June 17.7±1.6(48)b
Number of eggs/hen	14.8±1.4(64)a	21.9±1.3(64)b	18.4±1.3(64)b
Number of nests/hen	1.6±0.1(64)a	2.5±0.1(64)b	2.0±0.1(64)b

[1] Means not followed by the same letter are significantly different.

Table 4. Breeding bird weights (gms) for birds in Manitoba prior to the 1973 and 1975 breeding season.

Sex	Year	Group Adult Manitoba P1	Adult Manitoba F1	Novice Manitoba P1	Novice Michigan P1
Females	1973	1072±25(19)a[1]	1001±22(18)ab	945±24(22)bc	891±25(18)c
	1975	1160±29(16)	1104±22(20)	1149±23(22)	1075±28(18)
Males	1973	1073±25(20)a	1050±16(20)ab	1030±17(22)ab	984±26(18)b
	1975	1232±31(16)	1162±25(19)	1229±55(22)	1239±30(18)

[1] Any means in the same row followed by different letters are significantly different.

The 1975 body weight data indicate that by three years of age, there were no differences between the novice and adult groups. The 1973 and 1975 comparison indicates that the 1973 novices were lighter because of the age effect and not because they were actually smaller birds.

The significant difference in breeding bird weights in 1973, may have also led to the prediction that the novice groups would produce lighter eggs (that is, if hen body weight and egg weight are correlated). This was not the case. The correlation coefficient of hen weights and egg weight was calculated to be 0.10 ($r^2 = 0.01$) which is not significant ($p > 0.13$, $n = 129$). This result agrees with Labisky and Jackson (1969) for captive pheasants (*Phasianus colchicus*) but is contrary to findings for most field studies where egg size and body size are significantly correlated (Vaissanen *et al*. 1972).

Analysis of variance of individual female records for the three years showed significant differences between female mean egg weights but no significant year effects. A method of estimating the intra-individual correlation of repeat measurements over time is available. Repeatability is the ratio of between individual variance to the total phenotypic variance and can take values between 0 and 1. It is thus not a measure of product-moment correlation but is more analagous to the coefficient of determination. Using the method of Becker (1975:23) the repeatability of mean egg weight was determined to be 0.62 ± 0.08 (n of hens = 60). I conclude that egg weight is under effective genetic control and is independent of hen weight or age.

Dzubin (1969a:152) suggested that adult mallard hens may come into breeding condition first and thereby take the best habitat while yearlings are forced into less suitable habitat. Coulter and Miller (1968) found older mallards nesting earlier than younger ones. It appears that first year breeders may enter the breeding season in poor physical condition, and thereby may be less successful because of lack of experience at: 1) competing with older birds for resources or; 2) exploiting food and other resources to be used for reproduction.

The trend in the geographic origin comparison indicates a slightly earlier initiation of breeding by Michigan birds. This parameter was analyzed further in the comparison between the two geographic groups in each research location.

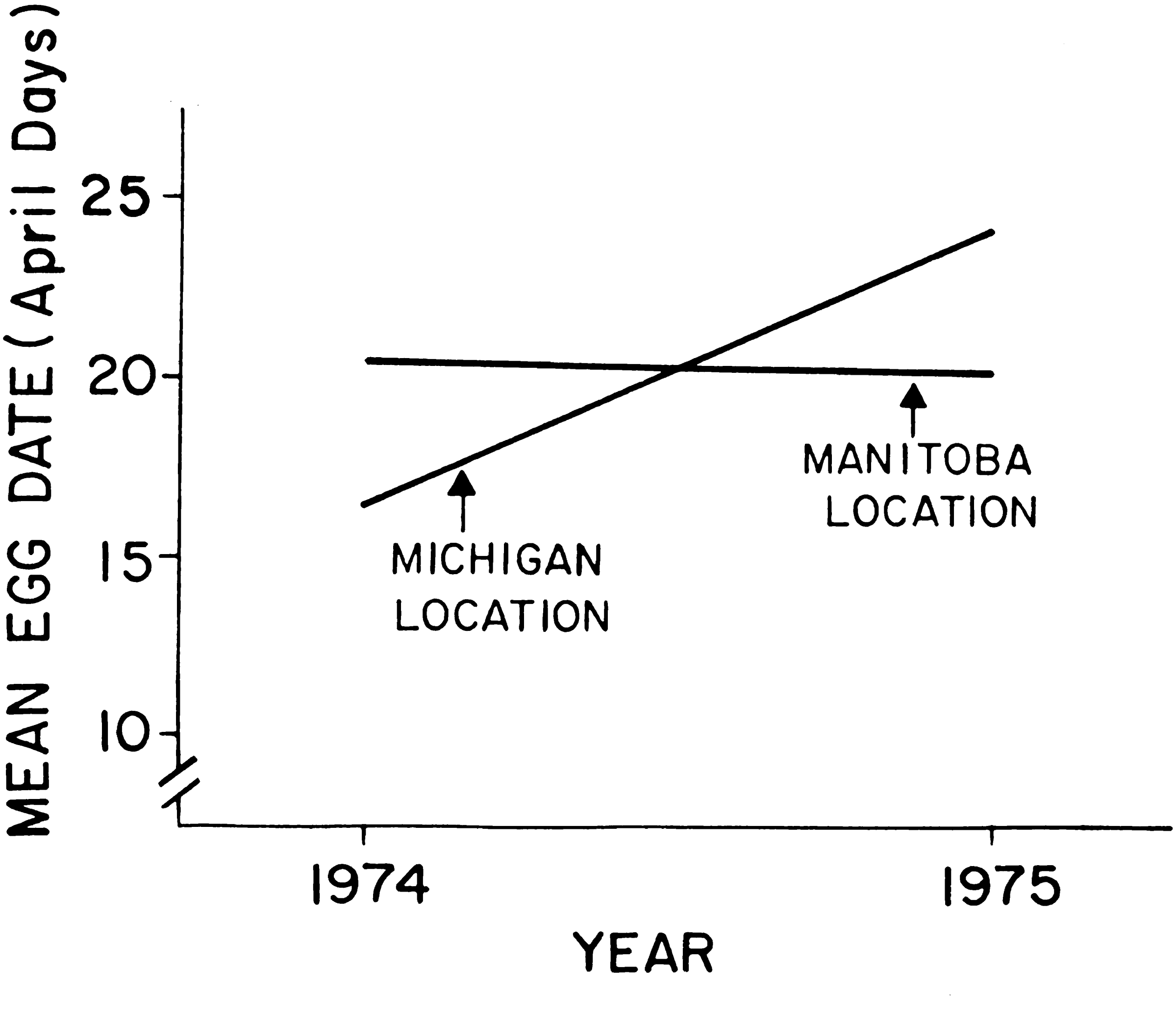
The analysis of variance of first egg dates between the two geographic groups located in each study area for the years 1974 and 1975, yielded a significant location x year interaction (Fig. 1) and a significant group effect (Table 5). The significant location x year interaction indicates set-back in the onset of breeding in Michigan in 1975. This is explainable on the basis of severe weather that occurred in Michigan during the normal initiation period. On April 2nd and 3rd, over 30 cm of snow fell on the Michigan State University Wildlife Research facility and on April 18th an additional 6.5 cm of rain fell. During the intervening period the daily mean temperatures were 5.15°C below the long term mean (U. S. Dept. of Commerce, Local Climatological Data). This result is consistent with other studies where breeding seasons of waterfowl were set back by harsh weather (*e.g.*, Sowls 1955:85, Dane 1966, Dane

Table 5. Mean first egg dates for the Manitoba and Michigan groups compared by location in which they were held in two successive breeding seasons.

		Group Origin	
Location	Year	Michigan	Manitoba
Manitoba	1974	April 20.0±2.0(17)	May 3.0±1.8(19)
	1975	April 28.6±2.0(16)	May 3.0±2.5(20)
Michigan	1974	April 24.7±1.3(14)	April 29.3±3.2(12)
	1975	May 3.0±2.3(9)	May 6.4±5.1(5)
	Totals[1]	April 28.8±1.0(56)	May 2.5±1.4(56)

[1] The means of the totals are significantly different.

Figure 1. The significant location x year interaction for mean first egg dates in the Michigan and Manitoba based experiment.


MEAN EGG DATE (April Days)
25
20
15
10
1974
1975
YEAR
MICHIGAN LOCATION
MANITOBA LOCATION

and Pearson 1971). It also supports the underlying assumption of this study that the birds responded normally to environmental cues for breeding.

Over the two areas the mean first nest initiation date for birds originating from Michigan was April 28.8 ± 1.0 (n = 56) whereas the mean for Manitoba birds was almost four days later at May 2.5 ± 1.4 (n = 56) (Table 5). The results of this portion of the study support the hypothesis that there is geographic variation in the timing of the breeding season within the continental mallard population. Conversely, they do not support the hypothesis that gene flow approaching 50% is sufficient to negate regional variation in waterfowl populations. Nor is the assumption of Hochbaum (1960:239), Mayr (1969: 189) and Johnsgard (1968:72) that there are no regional variations in populations of ducks because of the effects of the mating system. Endler (1973) predicted where selection gradients are uniform, it is possible for local differentiation to evolve parapatrically in spite of considerable gene flow. To my knowledge, the present study is the only one that has tested Endler's hypothesis as it may apply to species with a mating system and gene flow characteristics such as waterfowl (May *et al.* 1975). These results furnish experimental support for his hypothesis.

Differences in egg fertility for the three main effects were tested by Chi-square analysis. Comparison of adult (76.8%) and novice (71.4%) Manitoba P1's, using the 1973 data, yielded no significant differences between the two age groups (X^2 = 1.85, 1 d.f.). For examination of the generation and geographic origin effects the three year's data were pooled. Fertility of the adult

Manitoba F1 groups was significantly higher than the adult Manitoba P1 group (86.8% and 69.6%, respectively, $X^2 = 68.17$, 1 d.f.), thus giving further evidence of adaptation by the F1's to the captive environment (Table 6). Prince *et al.* (1970), also working with captive mallards, found an 18% increase in fertility by a semi-wild line of mallards contrasted to their wild counterparts. Another significant result was obtained when the novice Manitoba and Michigan groups were compared (78.3% and 83.0%, respectively, $X^2 = 7.35$, 1 d.f.). It is not clear why this result should be, as it implies that the Michigan birds made a better effort in Manitoba than did the Manitoba birds. The difference is not large, however, and is assumed to have little meaning.

Comparison of egg fertility between successive nests yielded significant results ($X^2 = 392.47$, 3 d.f.) which is a reflection of the obvious decline in later nests - particularly the fourth nest. I assume that this decline does not occur in the wild and is a characteristic of the captive environment since there would be no advantage to a hen's renesting if her eggs were not fertile. I assume the reason for this lies with the males. If the female is able to produce mature ova and lay eggs, it seems that infertility is likely a result of ova not being exposed to viable sperm. This probably does not occur in the wild where renesting females are able to seek out and find males that are still in reproductive condition. In the pen a hen was forced to remain with her assigned drake whether or not he could still fertilize eggs. Also, in the wild, the male is not forced to remain with sexually inactive females as may have been the case in the pens once the female began incubating.

Table 6. Percentage fertility of all eggs summarized for the three years of the study.

Group	Nest Number				Totals
	1	2	3	4	
Adult Manitoba Pl	80.4 (414)[1]	61.0 (356)	70.1 (147)	34.9 (43)	69.6 (960)
Adult Manitoba Fl	98.0 (454)	90.0 (368)	73.3 (202)	15.9 (63)	86.8 (1087)
Novice Manitoba Pl	81.4 (590)	77.3 (388)	70.9 (179)	-- (0)	78.3 (1158)
Novice Michigan Pl	89.1 (505)	88.1 (352)	71.3 (164)	26.4 (53)	83.0 (1074)
Totals	87.0 (1963)	79.1 (1464)	71.5 (692)	24.4 (160)	(4279)

[1] Numbers in parentheses denote sample size.

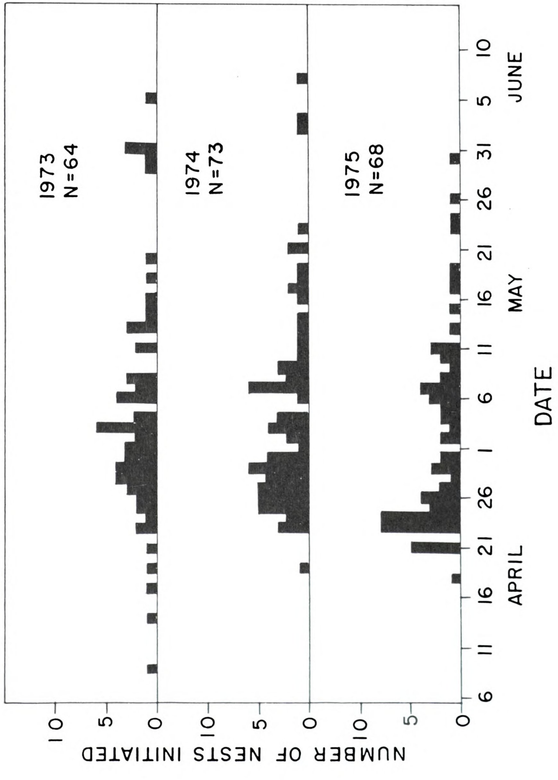
The analysis over years indicated that egg fertility significantly increased from 1973 to 1975 ($X^2 = 55.04$, 2 d.f.). Egg fertility for the three years was 74.8%, 81.1% and 86.7%, respectively. This result is consistent with the earlier finding where reproductive performance was shown to increase significantly from 1973 to 1974 but showed a slight but insignificant decline in 1975.

Fundamental Reproductive Parameters

Nest Initiation Dates

The earliest and latest first nest initiation dates for all hens of all groups were separated by 58, 50 and 43 days in 1973, 1974 and 1975, respectively (Fig. 2). The birds were held in the same breeding pen from year to year, diet was not changed, and the same birds were mated together each year. Year to year variation is thus assumed to primarily be the result of climatic influences confounded by experience. One-way analysis of variance indicated significant differences between hens for the three year's data. The repeatability of individual hen nesting date was determined to be 0.57 ± 0.07 (n of hens = 60). This suggests that individual hens are consistent and that within the population there is a wide range of individual phenotypic responses. In the wild, one would expect to find some pairs with a full commitment to nesting while at the same time others were paired but showing no breeding behavior. This may explain the difficulty that some investigators have had in separating the breeding population from other pairs that were: 1) transient and on their way to other breeding areas; 2) resident pairs nesting for the first time on different schedules or; 3) were pairs renesting after losing a first nest (Dzubin 1969b).

Figure 2. Distribution of the initiation of first nests by captive female mallards in isolated breeding pens by year.


1973
N=64
1974
N=73
1975
N=68
NUMBER OF NESTS INITIATED
10
5
0
10
5
0
10
5
0
6
11
16
21
26
1
6
11
16
21
26
31
5
10
APRIL
MAY
JUNE
DATE

Immelman (1971:373) has discussed intraspecific variations in breeding seasons and has accounted for most of it as being adjustments to localized ecological conditions or age-related factors. My results give more resolution to the concept of intraspecific variation and are consistent with the concept that the variability of temperate environments causes disruptive selection to maintain a wide range of genotypes in the population. Disruptive selection might also arise from population pressures that accrue some benefit to those genotypes that delay breeding until the density of nesting pairs is diminished and thereby they are able to use the breeding space when there is lower competition.

Individual consistency of laying dates has been found in the great tit (*Parus major*) (Kluijver 1951), the manx shearwater (*Puffinus puffinus*) (Harris 1966), the mutton bird (*P. tenuirostris*) (Serventy 1963) and the velvet scoter (*Somateria mollissima*) (Koskimies 1957a). Perrins (1970) interpreted these findings as reflecting the differential ability of individuals to find food. The results of this study, where food was supplied *ad libitum* suggests that food may not be the only explanation and that breeding response may simply be a reflection of an individual genotype-environment interaction.

Clutch Size

Clutch size data from all first nests and all renests for the three years were submitted to analysis of variance. A significant decline in clutch size was found between first nests and subsequent renests. Clutch size was 10.4 ± 0.2 (151), 9.5 ± 0.2 (116), 8.4 ± 0.3 (59) and 8.2 ± 0.8 (13) from the first through the fourth nest, respectively.

Regression analyses were next performed on first, second and third nests for each year to determine if clutch size declined within an individual clutch sequence. For first nests all three years data showed a significant decline of approximately 0.1 egg per day as the season progressed (Fig. 3). Covariance analysis indicated no significant differences between the means or slopes of the lines. For second nests, the 1974 data showed a corresponding significant downward linear trend. The equation for the line is $Y = 24.94 - 0.10\ X$ ($n = 54$, $r^2 = 0.20$, $p < 0.01$). Covariance analyses showed no differences between the means of all three years data nor between the slopes. The 1973 and 1975 data however, did not yield significant slopes ($F = 2.76$ ($n = 32$) and $F = 0.05$ ($n = 37$) for the two years, respectively).

For third nests, the 1973 data showed a significant decline ($Y = 20.79 - 0.07\ X$, $n = 13$, $r^2 = 0.36$, $p < 0.05$). Covariance analyses also showed no difference between the means or slopes for the three years data, but, the 1974 and 1975 slopes were not significant ($F = 1.30$ ($n = 31$) and $F = 0.04$ ($n = 20$) for 1974 and 1975, respectively). The evidence thus, generally describes a relationship in which clutch size declined within and between each nesting attempt.

To summarize the relationship of clutch size and laying date, all good nests for all three years were submitted to regression analysis. A significant curvilinear relationship between the date of initiation of laying and clutch size was determined (Fig. 4). The rate of decline in the number of eggs per clutch decreases in the latter part of the nesting season. This decrease may mean that clutches have a minimum size below which it is not advantageous to undertake the risks and expense of nesting. The number of young produced from

Figure 3. Relationship of clutch size to laying date for first nests only by year. All slopes are significant ($p < 0.01$).

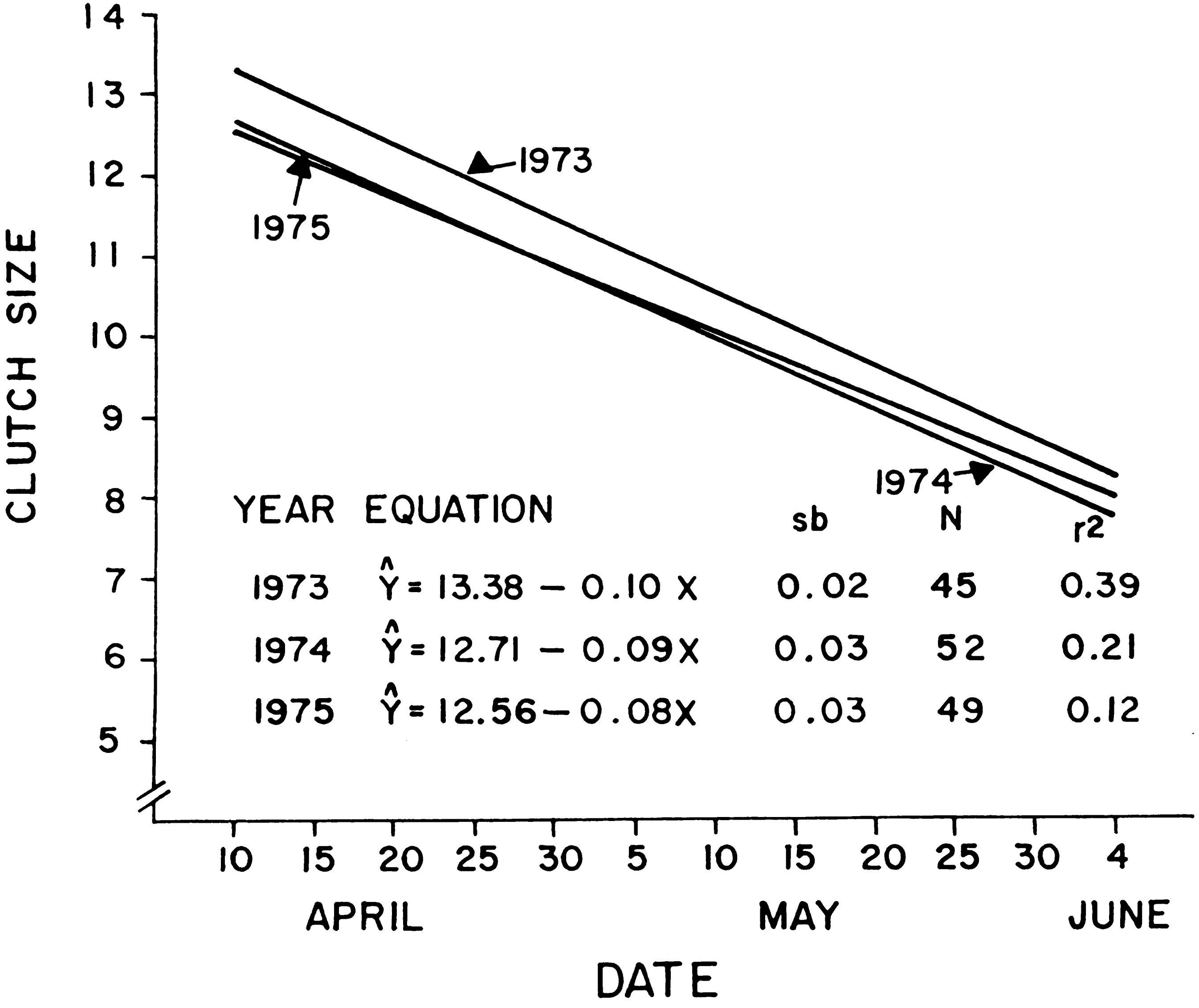
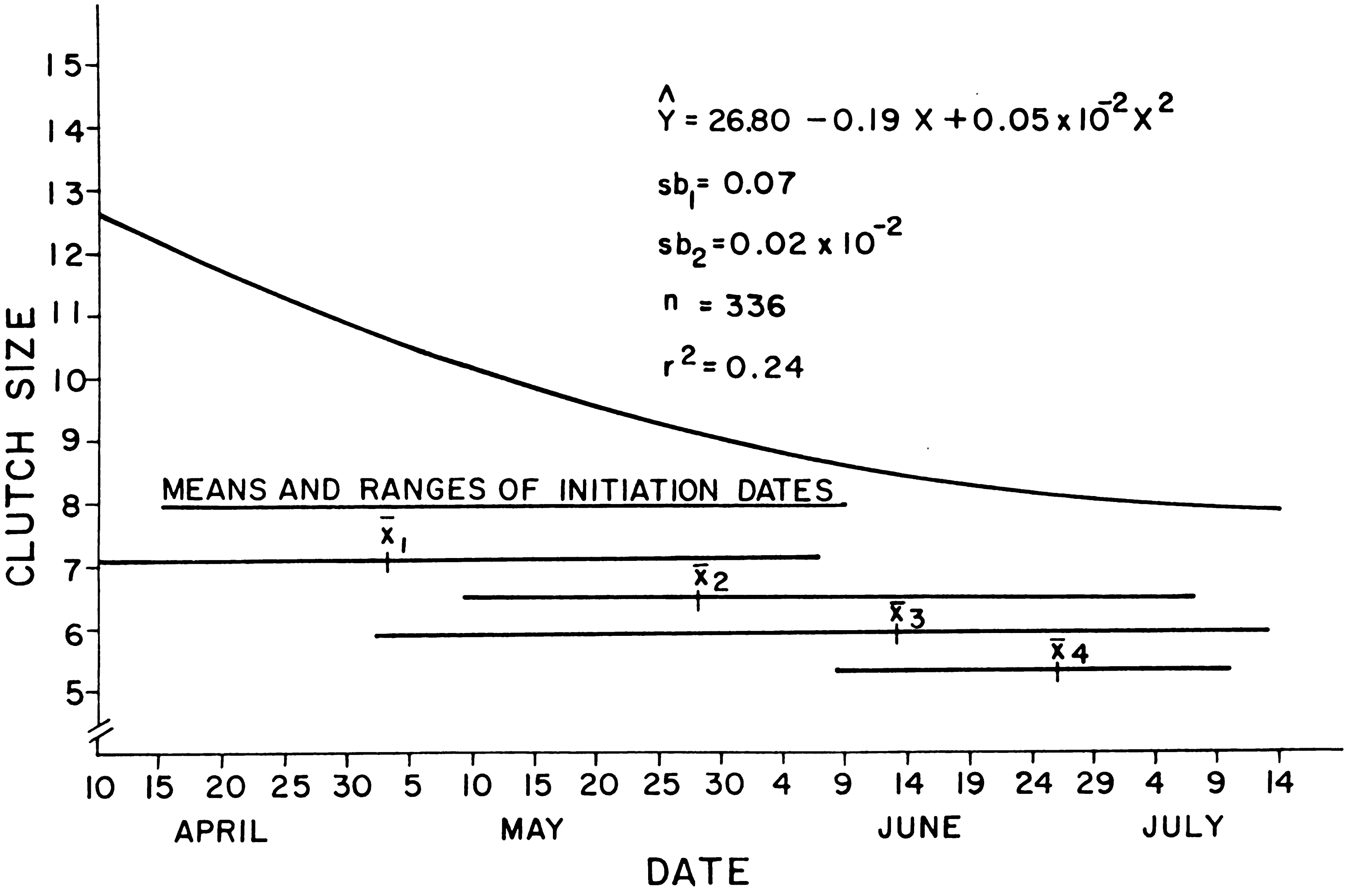

CLUTCH SIZE
14
13
12
11
10
9
8
7
6
5
1973
1975
1974
YEAR EQUATION sb N r2
1973 $\hat{Y} = 13.38 - 0.10X$ 0.02 45 0.39
1974 $\hat{Y} = 12.71 - 0.09X$ 0.03 52 0.21
1975 $\hat{Y} = 12.56 - 0.08X$ 0.03 49 0.12
10 15 20 25 30 5 10 15 20 25 30 4
APRIL
MAY
JUNE
DATE

Figure 4. Relationship of clutch size and initiation dates for all good nests for the three years data combined. Means and ranges for each clutch initiation are shown ($\bar{x}_1$ = mean date for all first clutches, etc.).

$\hat{Y} = 26.80 - 0.19X + 0.05 \times 10^{-2} X^2$
$sb_1 = 0.07$
$sb_2 = 0.02 \times 10^{-2}$
$n = 336$
$r^2 = 0.24$
MEANS AND RANGES OF INITIATION DATES
$\bar{x}_1$
$\bar{x}_2$
$\bar{x}_3$
$\bar{x}_4$
CLUTCH SIZE
15
14
13
12
11
10
9
8
7
6
5
10
15
20
25
30
5
10
15
20
25
30
4
9
14
19
24
29
4
9
14
APRIL
MAY
JUNE
JULY
DATE

late, minimum sized clutches, may only just balance the advantage accrued by the female if she does not renest but instead waits until the next year.

The decline of waterfowl clutch sizes as the breeding season advances has become an almost universally accepted relationship (see reviews by Dzubin and Gollop 1972:125, Klomp 1970, Johnsgard 1973). Numerous cause and effect relationships have been inferred but little consideration appears to have been given to the genetic aspects of the decline. Clutch size is known to decline between initial nests and renests but little is known about clutch size variation within an individual nest sequence.

Koskimies (1957a) showed that in the velvet scoter, which does not renest, clutch size declined in relation to the date on which the female initiated the clutch. He argued that there may be a genetic polymorphism that linked clutch size with laying date. My data for first nests for each of the three years of this study show a similar relationship (Fig. 3) and agree with Koskimies' proposal for the velvet scoter. One-way analysis of variance over the three years indicated a significant difference between individual clutch size. Repeatability for this trait (using only good first nests) was calculated to be 0.54 ± 0.07 (n of hens = 30). Thus, there is good evidence that laying date and clutch size are relatively consistent within individual females. These data do not refute Koskimies' hypothesis; but, I believe there is no need to employ the polymorphism concept to the observed relationship since both factors could be selected for independently and the same correlation of traits would conceivably still exist.

The results of the analyses of clutch size are consistent with the bulk of data obtained in the field by other investigators (see review of Klomp 1970). However, because of the simplicity of the environment in which this experiment took place and the *ad libitum* food supply, most cause and effect relationships reviewed by Johnsgard (1973) are not acceptable explanations; *i.e.* that 1) later smaller clutches may be produced by younger birds; 2) food supply might be limiting later in the season or; 3) population density might affect clutch size. Wagner (1960) suggested that the decline may result from exhaustion of the female's body stores. But this does not explain the decline within first nests. We are left with a conclusion that there is some ultimate reason why clutch size declines within the mallard. Prior analyses have only considered ultimate causes primarily as they relate to between species variability (*e.g.*, Johnsgard 1973, Lack 1967, 1968b).

Age-related effects are often considered to be proximate (Johnsgard 1973) - perhaps incorrectly so. I favor Lack's (1968a: 299) interpretation: *i.e.*, that species demonstrating this phenomena have "evolved physiological regulating factors to prevent earlier maturity because this, on balance, enables them to leave more offspring than if they mature earlier". Thus age-related reproductive effort may more appropriately be considered in relation to ultimate factors.

My results lead to the conclusion that there is (or has been) some over-riding advantage that favors clutch size decline as the season advances and that this advantage holds for all nesting attempts in the mallard. Dane (1966) suggested an adaptive mechanism by which

the bird is able to respond to changes in the stimulation provided by photoperiod and temperature. He found a relatively constant clutch size during the first half of the breeding season in the blue-winged teal (*Anas discors*) and Low (1945:48) recorded the same in the redhead (*Aythya americana*). These examples suggest different adaptive strategies between the three species. Presumably, the maintenance of relatively constant clutch size early in the season in the latter two species has some benefit that out weighs the advantage of the decline evident in the mallard.

The ultimate advantage of the decline discussed here may result from many and varied pressures. It is worth noting that the decline observed in this study occurred in an environment in which essentially all proximate inhibiting factors were minimized. This analysis strongly suggests an underlying genetically determined response that is the product of selective pressures that have ultimately favored genotypes that produce fewer eggs as breeding seasons advance.

Egg Weight

Mean egg weight data by clutch sequence for individual birds were submitted to paired t-tests to determine if egg weight changed through successive nesting attempts. The results indicate that mean egg weight increased significantly in second and third nests but that the fourth nest was not different than the first. All three years data were next pooled and analyzed by analysis of variance. Mean egg weights (gms) for second nests (51.5 ± 0.3 (118)) were significantly heavier than first nests (51.0 ± 0.3 (147)). Third nests (52.9 ± 0.4 (61)) were significantly heavier than all others.

Fourth nests were significantly lighter (50.1 ± 1.0 (13)) than the second and third nest but not different than the first nest.

Based on the above relationship I expected to be able to calculate a significant regression equation to show mean egg size to increase as the season advances. This is indeed the case when all nests for all three years are plotted (Fig. 5). Although the regression coefficient and y-intercept are significant, the coefficient of determination (r^2) indicates that the calculated equation only accounts for 1.24% of the variation. The relationship is only really clear when individual nesting attempts are compared as above.

I compared mean egg weight by clutch size for individual nest sequences to test the hypothesis that within a given nest sequence, later (thus smaller) clutches would have larger eggs (Fig. 6). Significant regressions were calculated with positive slopes which indicate that larger clutches also have larger eggs within a given clutch sequence. In agreement with the earlier finding, covariance analysis verified the relative differences in egg weight between clutches but there was no significant difference in the slopes of the lines. The biological meaning of this latter result is not clear but Kendeigh *et al.* (1956) recorded the same relationship in the house wren (*Troglodytes aedon*). Koskimies (1957b) found no significant relationship between clutch size and egg size in the velvet scoter but the trends in his data were negative rather than positive.

The increase in egg weight in renest clutches discussed previously, when combined with the evidence of clutch size decline from the preceeding section, suggests an interesting adaptation.

Figure 5. The relationship of mean egg weight to initiation date for all good nests. Data from all three years are combined.

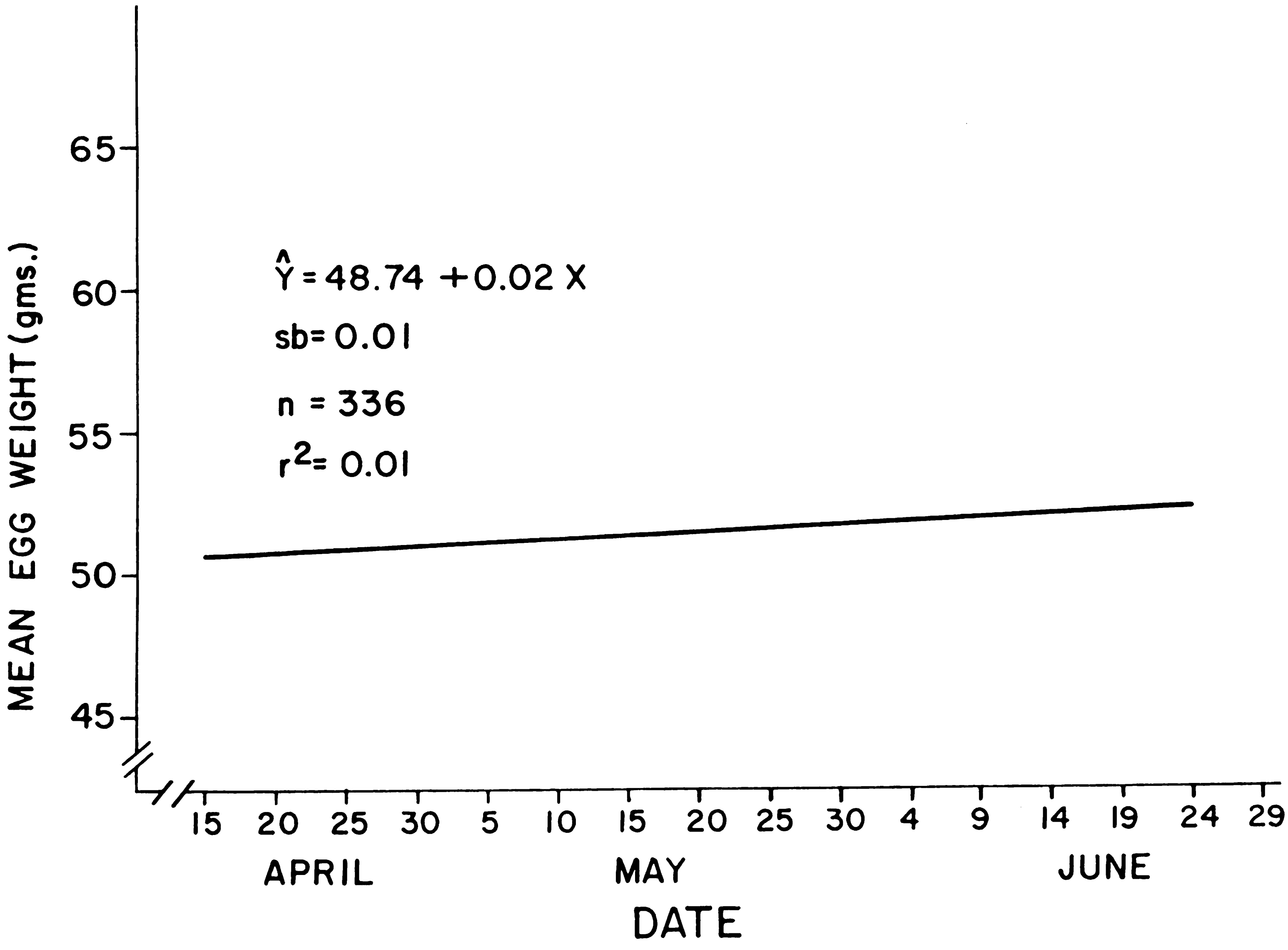
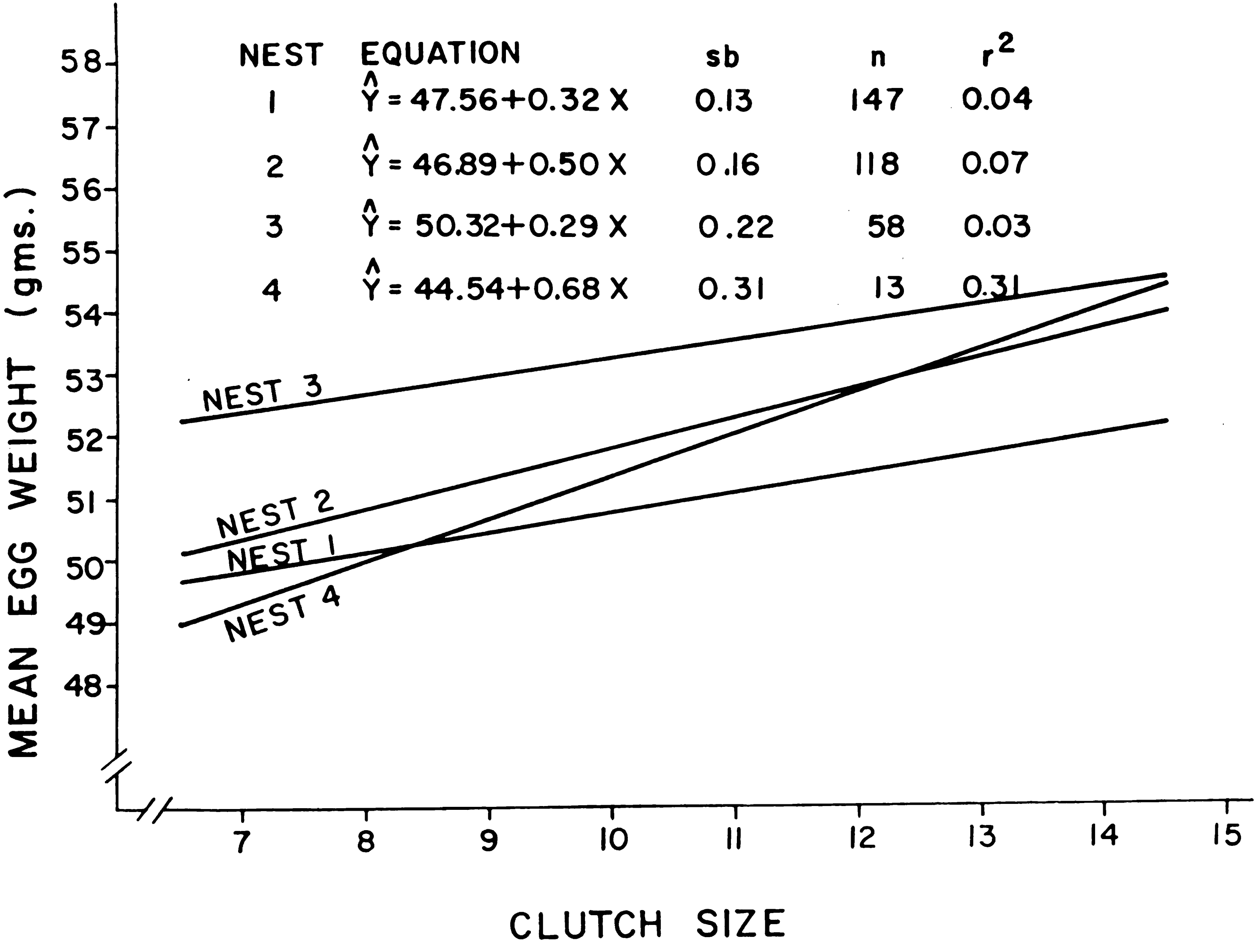
$\hat{Y} = 48.74 + 0.02X$
$sb = 0.01$
$n = 336$
$r^2 = 0.01$
MEAN EGG WEIGHT (gms.)
65
60
55
50
45
15
20
25
30
5
10
15
20
25
30
4
9
14
19
24
29
APRIL
MAY
JUNE
DATE

Figure 6. The relationship of mean egg weight and clutch size for first nests and all renesting attempts. All three years data are combined. All slopes are significant ($p < 0.02$).



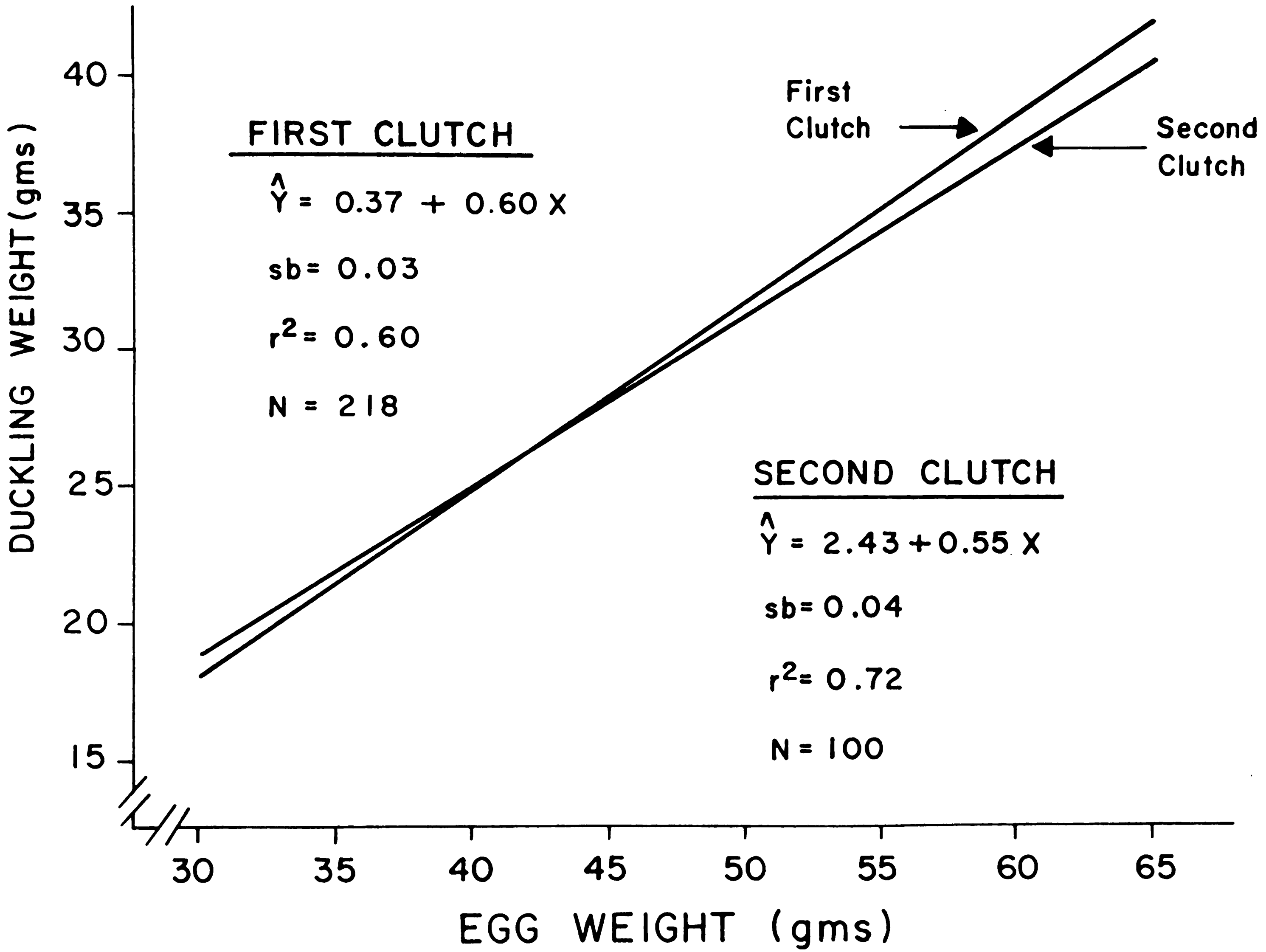
NEST	EQUATION	sb	n	r^2
1	$\hat{Y} = 47.56 + 0.32X$	0.13	147	0.04
2	$\hat{Y} = 46.89 + 0.50X$	0.16	118	0.07
3	$\hat{Y} = 50.32 + 0.29X$	0.22	58	0.03
4	$\hat{Y} = 44.54 + 0.68X$	0.31	13	0.31

Hypothetically, the decrease in potential numbers of young produced may be offset by the hen's laying larger eggs that presumably produce larger ducklings. These may have a greater potential for survival. The relationship between duckling weight and egg weight with eggs hatched in 1975 was found to be highly correlated (Fig. 7).

This analysis was not carried beyond the hatching of ducklings but a necessary assumption in the above hypothesis is that larger body size accrues some positive benefit to the ducklings. Parsons (1970) found that chicks from larger eggs of the herring gull (*Larus argentatus*) survived better during the first week than those from lighter eggs. In the great tit, Schifferli (1973) found young hatched from larger eggs to be significantly heavier up to the 14th day. There is thus, some prior evidence from other species to support this hypothesis.

As Schifferli (1973) pointed out, larger weight may provide two advantages to the young: 1) the chick may actually have a larger body size which may reflect a further stage of development, thereby shortening the fledging period or; 2) the chick may have more food reserves in the form of a larger yolk sac. In respect to energetic balance, ducklings from renest clutches are hatched later in the year when ambient temperatures are usually higher. The gain in energy available for the maintenance of homiothermy is probably far greater than just that reflected in body weight. Further, if ducklings from renest clutches are produced past the peak of their food supply, the added weight may give them a greater store to get started on before they are forced to feed themselves solely on food from the environment.

Figure 7. Regressions of initial egg weight and duckling weight for first and second clutches.


FIRST CLUTCH
$\hat{Y} = 0.37 + 0.60X$
sb= 0.03
$r^2 = 0.60$
N = 218
First Clutch
Second Clutch
SECOND CLUTCH
$\hat{Y} = 2.43 + 0.55X$
sb= 0.04
$r^2 = 0.72$
N = 100
DUCKLING WEIGHT (gms)
40
35
30
25
20
15
30
35
40
45
50
55
60
65
EGG WEIGHT (gms)

The increase in egg size in the later part of the season is not a unique finding but the literature is contradictory on this point and no single trend is apparent. Koskimies (1957b) found a tendency for eggs to get larger in the velvet scoter as the season advanced. He reviewed the literature up to 1956 and found records of egg size increase in such species as the red-winged blackbird (*Agelaius phoeniceus*), the common pigeon (*Columba livia*), the cuckoo (*Cuculus canorus*), the bobwhite quail (*Colinus virginianus*), and the song sparrow (*Melospiza melodia*). More recently, Perrins (1970) found an increase in egg size in the great tit as the season advanced. On the contrary, in the kittiwake (Coulson 1963), the shag (*Phalacrocarax aristotelis*) (Coulson *et al.* 1969), the gannet (*Sula bassana*) (Nelson 1966) and the herring gull (Parsons 1972) egg size has been shown to decrease as the breeding season progresses. The relationship of egg size, laying date and duckling vigor should provide a fruitful area for further research.

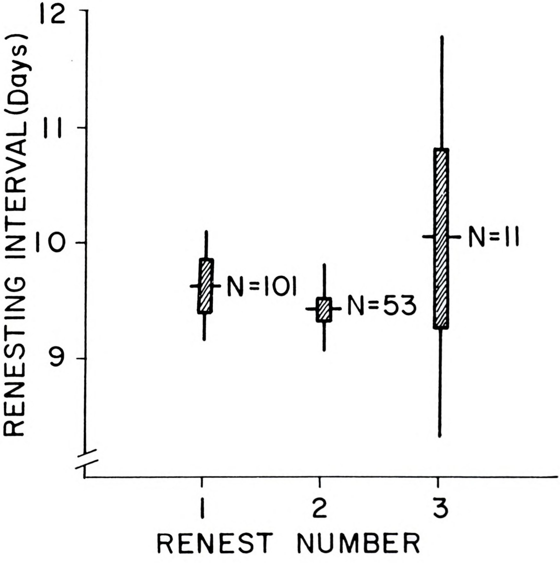
Renesting Interval

In this study renesting interval was defined as the time between my artificial destruction of one nest and the appearance of the first egg of the subsequent nest. For this analysis, only intervals between two incubated nests were used. Sowls (1955:134) showed that the renesting interval in ducks of the Tribe Anatini is positively related to the stage of incubation (the further advanced females taking longer to renest). He calculated a straight line regression that predicted the same rate of increase in renesting interval throughout the incubation period. However, Gates (1958) calculated a curvilinear relationship for the Gadwall (*Anas strepera*) that suggested a leveling off of renesting interval after mid-incubation.

Since all nests were collected at day 5 of incubation in this study, the main remaining variable was the sequence of the nest within the season. To my knowledge, these kinds of data are not in the literature probably because it is not possible to separate first renests from second or third renests in the wild. Analysis of variance indicated no differences in renesting interval between any renesting attempt and the break-up of the preceeding nest (Fig. 8). First, second and third renesting intervals were 9.7 ± 0.2 (101), 9.4 ± 0.2 (53) and 10.1 ± 0.8 (11) days, respectively. These results suggest that, where food is not limiting, renesting intervals may be independent of proximate environmental influences. They also suggest that the "decision" to renest must be made soon after nest break-up and that there is a physiological limit in how long it takes ovaries to reactivate and ova to mature to laying stage. Donham *et al.* (1976) have shown that female mallards are capable of a rapid endocrine adjustment after the loss of a clutch. Luteinizing hormone returned to levels equal to pre-laying birds within one day of nest loss.

Prince *et al.* (1970) found a renesting interval of 6.4 ± 0.2 (25) days after eggs had been collected at day 6 of incubation from a semi-domesticated strain of mallards. This is significantly shorter than my results and suggests that with succeeding generations in captivity, renesting interval may be shortened and may therefore be a reflection of increased domestication.

Figure 8. Renesting intervals for first, second and third renests. Values plotted are means, standard errors and 95% confidence intervals.

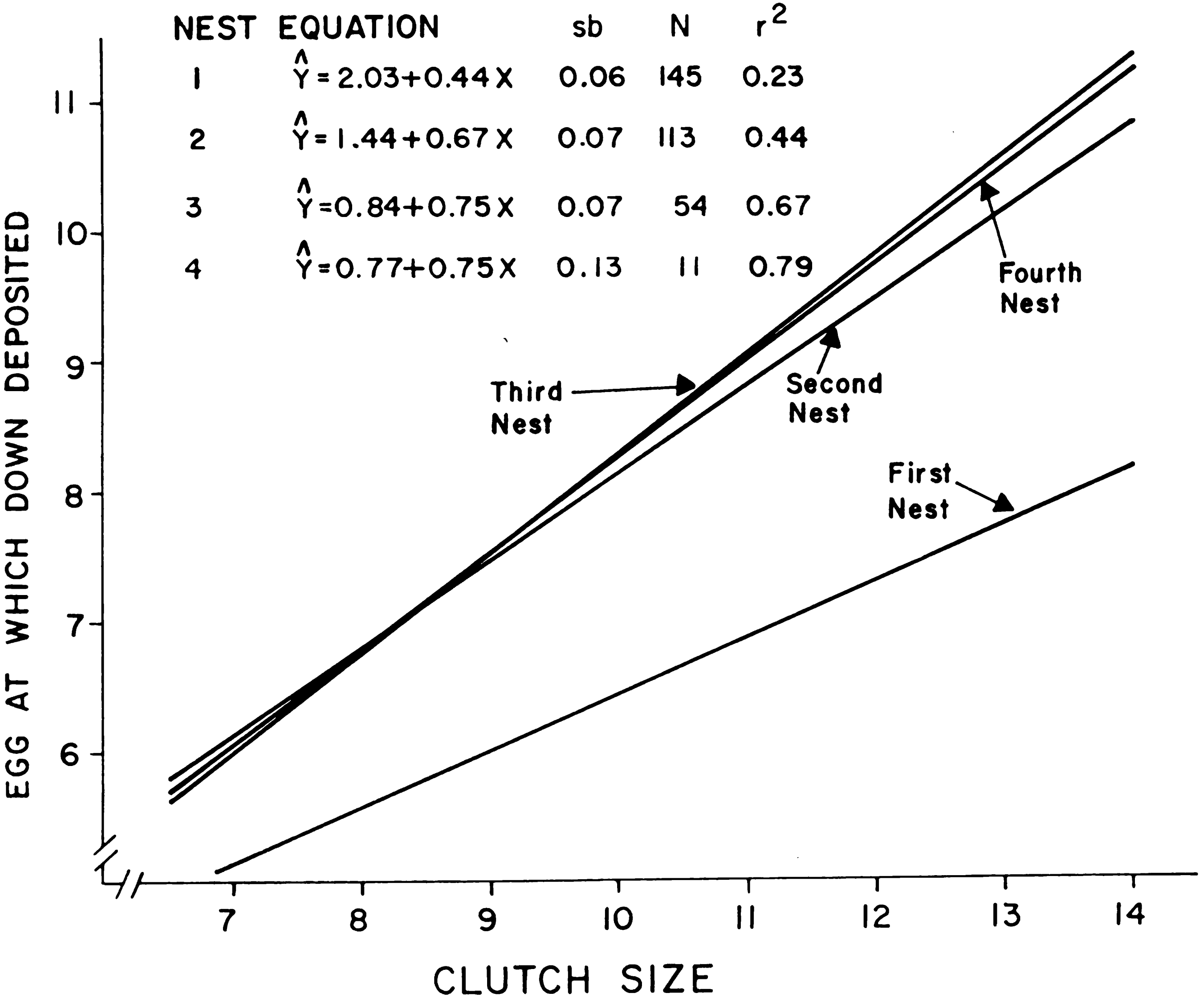

12
11
10
9
RENESTING INTERVAL (Days)
N=101
N=53
N=11
1
2
3
RENEST NUMBER

Down Deposition

Throughout the three years of the study the occurrence of the first down was recorded for all nests. Since nesting material was replaced after each nesting attempt, it was possible to get accurate data on down deposition in renests. A significant linear relationship exists between the egg at which down first appeared and the eventual clutch size (Fig. 9). Down deposition was significantly later in all renesting attempts but there were no differences in the regression coefficients of second, third and fourth nests. However, the fit of lines increased markedly from first through fourth nests (r^2 = 0.23, 0.44, 0.67, and 0.79 for first, second, third, and fourth nests, respectively). Coulter and Miller (1968:16) estimated that down deposition occurred at about the fourth or fifth egg in mallards and black ducks (*Anas rubripes*). This is much earlier than the relationship of Fig. 9 would predict but since they did not quantify their statement, it is not possible to evaluate this discrepency. In the hooded merganser (*Mergus cucullatus*) the egg at which down was first deposited was shown to be highly correlated (r^2 = 0.77) with the eventual clutch size by Morse *et al.* (1969). These same authors found a much weaker relationship (r^2 = 0.03) in the wood duck (*Aix sponsa*). The meaning and function of these differences is not evident at present. Cooper (1973:90) has described a similar relationship in Canada goose (*Branta canadensis maxima*) nests but, since that species has a low renesting potential, he was not able to expand the analysis to include renests.

Hanson (1959) has hypothesized that down deposition is related to the hormonal cycle as the hen proceeds through laying and into

Figure 9. Regressions of egg at which down was deposited in relation to eventual clutch size. The data from all three years are combined. All slopes are significant ($p < 0.01$).



NEST	EQUATION	sb	N	r^2
1	$\hat{Y} = 2.03 + 0.44X$	0.06	145	0.23
2	$\hat{Y} = 1.44 + 0.67X$	0.07	113	0.44
3	$\hat{Y} = 0.84 + 0.75X$	0.07	54	0.67
4	$\hat{Y} = 0.77 + 0.75X$	0.13	11	0.79

incubation. Although my data do not dispute this suggestion, the factors affecting down growth and/or deposition appear to be different for renesting females when contrasted with females laying the first clutch.

SUMMARY

1. A pen-based study was undertaken at the Delta Waterfowl Research Station and the Michigan State University Wildlife Research Facility with two main objectives. An attempt was made to evaluate the effects of: 1) age; 2) one generation of captivity and; 3) geographic origin, on the breeding performance of mallards. The second objective was to evaluate several existing hypotheses related to the timing and degree of reproductive effort in individual mallard pairs.

2. Four groups of birds were available for study. The base stock all originated from eggs collected from wild nests. Two groups were already on hand at Delta in 1972, the first was designated as the Adult Manitoba P1 group. Birds in the second group were progeny of the first and were at least two years old during the first year of the study. These were the Adult Manitoba F1 group. The last two groups were reared from eggs collected in 1972 - one group in Michigan and one group in Manitoba. These were named the Novice Manitoba and Michigan P1 groups.

3. Half of each of the latter two groups were exchanged between the two research locations during the summer of 1972. In Michigan two groups, while in Manitoba all four groups, were tested during the 1973-1975 breeding seasons.

4. In the Manitoba based experiment, the findings showed that the Adult Manitoba F1 group had a more extended breeding effort and

had higher egg fertility. These findings serve as a demonstration of the previously assumed adaptability of the mallard, and shows that measurable changes are evident after only one generation in a new environment.

5. Also in the Manitoba based experiment, the trend in the geographic origin comparison suggested that the Michigan birds initiated nesting earlier than the Manitoba birds. When the data for the two groups from each area were analyzed together, a significant difference was found between birds from each geographic origin in respect to the dates of first nest initiation. Michigan birds were earlier in each location. This result provides experimental evidence to support the hypothesis that regional variation can occur in species with mating systems such as the mallard. This may occur in the face of gene flow approaching 50%.
6. A marked set-back in breeding phenology occurred in Michigan in 1975 which was apparently in response to heavy snow fall and lower than normal temperatures. This finding is consistent with set-backs known to occur in the wild and supports the assumption that the birds used in this study responded normally to environmental cues for breeding.
7. First year breeders were found to be lighter in weight at the onset of the breeding season indicating that they may have been physiologically less prepared to breed than were older birds. The failure to detect age-related effects on reproduction suggests that, in the absence of competition with older birds and in an environment of abundant food, first year breeders may be capable of a reproductive effort approaching that of older birds. In

the wild proximate factors probably interact with ultimate adaptive strategies to lower reproductive potential of younger birds.

8. Egg weights were consistent amongst all groups showing no relationship to the weight of the female. Egg weight appears to be under effective genetic control. Significant differences were found between individual female egg weights over the three years and a high degree of repeatability was calculated for this trait.

9. Reproductive output increased significantly in almost all parameters, including fertility, in the second year of the study and declined slightly in the last year. This is believed to be a reflection of the familiarity of the birds with their breeding environment and with their assigned mates.

10. Fertility went down significantly between successive nests in the breeding season. Infertile eggs are probably the result of some males going out of breeding condition before the female. In the wild, renesting females are more likely to be able to seek out a sexually active male to assure that her eggs are fertilized.

11. Initiation of first nests by the flock extended over 58, 50 and 43 days for the three years of the study. Estimates of repeatability of individual female nesting dates indicate a high degree of fidelity by individual birds to a particular nest initiation date. This individuality helps explain why field investigators have had difficulty in separating pre-breeding, breeding, non-breeding and post-breeding segments of wild duck populations.

12. Repeatability of clutch size suggested that this trait also had a significant level of individual control. Clutch size declined within each nesting attempt and showed a consistent rate of decline from the beginning to the end of the nesting period. The hypothesis that laying date and clutch size might be linked as polymorphic characters was not felt to be necessary. It was argued that both characteristics could be selected for independently and still show the same correlation.

13. Most previous hypotheses of how proximate factors caused clutch size decline within the year were shown not to apply to the findings of this study as most proximate factors were controlled. Although these factors may emphasize clutch size decline in the wild, this study suggests that control of mallard clutch size is by underlying genetic influences regardless of seasonal variations.

14. Mean egg weight was shown to be significantly heavier in renest clutches. This suggests that mallards may make up for some of the lost reproductive potential of smaller renest clutches by producing larger ducklings which may have a greater chance of survival. This hypothesis needs to be tested for waterfowl but some data on other species support the concept of larger young having higher survival.

15. Mean egg weight was higher in larger clutches than in smaller ones for first nests and all renesting attempts. This showed that egg size did not increase as clutch size decreased within individual nest sequences as was predicted. Rather, it was necessary to check between nesting attempts to detect egg size increase.

16. Renesting intervals were not significantly different between first, second or third renests for nests interrupted on day five of incubation suggesting that the interval may be relatively fixed by a physiological time limit in how long it takes ovaries to reactivate and ova to mature.
17. Down deposition was significantly related to the eventual clutch size in all nesting attempts. Second, third and fourth nests showed significantly later first down deposition than did first nests.

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