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ASPECTS OF MALLARD BREEDING ECOLOGY IN CANADIAN

PARKLAND AND GRASSLAND

Alexander Dzubin and J. Bernard Gollop

Canadian Wildlife Service

Department of Fisheries and Forestry

1971

CONTENTS

	Page
INTRODUCTION	1
STUDY AREAS	3
Precipitation	4
Food resources	4
METHODS	7
Breeding pairs	7
Nests	7
Brood movement	9
Production	10
Brood mortality	10
Limitations of productivity estimates	11
Annual mortality rates	12
Statistical comparisons	13
Literature review	13
RESULTS AND DISCUSSION	15
Hatching chronology	15
Nest distances to water	17
Hatching success	18
Clutch sizes	21
Egg loss	24
Brood sizes	24
Brood movement	28
Brood loss, nest to water	28
Duckling loss	29

	Page
Mobility and pond dispersion	30
Distances moved	31
Movements and pond quality	32
Reproductive success	33
Local production and breeding populations	34
Drought impacts on production	37
Production indices	38
GENERAL DISCUSSION	41
SUMMARY AND CONCLUSIONS	45
ACKNOWLEDGEMENTS	50
LITERATURE CITED	51
APPENDICES	71

Aspects of Mallard Breeding Ecology in Canadian
Parkland and Grassland

by

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This paper has three purposes: (1) to present the summer dynamics of Mallards (Anas platyrhynchos) on representative areas of two types of breeding habitat, (2) to describe the major factors influencing seasonal fluctuations in numbers, and (3) to document drought effects on reproduction.

Although Mallards are found breeding near suitable waters from taiga to desert (American Ornithologists' Union, 1957; Godfrey, 1966), the center of abundance in North America is the northern great plains of the United States and southern prairies of Canada, viz., the grassland biome and the forest-grassland ecotone or aspen parkland (Hochbaum, 1946; Crissey, 1963). The major breeding grounds in Canada, some 220,000 mi² (570,000 km²), have a history of alternating high water and drought conditions (Kendall and Thomas, 1956; Lynch, Evans and Conover, 1963). Yearly precipitation patterns, particularly as reflected by snow melt, influence the quality and quantity of pothole or pond habitat. There are more than 10 million natural depressions capable of holding water in this region but between 1953 and 1965 the number of basins with water in May ranged from 1.5 to 6.5 million and in July from 0.6 to 5.6 million (Gollop, 1965a). Portions of the more northern parkland have relatively stable water levels and serve as waterfowl survival foci from which breeders can

disperse to colonize the less frequently suitable environments of the grassland (Lynch et al., 1963). In short, the center of abundance occurs in a most unstable and climatically unpredictable environment. A necessary consequence of this instability is the wide fluctuation in North American Mallard numbers.

Mallards are the major exploited waterfowl species in Canada and the United States. The factors and processes which regulate numbers have been the subjects of extensive and intensive study and speculation. Continent-wide schemes concerned with annual estimates of numbers of ponds, pairs and broods, mortality based on bandings, production from wing age-ratios and hunter harvests have led managers to a point where size of the fall flight can be predicted fairly accurately (Crissey, 1969; Geis, Martinson and Anderson, 1969). Yet, even with this wealth of population data and modelling on a continental basis there remains a dearth of published works on breeding ecology and local processes of numerical control. This paucity of natural history information has been stressed by Ryder (1961) in relation to the proportion of duck pairs producing fledged young and by Weller (1964:59) and Davis (in Giles, 1969:530) on Mallard clutch sizes. Lack (1966) did not discuss waterfowl ecology in his review but has more recently presented information on factors influencing clutch size and incubation periods in the Anatidae (Lack, 1967, 1968a, 1968b).

STUDY AREAS

Our study was conducted on two areas, one in aspen parkland near Roseneath, 9 miles south of Minnedosa, Manitoba, and the other in mixed grassland near Kindersley, Saskatchewan. At Roseneath, ponds averaged smaller in size than at Kindersley, were not as widely separated, were less ephemeral and contained edges of emergent aquatic vegetation (Fig. 1). Preferred nesting cover was widely dispersed at Roseneath but at Kindersley was restricted to dry stream courses and uncultivated uplands (Fig. 2). The parkland area was continuous with surrounding small pond habitat, while the grassland site formed one of several discontinuous pockets of habitat more suitable for breeding waterfowl than intervening landscapes. Increasing portions of both study blocks have been cultivated and grazed since the turn of the century.

Comparative climatic and edaphic factors are presented in Table 1. Maps of both areas are presented in Dzubin (1969b). More detailed descriptions of the vegetation, land-use, soils and upland cover of the Roseneath study area are presented in Evans, Hawkins and Marshall (1952), Dzubin (1954, 1969b), Kiel (1955) and for the Kindersley study area in Gollop (1965b) and Dzubin (1969b). Bird (1961) has described the ecology of the aspen parkland while Coupland (1950, 1961) presented detailed vegetative analyses of the Saskatchewan grasslands.

Throughout the text Roseneath is used synonymously with parkland study area and Kindersley with grassland study area.

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Table 1
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Precipitation

Ponds are recharged yearly through snow melt and summer thunderstorms. Trend lines of precipitation for prairie Canada, based on moving decadal means, show excesses at the turn of the century, a minor peak in the 1920's, a drying trend to the late 1930's, increasing precipitation through the 1940's and mid-1950's, followed by a decrease through the late 1960's (Thomas, 1965). Much of the parkland-grassland area has an annual evapotranspiration deficit of 2 to 10 inches (5 to 25 cm; Laycock, 1965; Atlas of Canada, 1957). During the study period summer precipitation excesses were experienced in 1953 and 1954 at Roseneath. On the grassland block snow and rainfall deficiencies and high temperatures from 1956 to 1959 led to progressively lower water levels and fewer ponds.

Food resources

Studies of the productivity and chemistry of small astatic ponds in prairie Canada have only recently been initiated (Hartland-Rowe, 1966; Rozkowska and Rozkowski, 1969; White and Hartland-Rowe, 1969; Driver, unpublished). Investigation of ponds annually subjected to partial or total drying show the classical effects of a reduction in organic matter accumulation through oxidation and the setting back of plant succession (Kadlec, 1962; Lynch, 1964:291; Jahn and Moyle, 1964:300; Cooke, 1964:570-573). Upon reflooding, the ready availability of chemical nutrients ensures that standing crops of zooplankton and other invertebrates are high, often exceeding 200 pounds per acre (224 kg per ha; Moyle, 1949, 1956, 1961; Dineen, 1953; Neel, 1963; Mackenthun and Ingram, 1967:42; 127-130). Yearly enrichment

also occurs through runoff from uplands. The planktonic and benthic biomass available as food for adult and young ducks has not been quantified. Qualitatively, it appears formidable through the summer but drying and increasing salinity changes faunas (Hartland-Rower, 1966). The use of foods by ducklings in relation to their availability has been studied by Collias and Collias (1963), Chura (1961) and Sugden (1971). Reflecting the food potential of potholes, Gollop (1954) reported that more than 1,000 ducklings were apparently raised on two adjacent ponds of 39 and 42 acres (16 and 17 ha) at Kindersley.

As in the breeding ranges of some other groups of birds, food does not appear limiting for adult ducks (Lack, 1954) but does influence dispersion of breeders (Lack, 1968b; but see Chitty, 1967). Most of the upland portions of both study blocks were seeded to small grain cereal crops (Table 1). Each spring approximately two-thirds of the cultivated uplands were in stubble with the remainder in fallow. Each acre of stubble contained sufficient waste grain to feed one pair of Mallards for a 50-day period, assuming (1) that grain lost by threshing with mechanical combines varied from 3 to 10% of the total harvest (Jordan, 1953; Bossenmaier and Marshall, 1958; Dodd, 1966), (2) that each Mallard consumed 6 ounces (170 g) of grain per day (Jordan, 1953; Bossenmaier and Marshall, 1958; Hammond, 1964), and (3) that the birds utilized only 50% of available waste grain. In effect, the potential waste grain food resources for the Mallard population on both study areas was two to six times more abundant than the pairs could use. A surplus existed even though Pintails (Anas acuta) and American Widgeon (Mareca americana) also ate grain. To this must be

added aquatic plant and animal life. While quantity of food did not appear to be a limiting factor on Mallard production, no information was available on whether the quality was adequate for breeding ducks.

METHODS

This paper is based on field studies by the senior author conducted during the spring and summer (a) from 1952 through 1955 at Roseneath, Manitoba, and (b) from 1956 through 1959 at Kindersley, Saskatchewan. Gollop conducted population surveys and banding programs in the Kindersley district from 1952 through 1959.

Breeding pairs

Pairs and lone drakes were counted at irregular intervals and assigned to the Roseneath study block while indicated pairs were censused every 7 to 10 days at Kindersley and average populations computed. Detailed procedures can be found in Dzubin (1969b). Pairs were trapped using cannon-projected nets and bait traps and marked with either soft plastic neck bands (Addy, 1956), aeroplane dope (Sowls, 1955) or colored celluloid leg bands and with USFWS aluminum leg bands. Hens were captured on nests using drop traps, hand nets, fish netting and dogs. Breeding pairs were censused at Kindersley through 1970 (Dzubin, 1969b) but our discussion is restricted to the drought years.

Nests

All of the preferred nesting cover on each study area was searched two or three times between 10 May and 10 July by walking through it and threshing the vegetation with stakes. Less attention was paid to stubble fields because experience showed generally low nesting densities (Dzubin, 1969b). Dogs were used in all nest searching. Nests were marked and revisited every 7 to 10 days for as long as needed to determine their fate. Distances of nests from nearest

water at calculated initiation and hatching dates were measured by tape, by pacing or from aerial photographs to the nearest 5 yards (5 m). Early and late nest-to-water distances were grouped at Roseneath because of small sample sizes and similarities in median values.

Clutch size during incubation was defined as the maximum number of eggs found in a nest, based on at least two checks. A successful nest was one in which at least one egg hatched. Seasonal (i.e., pooled early and late) clutch sizes were calculated for all successful and unsuccessful nests, both during incubation and at hatching. Clutches destroyed by predators during laying were rejected. Each year three to nine clutches, containing less than six eggs, and possibly suffering partial predation, were considered complete. Clutch sizes are, therefore, minimal. Other potential biases exist in precise clutch size determination (Hilden, 1964; Bezzel, 1966; Mednis, 1968) while valid yearly comparisons can only be made if a population age structure is known and average clutch sizes compared phenologically.

Hatching success was calculated for all clutches, both active (hen laying or incubating when found) and inactive (hatched, deserted or destroyed when found). Not all active and inactive nests were located. A portion of incubating Mallard hens (< 10%) were off nests during the pre-noon hours and, therefore, were unlikely to be found (Dzubin, unpublished). The nesting season was divided into early and late segments. Clutches initiated prior to the appearance of the first two broods were termed "early" and those initiated thereafter, "late". At Roseneath, the division occurred between 18 and 28 May in different years while at Kindersley it varied from 8 to 18 May. All

late nests were assumed to be renests.

All mallard nests located on the 1.4-mi² (3.6-km²) Roseneath area and within 0.5 mile (0.8 km) of the boundary were used in calculations. At Kindersley all nests located on the 10.5-mi² (27.2-km²) study area and on a 2-mi² (5.2-km²) block adjacent to it on the west were used.

Detached shell membranes and finely crushed eggshells in the bottom of the nest bowl were criteria used for hatched clutches. Membranes attached to shells and partially crushed or punctured shells with yolk or albumen remaining were criteria for unsuccessful clutches. Nest predators were identified by methods proposed by Sowls (1948) and Rearden (1951) while hen predators were classified after Einarson (1956).

Hatching dates were predicted by candling two or three eggs from each clutch (Weller, 1956) or by egg flotation (Westerskov, 1950) and corroborated by nest histories. Seasonal hatching peaks by weeks were calculated from clutches and by backdating Class Ia broods at Roseneath (Blankenship et al., 1953) and from successful and unsuccessful clutches combined at Kindersley. Annual sample sizes for Fig. 3 were 86, 89, 72 and 97, respectively, for 1952 through 1955, and 196, 251, 153 and 65, respectively, for the 1956-59 period. We assumed that one egg was laid per day (Sowls, 1955) and that the incubation period was 28 days (McKinney, 1970), even though there is some small variation in this rate (Prince, Siegel and Corwell, 1970).

Brood movement

Brood movement data resulted from the neckbanding of 109 hens on nests. In addition, 37 broods were marked by injecting food dyes

into eggs late in incubation (Evans, 1951).

Production

From mid-May to mid-August broods were counted a minimum of three times on the parkland area and weekly on the grassland block. Brood data were then compared to calculated and measured breeding pair figures. Broods that could have been counted previously were removed from final tabulation (Blankenship et al., 1953). "Beat-outs" were supplemented by evening and morning counts on ponds. Dogs were used during production surveys to aid in tracking hens and broods on the upland. Inherent in production estimates using brood counts is the major assumption that egress of broods from the area equals ingress.

Production and productivity were defined as the ratio of the number of flying young as of 1 September to the breeding population minus the estimated summer mortality of adults.

Brood mortality

Sizes of clearly visible broods were determined periodically on and within 1 mile (1.6 km) of the Roseneath block in 1952 and 1953 and within 5 miles (8 km) in 1954 and 1955. At Kindersley, brood counts were conducted on the study area and within 10 miles (16 km) of it. Based on plumage development, broods were assigned to three age classes: I, 1-18 days, II, 19-45 days, III, 46-55 days (Gollop and Marshall, 1954). Broods less than 1 week old were recorded as Ia. To estimate duckling loss from nest to water, 109 nest-trapped hens were marked with soft plastic neck bands at Kindersley and attempts were made to locate them and their broods after hatching. From late June to early August each year banding crews with retrievers

periodically covered all ponds within 5 miles (8 km) of the grassland study area.

The brood season was divided into early and late segments. These periods corresponded to those when broods from early and late nests would attain each age class. These segments varied annually by 10 to 15 days.

As an index to pond dispersion and availability during the brood period, measurements were made from the shoreline of each pothole which contained water on 1 July to the shorelines of the nearest four ponds. In addition, counts of the number of ponds on that date within 440 and 880 yards (402 and 805 m) of each pothole were made from aerial photographs. Data were calculated for the driest year (1952) at Roseneath and for each year from 1956 through 1959 at Kindersley.

Limitations of productivity estimates

Although reduction in average brood size from hatching to flying provides one estimate of mortality, the loss of entire broods is not accounted for by this method. The proportion of hens ultimately successful in producing young, therefore, is unmeasured. The data presented on seasonal brood size attrition, especially from the Kindersley area, were biased by the sampling of broods on more permanent ponds and by not sampling the same broods every week. Comparison of clutch sizes from the study area with brood sizes from a more extensive region, in which other limiting factors may be operative, is another source of bias.

Although brood mixing may occur in older brood classes because of weakened brood bonds and abandonment of nearly fledged broods by

hens (Miller and Collins, 1954:29; Boyd and King, 1960; Sapiteen, 1959; Beard, 1964:511; Cowardin and Higgens, 1967; Marshall and Campbell, 1969), aggressive behavioral mechanisms help maintain brood cohesiveness and do not favor inter-brood adoption. (Hochbaum, 1944:98; Collias and Collias, 1956; Eygenraam, 1957:138; Mendall, 1958:135; Beard, 1964:515; Raitasuo, 1964). However, crowding leads to strife between brood hens, straying of ducklings and possible loss of orphaned young (Beard, 1964:520). The last author found maximum concentrations of 0.15 Mallard broods/acre (1.2 /ha) on a 20-acre (8.1-ha) study marsh, while at Kindersley Gollop (1955) reported as many as two broods/acre (4.9/ha; one Mallard and one other species) on two ponds totalling 80 acres (32.4 ha). Under such densities brood size counts could be subject to wide error and were often difficult because of herding. Broods of mixed age classes and those with more than 12 young were not used in calculations of brood size.

Annual mortality rates

No significant numbers of immature Mallards were banded at Roseneath. Published mortality rates based on other North American investigations during the study period were applied. From 1954 through 1959, Gollop (1965b) banded 12,962 flightless young Mallards in the Kindersley area. Using the composite dynamic method of Hickey (1952) and the relative recovery method of Geis (Geis and Taber, 1963), average annual mortality rates for immatures and adults were computed.

The number of adults found dead on each study area in April, May and June was recorded. Adult deaths in July and August were estimated.

Statistical comparisons

Because the distribution of distances from nest to water was skewed, medians were used. A "biased" mean distance was computed for comparison with studies where this statistic has been used. Chi-square, t-tests, median tests and binomial confidence limits were used to test the acceptability of the null hypothesis (Steel and Torrie, 1960). Significance was inferred at the $P < 0.05$ level. In the text, sample means are followed by standard errors of the mean.

Literature review

For comparative purposes and as an aid to future population modelling we summarized both published and "unpublished" information on seasonal clutch sizes, brood sizes and hatching success of Mallards throughout North America, primarily for the 1950-60 decade (see appendices). Our review was not exhaustive. Means and ranges tabulated should be viewed as approximations only and are not amenable to statistical comparisons among years or areas. Biases inherent in reported seasonal clutch size means (Bezzel, 1959, 1966; Hilden, 1964) and pooled brood size data, from both early and late hatched clutches, or from coalesced broods (Miller and Collins, 1954; Marshall and Campbell, 1969) present formidable difficulties to any statistical refinement.

Readers should also be cognizant of the methodological and logistical constraints imposed in precise estimates of waterfowl breeding pairs (Diem and Lu, 1960; Dzubin, 1969b), nests (Sowls, 1955; Keith, 1961; Ryder, 1961), broods (Blankenship et al., 1953; Evans et al., 1952), age specific laying and hatching dates, per cent reneesting hens

(Coulter and Miller, 1968; Mednis, 1968), and subpopulation mortality, natality and emigration rates (Crissey, 1969). The attendant uncertainty of inferences drawn from short-term studies using small samples should also be recognized.

RESULTS AND DISCUSSION

Hatching chronology

At Roseneath the interval between arrival of the first pairs of Mallards and laying of first eggs was variable: 31 March-22 April 1953, 8 April-5 May 1954, and 2-20 April 1955. Snow cover in nesting substrate, frozen ponds and both minimum and cumulative temperatures above freezing appeared to be important threshold factors affecting ovulation and resultant hatching peaks (Sowls, 1955; Yocum and Hansen, 1960; Keith, 1961; Dane, 1966).

Hatching peaks showed an annual variation of 2 to 3 weeks (Fig. 3). From 1952-55 hatching dates extended over 86 days, from 15 May to 9 August. Recorded peak hatching weeks were 24-31 May in 1952 and 1955, 1-7 June 1953, and 8-15 June 1954. Secondary peaks occurred in late June and early July. In each year approximately 50% of all active clutches had hatched by 1 week after hatching peaks with 95% of all nests hatched by 16-23 July.

At Kindersley the first-arrival and first-egg dates for Mallards were as follows: 4-17 April 1956, 25 March-14 April 1957, 29 March-9 April 1958, and 23 March-11 April 1959. The 4-year average showed 47% of clutches at Kindersley and 22% at Roseneath hatched before 1 June (Fig. 3), reflecting earlier arrival dates (Dzubin, 1969a:188), higher average temperatures and earlier snow melt (Meteorological Branch, Canada Dep. Transport). The earliest hatching peak, 16-23 May, was recorded in 1958, and the next earliest, 24-31 May, in 1957. Bimodal peaks noted in 1956 and 1959 (24-31 May and 8-15 June) were associated with late April cold snaps that interrupted laying. Hatching

dates extended from 8 May to 12 July, a period of 66 days for the 4 years. The telescoping of the hatching period was associated with deteriorating pond quality through increasing drought. Also, higher nesting success led to fewer replacement clutches and earlier termination of laying.

In Alberta, Keith (1961:53) showed a 5-year average hatching period of approximately 75 days, 11-20 May to 21-31 July. For the Kindersley area, Gollop and Fyfe (1956:74) recorded a hatching span of 104 days, 17 May to 29 August, in a favorable water year whereas Gollop (1954) reported a span of only 58 days in a year with two spring cold spells.

Physiological-behavioral pathways which lead to initiation or termination of breeding in waterfowl remain subjects of study. Seasonal physiological changes affecting Mallard and Pintail reproductive behavior have been discussed by Johnson (1961, 1966) and Phillips and van Tienhoven (1962) while Lofts and Coombs (1965) tested the photoperiodic responses of drake Mallards during the refractory period. The relationship of habitat quality and weather on duration of laying or cessation of breeding have only now begun to emerge. Possible mechanisms which may terminate active gonadal function in a number of bird species have been proposed by Farner (1967). These include cessation of primary external environmental information, e.g., unavailability of water, and negative effects of essential supplemental mechanisms, e.g., low temperatures.

Nest distances to water

Parkland nests were generally situated closer to water than grassland nests. At Roseneath, medians of pooled early and late nest-water distances at both initiation and hatching were significantly smaller (< 7 yards, < 6.4 m) than those on the Kindersley area (50-255 yards, 46-233 m; Table 2, Fig. 4). At Kindersley, all median distances tended to increase from 1956 through 1959 with increasing drought, while at Roseneath median values remained relatively constant except for 1952. In the parklands, 95% of 217 nests were within 55 yards (50 m) of the nearest water at initiation and within 130 yards (119 m) at hatching. At Kindersley, 95% of 584 early nests were located 545 yards (498 m) or less from water at initiation and up to 880 yards (805 m) at hatching. Comparable figures for 108 late nests were 1,145 and 1,400 yards (1,047 and 1,280 m), respectively.

The shorter distances between nests and water in parklands were associated with a relatively high density of ponds (Fig. 1) and the restriction of much of the preferred nesting cover to pond edges. On the grassland site, greater distances were associated with a lower density of larger ponds, with much of the preferred cover being located in continuous uncultivated areas up to > 1.5 miles (> 2.4 km) from ponds (Fig. 2) and with hens being faithful to nest sites in spite of nearby ponds disappearing as the drought progressed. The same factors accounted for increasing distances from 1956 through 1959.

The nearest water, as given in our nest-to-water distances, was not always the pond used by hens ^{as waiting sites when} initiating laying (as shown by marked birds) nor the pond to which they moved broods at hatching. Therefore, these data are minimal in terms of distances actually travelled.

Table 2
Fig 4
Kind

Data from 12 other North American studies in pothole and large marsh habitats suggested a predisposition of Mallard hens to locate nests within 350 yards (320 m) of water (Appendix A). Such behavior might be adaptive. Broods hatching from nests near water would make a quicker journey to ponds and marshes and thus reduce risks of being taken by predators while on land. Any potential advantages accrued by nesting near water would have to be balanced against increased nest losses from predators searching shoreline cover (Keith, 1961:62). The ecological significance of nesting near water or at some distance from it on subsequent survival of broods requires testing.

Hatching success

At Roseneath, hatching success for early nests (34%) did not differ significantly from that for late nests (41%, Table 3). Avian predators, primarily crows (Corvus brachyrhynchos) and magpies (Pica pica), accounted for 44% of all destroyed nests while mammalian predators, chiefly striped skunk (Mephitis mephitis) and Franklin ground squirrels (Citellus franklinii), accounted for 35%. In 1952, eight pairs of crows and two pair of magpies nested on the study area while a 4-mi² (10.4 km²) block, which included the study area, contained 19 pairs of crows and six pairs of magpies. Pair numbers of both species did not appear to fluctuate yearly with only a slight reduction noted in 1954. Valid indices for the skunk population or for other buffer prey species were unavailable. Small sample sizes precluded meaningful comparisons between the causes of nest loss for early and late nests separately and also comparisons of hatching success among years.

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At Kindersley, a significantly higher proportion of early than late nests hatched (70 vs. 54%, Table 4). The proportion of early nests successfully hatching in 1956 and 1957 was significantly higher than in 1958, whereas late nests showed no significant differences in hatching success among years. Mammalian predators - striped skunks, badgers (Taxidea taxus) and coyotes (Canis latrans) - accounted for 60% of destroyed nests while avian predators were credited with 13%. The low impact of avian predators was a reflection of the relative scarcity of trees for breeding crows and magpies. Crow populations on and within 2 miles (3.2 km) of the study area varied from four to nine pairs, while two to six pairs of magpies were recorded in different years. Red foxes (Vulpes fulva) were virtually unknown until the 1960's.

Nesting success was significantly higher for early nests in grassland than in parkland but proportions of late nests hatching on the two areas were not significantly different. Optimal survival, in regards to hatching success, favored the primary clutches. In ephemeral water habitats or under drought conditions, broods originating from early clutches laid by adults, might have a greater chance of surviving to fledging before brood ponds dried, than those from later yearling clutches. Also, in years with low water levels the importance of high nesting success of primary clutches becomes paramount in terms of assuring survival of progeny to flying. Broods from replacement clutches find fewer ponds available in late July and August.

Overall hatching success of pooled early and late nests was significantly higher in grassland than parkland (67 vs. 36%). The hatching success of Kindersley Mallards was higher than in any previously reported study in either habitat type (Appendix E) and compared

favorably with nest success figures ($> 55\%$) given for island-nesting ducks by Vermeer (1970), Hammond and Mann (1956), Keith (1961), Townsend (1966), Duebbert (1966), and for California refuge studies by Miller and Collins (1954), Hunt and Naylor (1955), Anderson (1957), and Rienecker and Anderson (1960). The Kindersley figure was also similar to that for an island population in Scotland (49-78%, Marshall and Campbell, 1969), but lower than the almost complete success of Mallard nests reported from a South Dakota island (Drewien and Fredrickson, 1970).

Except in island nesting situations, upland nesting waterfowl generally experience high nest losses but their inferred high propensity to renest largely compensates for this initial loss (Cartwright, 1952; Sowls, 1955; Keith, 1961). Yet, of any aspect of waterfowl biology the proportion of hens which attempt to renest has been studied least. Over the past two decades only three published field studies have used marked birds for Mallard renesting studies: Sowls (1955), Hunt and Anderson (1966), Coulter and Miller (1968). A total of 62 Mallard hens have been marked with 29% renesting.

Coulter and Miller (1968) found that individual and age specific variations in renesting persistency and success were influenced by local population density and breeding environment. In the light of the apparent low nesting success and proportion of hens ultimately producing broods (Appendix E), there remains a need to determine renesting rates under the full spectrum of environmental conditions and habitat types. Inferences on the relative contribution of replacement clutches to overall reproductive output require validation.

Clutch sizes

Yearly variations in both clutch and brood sizes apparently occurred at Roseneath but because of small samples these could not be satisfactorily attributed to real changes and may reflect methodological inconsistencies. For discussion purposes data from all years were pooled for comparisons between early and late clutches.

Clutch sizes of successful nests during incubation were significantly larger in early nests than in late nests, 8.8 vs. 7.2 (Table 5), a trend reported by SOWLS (1955), Keith (1961), Ogilvie (1964), Mednis (1968) and Coulter and Miller (1968) (Appendix B). Mean clutch size at hatching was also significantly larger in early nests, 8.0 vs. 6.8.

At Kindersley, clutches, apparently complete, ranged from 3 to 14 eggs. Only one apparently multiple clutch was found (15 eggs) and only one mixed clutch, Mallard and Pintail, even though Mallard hens at the same stage of incubation nested within 3 feet (0.9 m) of each other.

The means of early clutches of all Mallard nests, successful nests and hatched nests in 1957 and 1958 were significantly larger than in 1956 (Table 6). The differences were attributed, partly, to earlier nesting in these two seasons (Fig. 3) and, possibly, to the age structure of breeding hens. High production of young in 1955 followed by high survival and homing of yearling hens, which lay smaller clutches (Grice and Rogers, 1965; Dane, 1966; Coulter and Miller, 1968; Mihelsons et al., 1968), could have decreased clutch sizes in 1956. With possibly a higher proportion of adult hens in 1957 and 1958 and with earlier nest initiation dates, mean clutch size increased. No similar significant difference was noted in late season clutches (Table 6). Comparing pooled 1956-58 means, all three categories of clutch size were

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significantly smaller in late than in early nests. In 1959, the mean of early season clutches was significantly smaller than each of the 3 preceding years. Two superimposed factors may have influenced clutch sizes, drought and increased partial predation. The individual influences were effectively obscured.

In Karelia, Russia, Ivanter (1968) recorded an average clutch size of 8.3 (N = 23, range 5-11) in first nestings and 6.4 in renests. In Finland, Hilden (1964) observed a seasonal clutch size of 8.24 while in Latvia, Mednis (1968) documented the reduction in mean clutch size from 10.8 in mid-April to 7.3 after late May and reported a mean of 9.06. Boyd and Campbell (1967) reported a mean clutch size of 8.2 and a mean hatching clutch of 7.5 on an island in Loch Leven. On the same island, Marshall and Campbell (1969) noted a decrease through the season but recorded no significant differences in clutch size from 1966 through 1968, i.e., 8.16 ± 0.18 , 8.58 ± 0.25 , 9.00 ± 0.17 with N = 126, 181, 109, respectively. In England, average clutch sizes of 13.3 have been reported by Boyd and King (1960), and 11 by Lack (1968b), while Ogilvie (1964) recorded a mean clutch of 12.6 ± 0.22 for early nests and 9.88 ± 0.20 for late nests.

Clutch size means varied from 10.1 in March to 7.0 in the first half of May in southern Moravia, 10.0 in March to 6.8 in the first half of June in Bavaria, and 10.9 in March to 8.0 in the last half of May in Switzerland (Kux, Bezzel, and U. Glutz in Bauer and U. Glutz, 1968:403). While reported clutches of nesting Mallards in England appeared significantly larger than those from North America, the other European averages are well within the range of the latter.

Variations in clutch sizes have been attributed to variations in age-composition of breeding pairs, population density, mean laying date and to direct and indirect effects of food supply for both adults and young (Klomp, 1970). A further variable was noted by Koskimies (1957) who concluded that clutch size in the Velvet Scoter (Melanitta fusca) was genetically fixed. Ryder (1970) proposed that physiological condition of the female Ross' Goose (Anser rossii) on arrival and during the incubation period influenced clutch size. Lack (1967, 1968b) has suggested that average clutch size of the Anatidae has been evolved in relation to the average availability of food for the hen around the time of laying, modified by the relative size of the egg, while Hilden (1964) proposed that annual variation in clutch size in ducks was due to availability of both winter and spring foods. The last author also reported that the proportion of unhatched eggs rose as clutch size increased and, on the average, the mortality rate was higher for broods originating from larger clutches in both the Tufted Duck (Aythya fuligula) and the Scaup (Aythya marila).

Any inverse relationship between increasing pair density and clutch size was difficult to ascertain because of the asynchrony of adult and yearling laying periods (when hostile pair interactions peak) and the time lag in arrival of pairs. Although the highest nesting population was recorded in 1957, no concomitant reduction in clutch size was evident (Table 6) but we could not separate possible effects of age specific clutch sizes. In Finland, Hilden (1964) reported no significant decreases in clutch sizes of Scaup and Tufted Duck with increasing pair abundance. Nor did Drewien and Fredrickson (1970) show decreases in average clutch size of Mallards nesting in 9 acres (3.6 ha)

of cover on a South Dakota island. Clutch sizes averaged 10.4 in 1967 and 8.8 in 1968 ($N = 39$ and 28 , respectively) but ranged from 6 to 18 eggs, the latter suggesting laying by more than one hen in each nest, a phenomenon also reported for dense nesting Gadwall hens (Duebbert, 1966). In-depth considerations of the many variables influencing clutch size cannot be attempted on the agricultural habitats such as we studied.

Egg loss

Not all eggs hatch in successful nests. Comparison of clutch size means of successful nests during incubation and at hatching at Roseneath showed 9% of the eggs were unhatched or lost in early nests and 6% in late nests. Unhatched eggs at Kindersley accounted for a 9% loss of pooled means for successful early clutches and a 3% loss in late clutches. The major factors were death of embryo, freezing, infertility and partial predation.

Our results follow closely those reported in seven North American studies summarized by Hilden (1964:215). Of nearly 10,000 Mallard eggs whose fate was determined (primarily on refuges), unhatched eggs made up 4.2 to 12.7% (average 6.7%) of the total. In other studies conducted from 1949 through 1960, unweighted mean loss was 8% and ranged from 1 to 19% (Appendix C). In successfully hatched nests, Keith (1961:52) found that 7.3% of 1,446 duck eggs of 11 species were nonviable and a further 1.5% were lost to predators, etc.

Brood sizes

At Roseneath, Class Ia brood sizes were significantly smaller than hatched clutch means in both early and late nests (Table 5). In

early clutches the average decrease between hatching and downy broods, less than 1 week old, was 20% (8.0 vs. 6.4); in late clutches it was 10% (6.8 vs. 6.1). There was a tendency for Class Ia brood sizes to be larger in years when hatching peaked early, 1952 and 1955 (Fig. 3), but we could not validly test these observations. No statistically significant differences in mean size of early and late Ia, II or III broods could be detected. Either survival of broods is high in parklands or methodological biases masked any seasonal reduction in size.

Overall reduction between successful clutch size during incubation and prefledged Class III broods was 31% in the early period (8.8 vs. 6.1) and 14% in the late season (7.2 vs. 6.2). The data suggest that survival of late broods is somewhat higher than early broods. Most of the mortality in both early and late periods occurred within 1 week of hatching.

At Kindersley, using 3-year pooled means, the loss of young between hatching and Class Ia was 27% for early broods (8.6 vs. 6.2) and 30% for late broods (7.7 vs. 5.4, Table 6). Reduction in mean brood size from Classes Ia to III averaged 18% early in the season and 13% for late broods (Appendix C). Overall reduction between clutch size of successful nests in incubation and prefledged Class III broods was 46% for the early (9.4 vs. 5.1) and 40% for the late period (7.9 vs. 4.7, Table 6). Average losses from seasonal complete clutches to Class III broods in four other studies was 36% (Appendix C).

In Holland, Eygenraam (1957) recorded the 4-year averages of 1-day-old Mallard broods as 10.59 ducklings in April, 10.42 in May and 8.92 in June. Comparable averages of 5-week-old broods were 6.99, 6.99 and 5.56, respectively. From 1951 through 1954, he reported no

significant difference in prefledged brood size, i.e., 6.02 to 6.91. In England, Boyd and King (1960) reported an average fledged brood of 6.6 young. Because of coalescing of older broods, average brood size at hatching, 6.1, increased to 6.8 for well grown young from first nestings but decreased from 6.9 to 5.6 in renests. In a more recent study Boyd and Campbell (1967) reported a Ia brood mean of 6.5 and a Class III mean of 4.4. Of 1,640 ducklings leaving the nest, 67% survived to flying. In Karelia, Russia, reduction from mean clutch size (8.3), to early hatched young broods (5.7), to "flapper" stage broods (4.3) was 48.2% (Ivanter, 1968). Elsewhere in European Russia, Sapiteen (1959) reported a reduction from an average clutch of 9.3 eggs to an average brood of 8.2 young in May, 7.9 to mid-June, 6.8 in late June, 5.4 in mid-July, 6.1 in late July and 5.5 in August. Approximately 58% of all eggs laid hatched successfully while brood loss from hatching to flying was 42%.

European studies showed a higher hatching success than those in North America, but similar clutch and brood sizes, both at hatching and fledging. All studies with comparable data (two in Russia and one at Loch Leven) show the high post-hatching reduction in brood size. The loss was associated with "insufficient" viability, unfavorable weather conditions and predation by Eygenraam (1957) while Boyd and Campbell (1967) noted the periods of greatest duckling loss were during periods of wet, cold weather. In the latter study, predation was not a major brood decimating factor.

Attrition through the brood period was negligible in the parkland but was more severe in the grassland. At Kindersley, avian and mammalian predation appeared a minor factor in brood mortality but it

could not be quantified. Both Marsh and Swainson's Hawks (Circus cyaneus and Buteo swainsoni) were observed diving at broods and were also flushed from dead ducklings. Few carcasses of defleshed young were encountered during banding or census operations.

Some morbidity in ducklings was attributable to the proventriculus worm (Echinuria uncinata; Cornwell, 1963). Infected ducklings appeared more prevalent during the worst year of drought, 1959. Bleached and worn scapular feathers, light weight and delayed plumage development in summer- and autumn-trapped birds were correlated with such infections at Kindersley. The extent of brood or adult loss due to echinuriasis is unknown but Cornwell (1963) suggested that losses would be greater in drought years when broods concentrate on the more permanent ponds, which also contain masses of the zooplanktonic, intermediate hosts. Similarly, no mortality could be attributed to heavy loads of helminth parasites observed. Cornwell and Cowan (1963) propose that severe nutritional host stress might increase mortality in Canvasback (Aythya valisineria) ducklings.

Differential survival of young originating from average-sized broods and those larger and smaller than average could not be determined. Eygenraam (1957) noted that broods of 9 to 12 downy young and those smaller than four showed proportionally higher losses than those with five to eight young. The chances of broods of one or two surviving were small because of early abandonment by the hen. Differential survival of early and late hatched broods has been documented by Gollop (1965b). He calculated a 1st year mortality rate of .55 for young hatched prior to 9 June and a .64 rate for those hatched after 29 June.

In summary, comparison of pooled means for each study area showed that mean sizes of successful clutches during incubation and at hatching were significantly higher at Kindersley than at Roseneath for early nests and showed a tendency to be higher for renests. Class Ia broods were significantly smaller at Kindersley late in the season (5.4 vs. 6.1) but mean size of early broods showed no significant difference between areas. Flightless Class III brood sizes were significantly lower at Kindersley than Roseneath for both early (4.7 vs. 6.1) and late parts of the season (5.1 vs. 6.2). The smaller brood sizes and higher percentage loss from Classes Ia to III at Kindersley were attributed to increased mortality from longer overland movements.

Brood movement

Mallard ducklings generally leave the nest within 12 hours of complete hatching of the clutch (Girard, 1941; Weidmann, 1956; Raitasuo, 1964; Kear, 1965; Ivanter, 1968) but may remain from less than 9 to more than 46 hours (Boyd and Fabricius, 1954; Hori, 1966; Bjärvall, 1967, 1968). Departure is during daylight hours, usually before noon (Bjärvall, 1968). Mallard broods have a fledging period of 52-60 days (Gollop and Marshall, 1954).

Brood loss, nest to water. From weekly censuses at Kindersley we found that 60% (117 broods) of clutches that hatched reached water in 1956, 35% (103) in 1957 and 65% (66) in 1958. Estimated survival of newly hatched broods from nest to water for the 3 years was 48% (95 of 197 hatched clutches). Evidence to corroborate such losses was collected in 1957 and 1958 when 109 hens, well along in incubation, were marked with plastic neck bands. Of 94 successful nests only 19%

of the marked hens were subsequently located on ponds through the two summers. Furthermore, only 24% of the colored broods from 37 hatched clutches injected with food dyes were observed after leaving the nest in 1957 and 1958.

Comparison of the measured number of hens raising broods to flying age (Table 9) with the number of brood hens estimated to have reached water from the nest site gave first approximations of total brood mortality associated with inter-pond movements during the fledging period. Our data suggest that only 66% of 117 broods reaching water survived to fledging in 1956, 39% of 103 in 1957 and 73% of 66 in 1958, for a 3-year pooled average survival of 58% (55 of 95 broods).

The high loss of entire Mallard broods from nest to water at Kindersley was associated with the greater distances that hens nested from water in grassland (Table 2, Fig. 4). The majority of broods had to travel more than 200 yards (183 m) to water after hatching. These distances may be a function of three factors: (1) high faithfulness of hens leading to persistent reuse of nesting cover through a drought period, particularly if the previous year's nest was successful, (2) crowded pair populations leading to increasing pursuits by drakes which forces hens to nest at some distance from ponds to avoid being molested (Dzubin, 1969a), and (3) preferred shrub nesting cover being available in continuous strips for more than a mile ^(1.6 km) from water in some cases.

Duckling loss. As with many nidifugous birds, the major mortality period in this study occurred immediately after hatching (Tables 5, 6). No specific cause could be determined for the high initial mortality. Most ducklings tended to "disappear" probably because their carcasses quickly decomposed. Starvation, heat stress, dehydration or entanglement

in the heavy rose-shrub (Rosa spp.) vegetation during nest-to-water movement may have been responsible. However, Mallard young are able to mobilize nutrients from the yolk sac, liver and subcutaneous fat deposits (Kear, 1965; Marcstrom, 1966) and to survive without food or water for more than 2 days. Lack (1967:127) suggested that the large internal food stores have survival significance in that "ducklings can walk a long way from the nest before their first meal", thus allowing the hen more latitude in selecting a safer nest site.

High losses may also involve exposure and chilling (Eygenraam, 1957; Nye, 1964; Boyd and Campbell, 1967). Newly hatched Mallards exhibit a low tolerance to cold as their thermoregulation is imperfect (Koskimies and Lahti, 1964). To survive they must be periodically brooded by the hen. Inability to maintain body temperature could occur after prolonged exposure to temperatures below 50°F (10°C) before reaching water or when internal food reserves were exhausted. Energetic stress of long distance movement may handicap cold hardiness. Thermal insulation of the body is also reduced during the first 48 hours as fat reserves are used. Therefore, excessive rainfall, cold and high winds could lead to increased brood mortality. Heat prostration might also occur.

Mobility and pond dispersion. In brood rearing habitat high seasonal mobility of hens and ducklings is a well documented phenomenon (Hochbaum, 1944:104; Evans et al., 1952:54; SOWLS, 1955:144; Berg, 1956; Marshall, 1958; Beard, 1964:505; McKinney, 1965). In our studies, we accepted the high mobility of broods as a natural phenomenon and not an artifact of our presence. Pond densities and the distances between ponds on 1 July showed major differences on the two areas (Table 7).

Table 7
Bird

In the driest₂ year at Roseneath (1952) there were 63 ponds/mi²₁ (24/km²) compared to 4.7₁ in the wettest year at Kindersley. At Roseneath, the mean distance from each pond to the nearest pond was 59 yards (54 m) while at Kindersley it was 245 yards (224 m). Comparable differences for the mean distances from each pond to the second, third and fourth nearest ponds were 96 vs. 400 yards (88 vs. 366 m), 138 vs. 524 yards (126 vs. 479 m) and 180 vs. 636 yards (165 vs. 582 m). At Kindersley, with increasing drought in 1957, 1958 and 1959, mean distances to nearest ponds increased to 938, 910 and 1,280 yards (858, 832 and 1,170 m), respectively, and the mean number of water areas within 0.5 mile (0.8 km) of each existing pond dropped from 3.0 to 0. The average number of ponds/mi² decreased to 0.7, 0.8 and 0.4, respectively.

At Roseneath, the mean number of ponds within 440 yards (402 m) of any pond was 14.8 compared to only 2.5 at Kindersley in 1956. Comparable pond number means within 880 yards (805 m) were 50.5 vs. 3.0.

Mobile broods, therefore, had to travel much longer distances between ponds in grassland area than in parkland. The chances that nonoriented broods, leaving one pond, would wander into another were excellent in parkland but poor in grassland.

Distances moved. Mallard hens and broods make frequent overland trips between ponds although no complete Mallard brood range has been documented in the literature. Mallard broods have been reported moving up to 2 miles (3.2 km) (Salyer, 1962:75; Young, 1967). At Kindersley, the greatest distances recorded were for two marked hens with broods moving 3 miles (4.8 km) in 1 week and 5 miles (8 km) in 9 days. Eighteen of 123 Mallards marked as Class I and II young were known to have moved 1.6 miles (2.6 km) from a drying slough to the nearest

pothole (Gollop, 1965b:17). In the same area, Heyland (1965:41) records a Class II brood moving 1.2 miles (1.9 km). At Minnedosa, Mallard broods remained on ponds for an average of only 7 days while the longest residence on a single pothole at Waubay, South Dakota, was 37 days (Evans and Black, 1956).

In short, Mallard broods are highly mobile and often change water areas during the fledging period. In marshes and large ponds several parts of shorelines are used during this period.

Movements and pond quality. Brood movement is a function of the hen's presence (Stoudt, 1969:128). At Minnedosa, all seven broods without hens remained on the ponds where they were found (Evans et al., 1952:34). However, factors causing brood movement are unclear. While drying of a slough is an obvious cause, food shortage and disturbance have also been suggested (Stoudt, 1969:128). Evans and Black (1956:45) could find no cause for movements which "were not always from poor to perceptibly better potholes, but were never to areas obviously poorer than those last occupied". Berg (1956) and Keith (1961) reported that movements were to larger, more permanent ponds. Evans and Black (1956) concluded that the hen was oriented to the landscape because she frequently left her brood for an hour or more to feed in nearby ponds and fields. In southeastern Saskatchewan, Stoudt (1961:32) noted that, although broods visited a number of ponds in moving several miles in years of favorable water conditions, during severe droughts (e.g., 1961) "hens would not move broods a half mile to the nearest good water even though the hen herself would fly to the pond".

Although one author concluded that food was not an important factor in pond selection (Benson, 1948), others have suggested that

hens search for favorable food and cover requisites (Beard, 1964:519; Mendall, 1958:134; Stoult, 1969) while still others (Evans et al., 1952:22; Sowls, 1955:150) noted that broods moved in "random" directions. Heyland (1965:33) found that wing-clipped incubating Mallards could return to nests from at least 870 yards (796 km) away, suggesting precise orientation even at ground level.

Our evidence from marked hens does not affirm any consistent pattern of movement by broods; some move steadily away from nests, while others may return to a pond after visiting one or more other potholes. Brood mobility patterns and orientation of brood hens require further field study, especially under conditions of minimum human disturbance.

Reproductive success

Two estimates of the number of young produced on both study areas were made: (1) a calculation from censuses of breeding pairs, hatching success, renesting rates, spring mortality of adults and average brood sizes, and (2) a measurement from censuses of nearly fledged broods and successful brood hens originating on the study areas (Tables 8 and 9). A major assumption was that all hens counted during spring breeding pair censuses attempted to lay one or more clutches. Observational evidence relating censused breeding pairs with nests found and pair behavior supported this assumption. However, evidence of nonbreeding by some apparently resident hens was obtained from specimens collected in 1959, a year of drought. Examination showed ova atresia and lack of ovulated follicles in hens collected from late-May flocks. Production calculations were rejected for that year.

Tables 8 + 9
here
from each
other

At Roseneath, the calculated production of young averaged 1.4 immatures/adult and varied from 1.1 in 1954 to 1.7 in 1955 (Table 8). Measured production averaged 1.2 and varied from 0.6 immatures/adult in 1954 to 1.6 in 1955. Because of the small size of the study area and evidence of brood movement across its boundaries, we accepted the calculated production as the best approximation of the 1 September population. Because there was apparently no loss of entire broods at Roseneath, this method could also be used.

At Kindersley, associated with the significantly higher hatching success (Table 4), calculated production averaged 1.8 immature/adult and varied between 1.4 in 1958 to 2.0 in 1957 (Table 9). Measured production was much lower: an average of 0.5 immatures/adult with a low of 0.3 in 1957 and a high of 0.7 in 1956 and 1958. Because of the lack of emergent vegetation resulting in high potential visibility of broods, and because of loss of entire broods, we accepted the measured method at Kindersley as giving the best estimate of actual production.

Local production and breeding populations

From the production estimates calculated and measured for the two areas we computed a theoretical population model for the April through August period (Table 10). Weighing the yearly decreases in spring breeding populations at Roseneath, 54 to 33 pairs from 1952 to 1955 (Table 8), we calculated implied mortality rates for this decrease. Using a formula developed by Hickey (1952), Balham and Miers (1959), Fog (1965), Henny (1969), and Henny, Overton and Wight (1970), we calculated the production of immatures required to balance the mortality rates for the two areas. At Roseneath, each hen had to

11/10
here

produce 1.7 immatures to maintain a stable population while at Kindersley the figure was 1.2 young.

Post-breeding season production indices should include some measure of the summer mortality of adults or such indices could be biased upward if reproductive output is compared to the original breeding population (Henny, Overton and Wight, 1970). Our estimated April-to-June drake and hen death rates of 2 and 5%, respectively, at Kindersley, and 4 and 7% at Roseneath (Tables 8 and 9), were similar to estimated drake mortality of 2% and hen mortality of 8% reported for the 6-May-to-15-July period by Keith (1961:44) in Alberta. Crissey (1969:163) estimated the adult mortality between May and September as averaging 4-5%, while Cartwright (1952) assumed that 2% of nesting hens were killed by predators. In our model, although we estimated an average loss of one hen and brood per year in the parkland (Table 10) we could not determine whether a hen was removed by predation or whether she abandoned her brood as early as the 5th week. We assumed the former had occurred.

The reproductive outputs at Roseneath, 1.3, 1.5 and 1.1 immatures/adult on 1 September (for the 3 years where subsequent breeding populations were known), averaged 1.3 and were sufficient to balance mortality rates of .40 for adults and .55 for immatures. These figures are at the lower limits of estimates given for various North American localities, i.e., .38 to .50 for adults and .55 to .69 for immatures (Crissey, in Smith, 1956:60; Keith, 1961:75; Jahn and Hunt, 1964:48). We concluded that the critical mortality occurred away from the study area from September through March. The proportion of new recruits to the spring population was determined on the fall migration and

wintering grounds.

Reproductive outputs in the grassland, 0.3 to 0.7 immatures/adult in fall, also resulted in a declining population which continued to 1963, 1964 and 1965 when 37, 40 and 39 pairs were counted (Dzubin, 1969b:206).

Under drought conditions at Kindersley, high brood mortality was considered the single most important proximate factor controlling fall population size. Concurrently, other disturbing forces also interacted to dampen summer gain: (1) increased predation on nests in 1958 and 1959, (2) telescoping of nest initiation period with fewer hens re-nesting and (3) nonbreeding.

Immigration of drought-displaced pairs onto the study area obviously increased the population in 1957 and, while not adequate to offset a decline, did contribute to the 1959 population.

The highest breeding population (1957) had the poorest breeding success, not because of significant decreases in clutch size or hatching success, but because of the highest loss of broods from nest to water and the lowest overall percentage of hens fledging broods during the study. From one year's data we could not assess any inverse effects of increased density on reproductive success.

Immigration obscured the effects of varying birth and death rates on population levels. Local populations may be reduced by low birth rates or high death rates but sustain themselves by influxes of pioneering birds from other more successful subpopulations. In general, breeding population changes between seasons are dependent on a number of factors: reproductive output, homing of adults and young, hunting and natural mortality during the winter, immigration and

emigration.

Drought impacts on production

The effects of drought on habitat quality and reproductive success of waterfowl has been documented both in North America (Yeager and Swope, 1956; Crissey, 1969) and Australia, where species show various adaptations to drought from nomadism to a periodic breeding season dependent on water levels (Frith, 1959).

In North America, the emigration of Mallards from drying grassland and parkland breeding grounds to boreal habitats of the Mackenzie River Basin and Alaska has been described by Crissey (1969). Smith (1969:118) also elucidated these periodic northward shifts and documented non-breeding during the 1959 drought, wherein Mallard pairs gathered in large concentrations through the regular breeding season and passed the summer as nonbreeding pairs until the molting period. Stoult (1969:126) suggested that weather plays a role in reneating effort of the Canvasback. Hens were more prone to reneat under conditions of cool temperatures and stable water levels, than under high temperatures and receding levels. Rogers (1964) recorded that a high proportion of Lesser Scaup (Aythya affinis) hens failed to nest when their nesting substrate was not flooded. In North Dakota, Salyer (1962) noted decreases in pair numbers and increased brood mortality with drying habitat. In South Dakota, Drewien and Springer (1969) described abandonment of drying ponds by Blue-winged Teal (Anas discors) but noted quick recolonization when water levels improved. Weller, Wingfield and Low (1958) observed increased nest predation with decreasing water levels on a Utah marsh. Evans and Wolfe (1967)

documented the reinvasion of a periodically flooded rainwater basin by ducks in Nebraska and the subsequent disappearance of the breeding population during 4 years of deteriorating water levels. Mayhew (1955) postulated that during drought low humidity in Mallard nests led to decreased hatching success, but Anderson (1957) found no evidence to support this theory. Our data from the grassland area suggest that even under drought conditions Mallards have a high "condensation potential" (Frank, 1957), i.e., they readily adapt to increasing pair densities, up to some unknown critical point. Hens successfully nested at densities approaching five pairs/acre (2/ha) of water on one pond at Kindersley (Dzubin, 1969a:148). High brood mortality from nest to water and during inter-pond movements plus lower mean brood sizes were the most obvious effects of drought on Mallard production in the grassland area.

Production indices

The estimation of summer replacement rates requires precise information on the number of breeding pairs, the proportion producing young, the summer mortality of adults and the true brood size at fledging. Data on clutch sizes, nesting success and renesting are useful in estimating production but are not in themselves sufficient to arrive at fall age ratios because no account is taken of hens losing entire broods.

Comparison of our results with other North American studies showed that clutch sizes were below average at Roseneath but above average at Kindersley (Appendix B) while brood sizes for both areas were generally lower than elsewhere (Appendix D). Hatching success

at Kindersley (67%) was higher than in any other study in the pothole-stockpond habitat but the average proportion of hens ultimately successful in producing fledged broods (21%) was lower in only one year in one other area (Appendix E) and reflected losses of entire broods. Loss of broods or no renesting lead to early abandonment of unfavorable brood rearing habitat by hens. Although overall reproductive output is reduced, the hens' survival for another breeding year may be enhanced, as they are not tied to suboptimum habitats for the fledging period and they undergo the stressful molt period earlier and in more favorable habitats.

Superficially, there was little indication of regional, latitudinal or habitat differences in seasonally pooled clutch size means from various North American locations (Appendix B), although valid statistical comparisons were precluded by lack of supporting variance and age-structure data. In Maine, clutch size means reported by Coulter and Miller (1968:24) for the 1951-56 period were significantly higher (10.6 ± 0.25) than means obtained in the same region from 1957-63 (9.2 ± 0.22). They were further significantly higher than those reported for 1953-57 by Keith (1961:52) in central Alberta (8.8 ± 0.15), from Roseneath (8.21 ± 0.14), and from Kindersley (8.91 ± 0.07) ($N = 48, 83, 88, 166$ and 627 , respectively, for each sample mean \pm S. E. of the mean).

In our studies the major percentage loss of young occurred within a week of hatching. In other studies (Appendix C) losses between Class I and Class III broods were variable but averaged higher than nest-to-water losses (Appendices C and D). From continental production ratios of 0.6 to 1.7 immatures/adult recorded for the 1955 to 1965 period by Crissey (1969:163), we calculated that a maximum of 54% and

a minimum of 19% of the hens successfully fledged flying broods, assuming (1) an average brood size of 6.3 on 1 September, and (2) balanced sex ratios. On the basis of average annual production of 1.1 immatures/adult and the above assumptions, 35% of Mallard hens must ultimately be successful in bringing broods to flying stage.

The latter figure is similar to the average index of per cent successful hens given in Appendix E - 34.7 - which is also similar to the average hatching success - 33.8%. These data suggest that either loss of entire broods may be a key decimating factor or that reneating does not contribute as much to overall continental reproductive success as previously inferred. The only long-term estimates of the proportion of hens ultimately successful in producing broods are those published by Stoult for southeastern Saskatchewan which show a 13-year average of 34.8% (range 21-70) and by Smith for central Alberta which show a 12-year average of 46.6% (range 15-92) (in Dzubin, 1969a:147). Data for European studies show 66% of hens successful in fledging broods in England (Boyd and King, 1960), 76% and 77% in Holland (Eygenraam, 1957) and 70% in the province of Zeeland, Holland (Lebret, 1961).

As mean brood size at fledging decreases, the proportion of hens required to produce broods to maintain population equilibrium under prevailing mortality rates must rise accordingly. For example, to maintain population balance (assuming equal sex ratios and average annual mortality rates of .40 for adults and .65 for immatures, none of which occurs in the summer), 68% of hens must be successful in producing an average brood of 5.0 young, while only 53% of the hens must be successful if the average number fledged is 6.5.

GENERAL DISCUSSION

Long-term fluctuations of the North American Mallard population over the last three decades have been associated primarily with climatic factors per se and as they affect the number of May and July ponds on the breeding grounds (Bellrose et al., 1961; Watt, 1968:172; Crissey, 1969). Hunting mortality is also a major factor regulating populations (Hickey, 1952; Crissey, 1969; Geis et al., 1969) with high local exploitation rates leading to population declines (Hochbaum, 1947; Moyle, 1964; Jessen, 1970). Under low population levels, Watt (1968:175) speculated that mortality factors may operate more severely against hens with many being lost through increased predation, hunting, botulism and drought. As with other nest loss factors, the role of predation in depressing reproductive success is complicated by re-nesting (Cartwright, 1952; Hickey, 1952; Errington, 1956; Balser, Dill and Nelson, 1968). In artificially altered habitats with restricted nesting cover, predators may become a major decimating factor. Density-dependent factors may be operative in reducing summer gain when populations exceed the carrying capacity of prairie pothole habitat (Bellrose et al., 1961; Crissey, 1969; Dzubin, 1969a). Parasites and diseases cause spectacular local die-offs but are not considered to be a major regulatory factor (Weller, 1964).

Reproductive output is dependent on a multiplicity of inter-related factors which acting in concert tend to depress summer gain. Subpopulations separated into a mosaic of habitats undergo annual fluctuations as a consequence of the effects of these many factors. On a number of intensively studied areas (Ellig, 1955; Stoudt, 1956;

Smith, 1956; Steel, Dalke and Bizeau, 1956; Keith, 1961; Jahn and Hunt, 1964; Moyle, 1964, Stouidt, 1969; Smith, 1969) a whole spectrum of factors has been proposed for reducing summer gain, e.g., land-use practices, plant succession, freezing and wet weather, hail, predation of eggs, nests and young, nest desertion, density effects, diseases, parasites, human disturbance, nonbreeding emigration, droughts and low renesting rates. On some study areas, one factor or a combination of factors was dominant every year and could be considered key, proximate controlling factors while the same or other factors in other areas fluctuated greatly in their annual impact. Geographically, different subpopulations of a species apparently fluctuate independently as the effective environmental factors influence them in different ways.

The role of Mallard spacing behavior and mutual intolerance as a contributory force controlling breeding population density or leading to more efficient resource apportionment is complex (McKinney, 1965, 1970). Only one aspect was considered here, i.e., greater nest distances from water, with density-associated increasing rates of aerial pursuits of hens by drakes. Agonistic and sexual motivated coactions plus the dispersion of small ponds themselves lead to pair spacing, with its implied regulatory role. Pairs show activity localization and site tenacity to specific small ponds or portions of shorelines, and drakes launch aerial pursuits against hens of transgressing pairs for periods up to 4 weeks. Where a preponderance of ponds are less than 1.5 acres (0.6 ha) in size, e.g., in parkland, spacing behavior disperses pairs amongst ponds and may play an important role in determining breeding densities or dispersing some later arriving pairs to other habitats. No definitive data exist

which show increased adult deaths or reduced progeny output from pairs so displaced. The social structure of pairs is further complicated in habitats which contain ponds larger than 3.5 acres (1.4 ha) in size on which spaced pairs aggregate but show greater tolerance to neighboring pairs as in some grassland habitats. Here, drakes are incompletely dominant, waiting site and activity centers are not exclusive use areas and pursuits may be initiated from many portions of the home range.

Considering the compensatory processes of emigration, delayed breeding and high mobility in prairie pond habitats, we suggest that spacing mechanisms play a minor, but little understood, role in regulating local pair abundance and further influencing continental reproductive output (for other views see Crissey, 1969). Arguments for density regulated reproductive success and proposals that social behavior is the ultimate factor limiting populations remain speculative (Dzubin, 1969a). Grassland breeding Mallards may differ genetically from parkland birds in inter-pair hostility and condensation potential (see Chitty, 1960). Any such proposed racial differences are conjectural.

Movements of brood areas with a high density of ponds may have some adaptive significance, e.g., on the average, more young survive by moving than by remaining on one pothole. Other than leaving a pond that will dry before the birds can fly, increased survival through movement may be associated with (1) an anti-predator mechanism, (2) food deficiencies affecting development on a particular pond, (3) a decrease in inter-brood competition for food or cover, and (4) developing toxicity, e.g., algae or alkalinity. However, the behavioral attribute of recurrent mobility that has positive survival

implications where ponds are aggregated is negated during periods of drought. The ultimate selective advantage favoring movement of broods from small astatic ponds to potholes where the young are assured of reaching flight stage is obvious. During drought, selection would favor hens and broods remaining on permanent ponds but other pressures, e.g., predation and lack of adequate food, might outweigh any such tendency.

Where mallard brood hens utilize large, i.e., > 3 acres (1.2 ha), widely dispersed stock ponds in grassland habitats, the movement of hens from one shoreline to another may suffice to fulfill any appetitive mobile behavior. On the other hand, any behavioral or racial adaptations which lead to decreased inter-pond mobility in habitats where stock ponds are widely dispersed, would favor increased progeny survival and population maintenance.

We suggest that the high correlation obtained by Crissey (1969) and by Geis et al. (1969) between July pond numbers and productivity, as measured by immature:adult ratios, can, in part, be explained by the following proposal. Optimum Mallard brood habitat in both parklands and grasslands must contain densities of at least four to six ponds per 160 acres (65 ha). Strategically dispersed aggregations of permanent ponds are the critical factor, not numbers alone. Aggregations increase the chance that wandering brood hens will find water. Where drought leads to greater spacing of ponds the mortality of young will increase, resulting in lower productivity.

SUMMARY AND CONCLUSIONS

From 1952 through 1959, the reproductive success of Mallards was estimated in successive periods on two study areas in the southern prairies of Canada. Roseneath, 895 acres (362 ha) in the aspen parklands near Minnedosa, Manitoba, contained many small ponds, while Kindersley, 672 acres (2,720 ha) in the mixed grasslands of Saskatchewan, contained fewer but larger ponds. During the 4-year study period on the latter area, increasing drought was experienced.

Nests in parkland were significantly closer to water than those in grassland, their hatching success was much lower, clutch sizes were smaller and losses from downy young to fledging were lower. The proportion of hens producing broods on the parkland area was double that of the grassland block (46 vs. 21%).

In neither of the two areas was production of immatures sufficient to maintain population levels in the face of prevailing hunting losses and other mortality factors. At Roseneath, the mean annual production per 100 nesting hens was 267 young or 1.4 immatures/adult on 1 September (after subtracting summer adult mortality); at Kindersley it was 106 young or 0.5 immatures/fall adult.

The major factor restricting population growth in the parklands was the high exploitation rate of adults and young after 1 September, either on the breeding grounds prior to migration or on migration and wintering areas. On the grassland block most of the 1st-year mortality of young occurred during overland movements of broods between nest and water and between ponds. Mallards were sensitive to environmental controls and the limiting effect of early deaths was evident under

drought conditions. Immigration at Kindersley obscured meaningful evaluation of the effects of reproduction on the subsequent year's breeding population.

Production of young by homing and immigrant Mallards in relatively favorable grassland habitat (prior to 1956) was apparently not limited by nest predation nor inter-pond brood mortality. Subsequent breeding population peaks were not realized because of brood mortality between nest and water resulting from (1) the drying of ponds after nest initiation in habitat already suboptimum in pond density and (2) the crowding of pairs causing hens to locate nests at greater distances than normal from water, probably in order to avoid harassment by drakes. Breeding populations were reduced to 10% of peak levels during prolonged drought (through 1965) primarily because of continued reproductive failure, emigration of adults from unsuitable habitat and, perhaps, fall and winter exploitation by hunters.

Two behavioral characteristics of Mallard hens are important factors in drought situations: (1) a strong fidelity to a previous nesting site and (2) a tendency to move broods periodically and without orientation to other ponds. The appetitive mobile behavior apparently cannot be adapted to drought conditions. Any selective advantages that accrue over the long term from persistent reuse of deteriorating habitat and disoriented brood movement are negated during droughts.

Considering the methodological imprecision and approximations inherent in many waterfowl investigations published to date, we conclude that there remains an urgent need for more precise estimates of natality and mortality by regions. Long-term ecological and behavioral studies with supporting marking programs carried through

entire precipitation and population cycles are a necessity if we are to better understand the processes of population regulation in any waterfowl species. Four areas require special consideration: (1) the formulation of statistically and biologically sound pair and brood surveys, (2) a more precise estimate of the proportion of hens which attempt to nest and reneest under varying climatic and edaphic conditions and, further, the proportion which successfully fledges broods, (3) more quantitative data on seasonal mobility and natural mortality of adults and young on the breeding grounds through individually identifiable birds, and (4) the effects of food supplies and spacing behavior on breeding densities and survival, growth, and output of progeny.

Intensive studies on local or regional subpopulations should be initiated to test specific hypotheses. The size of a study area should depend primarily on the factors affecting adequate sample size: breeding pair density, density and mobility of broods, etc. The ideal would be to continually record the activity of at least 30 successful pairs from spring arrival to fledging of their broods each year. In a grassland area such as Kindersley at the time of this study, $150 \pm$ pairs would have to be marked and tracked to obtain this output of data on Mallards. The area would then start off as the smallest piece of land with 150 markable pairs and end up as the area covered by the 30 marked broods from hatching to fledging.

Long-term marking would also be needed for an understanding of homing, immigration, emigration, age structure, etc., on production. Such research should permit the modelling of production from each important habitat unit. Along with banding and other techniques, it

would allow annual predictions of the geographical and temporal contribution to hunting, based on routine measurements of breeding pairs and the effective environmental limiting factors. Adequate research may also provide practical methods for significantly reducing the heavy losses to potential gain occurring during nest and brood periods: 89% at Kindersley (940 eggs for 100 fledged young) and 68% at Roseneath (880 eggs for 280 young).

The current concept of a subpopulation of breeding waterfowl is apparently that of a group of birds faithful to a particular block of breeding habitat (whether a few mi^2 or a few thousand mi^2) with no significant dilution from or dispersal to other areas. Ideally, it would have a restricted migration route and wintering area. While this concept holds for geese, it may not be acceptable for ducks as suggested above because of immigration and emigration and because of divergent migration routes and extensive wintering areas, even for Mallards raised on one pond (Gollop, 1965b). With ducks it is necessary to learn how the entire range of each disturbing factor in a habitat type affects the contribution of birds to the fall flight, whether the breeding population is made up largely of homing or immigrant birds.

To implement this proposal, it would be necessary to classify waterfowl habitat considering such obvious factors as large and small ponds, high and low pond densities, drought susceptible and resistant areas, and major differences in other factors, such as predators. A gross classification and delineation would suffice for management purposes at this time.

Current management concepts and data gathering schemes are oriented to some wide ranging "continental" Mallard population. Use of the best data available has apparently resulted in serious errors

in population plots which, in turn, have been adjusted and weighted to agree with what is believed to be a new best estimate of the population. We suggest that the imprecision of recent predictions should be attacked by research and data collection on subpopulations by learning to count and predict breeding populations from each habitat type under varying conditions, measuring production in the field and from wing surveys related to each subpopulation and directly identifying the harvest from each area. If adequate technology is not available, emphasis should be put on its development.

Wild Mallards breeding under natural conditions are poor subjects on which to accumulate statistically sound population parameters. The species is particularly sensitive to human interference, especially during the brood period. Statements such as "unstudied Mallard populations easily maintain themselves" might be viewed as a general truism. Field workers concerned with duck population dynamics should periodically remind themselves of the Heisenberg Uncertainty Principle (TIME, Canadian Edition 04/15/63, p. 51), "the very act of observing or probing a phenomenon changes the phenomenon".

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Appendix A. Recorded distances of Mallard nests from water.

Area	Number of nests	Average distance to water yards (m)	Remarks	Author
Montana	252	118.7(109)		Girard, 1941
"	10	319.9(293)	82% < 100 yards (91 m)	Smith, 1953
"	20	90 (82)	Grass cover	Ellig, 1955
"	12	55 (50)	Greasewood cover	"
California	13	51.2 (47)		Mayhew, 1955
"	209		78% < 50 yards (46 m) 16% over water	Miller & Collins, 1954
Manitoba	123		90% < 200 yards (183 m)	Sowls, 1955
Wisconsin	68	229 (209)		Labisky, 1957
Alberta	135	18 (16)		Keith, 1961
Minnesota	50	317 (290)	Maximum 1120 yards (1024 m)	Ordal, <u>in</u> Moyle, 1964:95
"	62	17 (16)	90% < 50 yards (46 m)	Jessen, Lindmeier & Farnes, <u>in</u> Moyle, 1964:64, 17.
"	9	130 (119)	Maximum 352 yards (322 m)	Benson, <u>in</u> Moyle, 1964:119
Saskatchewan	12	2 (2)		Townsend, 1966
.....				
Manitoba	217	33 (30) 6 (5)*	At hatching	This study - Table 2
Saskatchewan	584	275 (251) 190 (174)*	At hatching - early	" " "
	108	351 (321) 255 (233)*	" " - late	" " "

* Median value.

Appendix B. Seasonal clutch sizes of Mallards in North America.

Year	Area	Clutch size	N	Author(s)
1949	California	5.7	35	Mayhew, 1955
1950	"	8.2	5	"
1951	"	8.9	38	Hunt & Naylor, 1955
1952	"	8.9	178	Miller & Collins, 1954
1953	"	8.3	64	Hunt & Naylor, 1955
1949	Colorado	8.1	165	Flinn, 1949:138
1950	"	8.3	370	Flinn, 1950:163
52-56	Great Plains	8.3	40	Weller, 1959:354
1951	Idaho	8.9	22	Wolf, 1955
51-56	Maine	10.6	48	Coulter & Miller, 1968:24
57-63	"	9.2	83	"
1949	South Dakota	8.9	27	Stoudt, 1949:149
1950	Utah	8.9	37	Nelson, 1950:136
1950	"	9.4*	63	Weller, 1959:354
1951	"	9.4	103	Nelson et al., 1951:128
1951	"	8.2	28	Wolf, 1955
1956	"	9.6	19	Ryder, 1961
1957	"	8.4	11	"
53-57	Alberta	9.6	(prior 5/16)	
		8.1	58 (post 5/31)	Keith, 1961

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Appendix B Concluded.

Year	Area	Clutch size	N	Author(s)
47-50	Manitoba	10.0	23	(prior 5/15) Sowls, 1955:132
"	"	8.3	25	(5/15 to 6/15) "
1955	Saskatchewan	9.9	84	Gollop & Fyfe, 1956:74
Weighted mean**		8.72 (1468) Range, 5.7-10.6		
52-55	Manitoba	8.6	111	(prior 5/25±) This study
		7.2	55	(post 5/25±)
56-59	Saskatchewan	9.1	529	(prior 5/15±) This study
		7.7	98	(post 5/15±)

* Average 9.2 in 223 parasitized clutches.

** Excluding Keith, 1961.

Appendix C. Estimated seasonal losses in Mallard clutches and broods.

Average clutch size (eggs)		Loss un-hatched eggs %	Mean brood sizes		Loss hatched clutch to I %	Loss I to III %	Total loss completed clutch to III		Area	Year	Author(s)
Seasonal complete	Hatched		Ia, I	III			No.	%			
8.1	7.4	9	6.8	5.0	8	26	3.1	38	Idaho	1949	Bizeau & Steel, 1950:132.
										1951	Steel, Dalke & Bizeau, 1956.
8.3	7.0	16	7.1	5.6	0*	21	2.7	33	Calif.	1949	Chattin, Miller & Foster, 1949:123.
8.9	8.3	7	6.8	6.2	18	9	2.7	30	Calif.	1952	Miller & Collins, 1954:26,28.
8.4	6.9	18	4.8	3.6	30	25	4.8	57	Calif.	1949	Earl, 1950.
8.1	7.9	2	-	7.2	-	-	0.9	11**	Colo.	1949	Flinn, 1949:138.
7.6	-	-	6.6	-	-	-	1.9	24**	Alta.	1949	Smith, 1949:46.
8.9	-	-	6.1	5.4	-	11	3.5	39**	"	1950	Smith, 1950:35.
8.5	7.5	12	-	-	-	-	-	-	"	1952	Smith, 1956:51,58.
8.0	6.5	19	5.5	4.6	15	16	3.4	43	"	1953	"
8.0	7.7	4	6.6	4.7	14	29	3.3	42	"	1954	"
8.6	8.5	2	7.0	3.5	18	50	5.1	59	"	1955	"

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Appendix C continued.

Average clutch size (eggs)		Loss un-hatched eggs %	Mean brood sizes		Loss hatched clutch to I %	Loss I to III %	Total loss completed clutch to III		Area	Year	Author(s)
Seasonal complete	Hatched		Ia,I	III			No.	%			
8.50	8.24	4	6.96	6.13	16	11	2.4	28	Sask.	1952	Stoudt, 1956:25,47,49.
8.36	7.92	5	6.91	6.55	13	6	1.8	22	"	1953	"
8.07	7.69	5	6.14	5.86	21	5	1.8	22	"	1954	"
8.38	8.16	2	7.56	6.24	7	17	2.1	25	"	1955	"
-	8.6	-	7.6	6.5	12	14	-	-**	Sask.	1955	Reeves, Lundy & Kreller, 1956.
9.9	-	-	6.2	-	-	-	-	-**	Sask.	1955	Gollop & Fyfe, 1956:74.
8.8	-	-	7.2	-	-	-	-	-	Alta.	53-57	Keith, 1961:72.
8.5	7.7	9	6.4	-	17	-	-	-	Minn.	57-60	Moyle, 1964:72.
10.3	10.2	1	8.8	-	14	-	-	-	"	"	" 1964:96,103.
8.3	7.7	8	6.6	5.3	14	20	3.0	36			Unweighted average.
8.6	8.0	7	6.4	6.1	20	5	2.5	29	Man.	52-55	This study - early nests.
7.2	6.8	6	6.1	6.2	10	0*	1.0	14	"	"	- late nests.

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Appendix C concluded.

Average clutch size (eggs)		Loss un-hatched eggs %	Mean brood sizes		Loss hatched clutch to I %	Loss I to III %	Total loss completed clutch to III		Area	Year	Author(s)
Seasonal complete	Hatched		Ia,I	III			No.	%			
9.1	8.6	7	6.2	5.1	27	18	4.0	44	Sask.	56-58	This study - early nests.
7.7	7.7	0	5.4	4.7	30	13	3.0	39	"	"	- late nests.

* Anomaly in data: increase treated as no change.

** Not used in averages because data incomplete. Sample sizes generally exceed 30 in each category.

Appendix D. Seasonal attrition of Mallard broods in various North American habitats.

Year	Area	Mean brood sizes			Total number broods	Loss	Loss	Estimated total loss		Authority
		I	II	III		I to II %	II to III %	No.	%	
50-56	Wisconsin	7.7	6.8	6.5	330	12	4	1.2	16	Jahn & Hunt, 1964:45
37-50 (9 yrs)	Minnesota	8.4	7.5	6.9	838	11	8	1.5	18	Stoudt, 1950:185
1951	"	6.6	6.8	6.3	92	0*	7	0.3	5	Ellerbrock, 1956:205
1952	"	4.5	7.2	6.7	127	0*	7	0*	0*	"
1953	"	7.5	5.7	5.6	18	24	2	1.9	25	"
1954	"	7.8	7.0	5.5	44	10	21	2.3	29	"
1955	"	7.0	7.1	7.0	51	0*	0*	0	0	"
1948	"	6.8	6.9	6.4	103	0*	7	0.4	6	Lee, 1949:182
1949	Dakotas	6.97	6.77	6.67	130	3	1	0.3	4	Stoudt, 1951:173
1950	"	7.05	7.00	6.25	193	1	10	0.8	11	"
1951	"	6.92	6.40	7.24	153	7	0*	0*	0*	"
1948	N. D.	9.1	7.5	7.1	-	18	5	2.0	22	Stoudt & Davis, 1948:135
1948	S. D.	8.2	6.5	6.8	-	21	0*	1.4	17	"

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Appendix D Continued.

Year	Area	I	II	III	Total number broods	Loss I to II %	Loss II to III %	Estimated total loss I to III No.	%	Authority
1950	S. D.	7.1	7.4	6.9	69	0*	7*	0.2	3	Murdy, 1950:151
1954	N. D.	6.7	6.9	6.4	124	0*	7	0.3	4	Fashingbauer & Sjoldal, 1955:208
1951	Colorado	6.0	6.6	6.4	240	0*	3*	0*	0*	Grieb & Wampole, 1951:140
1951	"	6.3	6.7	6.3	148	0*	6	0	0	Grieb et al., 1952:179
1952	"	6.6	6.5	6.3	167	2	3	0.3	5	"
1946	Washington	6.6	5.3	5.4	102	20	0*	1.2	18	Yocum, 1951:91
1948	"	7.6	6.2	6.8	104	18	0*	1.8	24	"
1948	"	7.5	6.3	5.8	145	16	8	1.7	23	Yocum & Hansen, 1960:244
1949	"	8.1	6.4	6.4	352	21	0	1.7	21	"
1950	"	6.5	5.4	5.5	227	17	0*	1.0	15	"
1951	"	6.5	6.5	6.1	218	0	6	0.4	6	"
1952	"	7.6	6.8	6.2	386	11	9	1.4	18	Moreland, 1952:131
1954	"	6.1	5.1	5.8	281	16	0*	0.3	5	Hansen, Oliver & Jeffrey, 1955:158

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Appendix D Concluded.

Year	Area	I	II	III	Total number broods	Loss I to II %	Loss II to III %	Estimated total loss I to III		Authority
								No.	%	
1952	Idaho	7.2	5.6	6.1	269	22	0*	1.1	15	Salter, 1952:158
1953	"	6.2	6.2	5.7	270	0	8	0.5	8	Salter, 1954:154
1954	"	6.3	5.6	5.6	321	11	0	0.7	11	Salter, 1955:183
1953	Oregon	7.5	7.3	7.1	181	3	3	0.4	5	Kebbe, 1954:137
1954	"	8.2	7.5	7.6	41	9	0*	0.6	7	Kebbe, 1955:162
1955	"	7.3	6.3	6.6	34	14	0*	0.6	8	Kebbe, 1956:140
1948	Alberta	7.0	6.6	6.1	60	6	8	0.9	13	Smith, 1948:54
Unweighted average		7.1	6.6	6.4	6,403	9	4	0.8	11	
52-55	Manitoba	6.4	6.3	6.1	322	2	3	0.3	5	This study - early nestings
"	"	6.1	5.8	6.2	157	5	0*	0*	0*	" - late "
56-58	Sask.	6.2	5.5	5.1	574	11	7	1.1	18	" - early "
"	"	5.4	5.2	4.7	341	4	10	0.7	13	" - late "

* Data anomaly; increase treated as no change.

Appendix E. Mallard hatching success and per cent hens successful in fledging broods in pothole-stockpond habitat of the Dakotas and southern Canada.

Nests			Breeding pairs	Broods	Index % hens successful	Area	Year(s)	Author(s)
Number nests	Hatched	Hatching* success %						
			46	13	30	Man.	1949	Evans et al., 1952:38
68	26	38				"	1949	Hawkins, 1949:64
27	2	7				S. D.	1949	Stoudt, 1949:149
			84	56	67	"	1950	Bue, Blankenship &
			100	66	66	"	1951	Marshall, 1952
			61	19	31	N. D.	1949	Stoudt, 1949:150
			61	13	21	S. D.	1949	"
			31	13	42	Sask.	1950	Leitch, 1956:103, 104
			34	10	29	"	1951	"
			111	58	52	"	1952	"
			154	53	34	"	1953	"
			193	47	24	"	1954	"
			106	22	21	"	1955	"

. . . cont'd

Appendix E continued.

Nests								
Number nests	Hatched	Hatching* success %	Breeding pairs	Broods	Index % hens successful	Area	Year(s)	Author(s)
			13	5	38	Sask.	1952	Leitch, 1956:105
			19	9	47	"	1953	"
			27	13	48	"	1954	"
			23	17	74	"	1955	"
			113	19	17	S. D.	1950	Evans & Black, 1956:25
			96	27	28	"	1951	"
			104	24	23	"	1952	"
			81	31	38	"	1953	"
58	33	57	264	122	46	Sask.	1952	Stoudt, 1956:41
219	107	49	255	101	39	"	1953	"
266	64	24	211	45	21	"	1954	"
245	95	39	168	71	42	"	1955	"
11	5	46	-	-	-	Alta.	1952	Smith, 1956:55, 56

. . . cont'd

Appendix E concluded.

Nests								
Number nests	Hatched	Hatching* success %	Breeding pairs	Broods	Index % hens successful	Area	Year(s)	Author(s)
13	4	31	96	25	26	Alta.	1953	Smith, 1956:55, 56
132	9	7	141	30	21	"	1954	"
40	15	38	152	44	38	"	1955	"
186	69	37				Man.	1953	Kiel, 1954:84
63	21	33				"	1953	Howard, Pospichal & Reid, 1954:89
80	39	49	234	69	30	Sask.	1955	Reeves, Lundy & Kreller, 1956:54-62
101	21	21	82	40	49	Alta.	1953-57	Keith, 1961:61, 62
1509	510		3060	1062				
	Avg.	33.8		Avg.	34.7			
257	93	36	177	71	40	Man.	1952-55	This study
709	477	67	779	165	21	Sask.	1956-58	" "

* Seasonal figures - primary and replacement clutches lumped.



Fig. 1. A 110-acre (44-ha) portion of the Roseneath Study Area, April, 1954. Note wide dispersion of small ponds and potential shrub-grass nesting cover near ponds and waste uplands. Seven Mallard pairs utilized shorelines of the more permanent ponds for waiting areas.

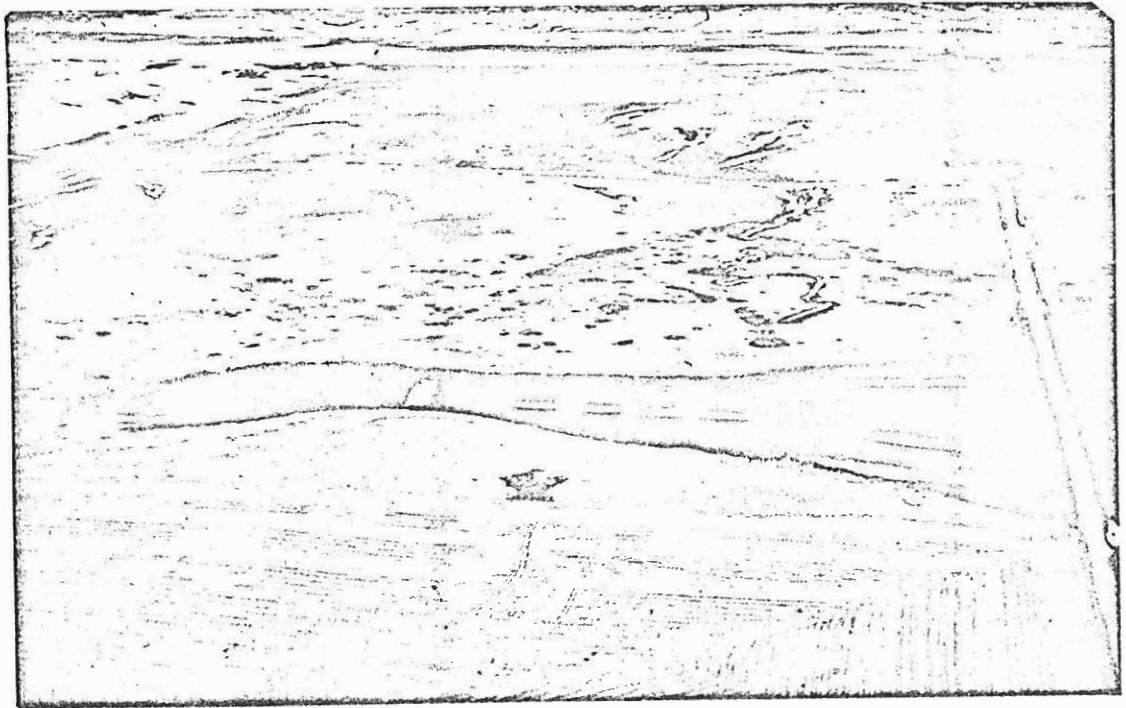


Fig. 2. Portion of the Kindersley Study Area, April, 1958. Note the 20-acre (8-ha) pond containing islands, lack of small upland potholes, and dark Symphoricarpos-Rosa nesting substrate restricted to dry water courses. The 14.2 acres (5.7 ha) of nesting cover in the lower center contained 77 Mallard nests in 1957.

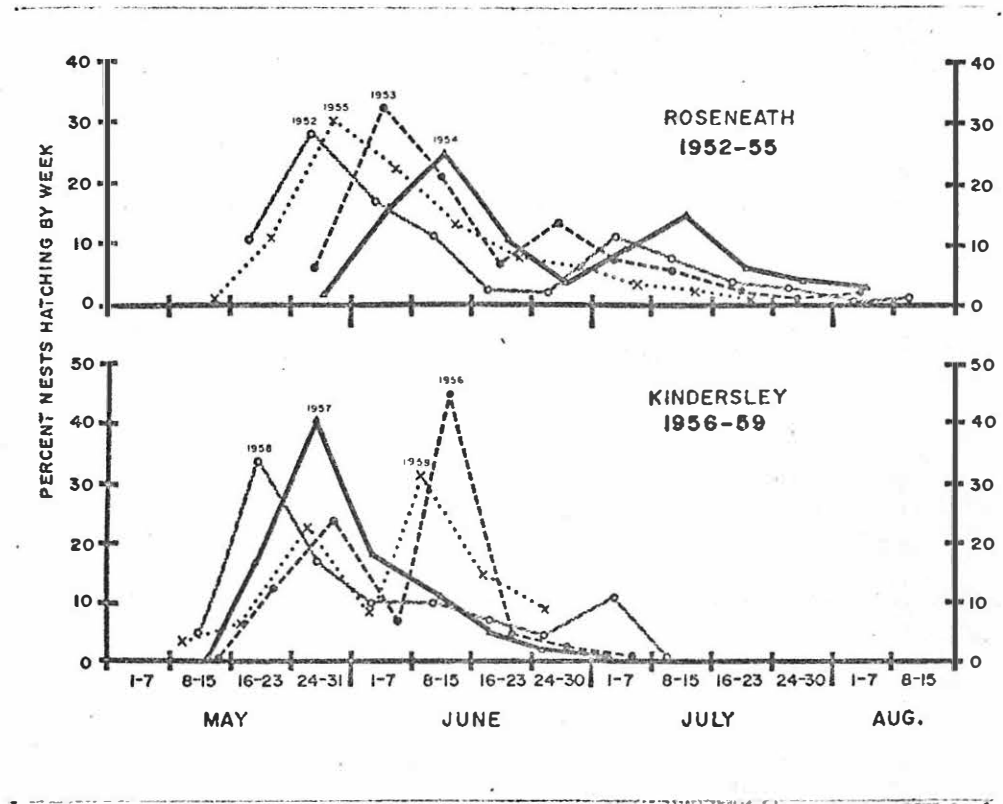


Fig. 3. Hatching peaks and duration of hatching season.

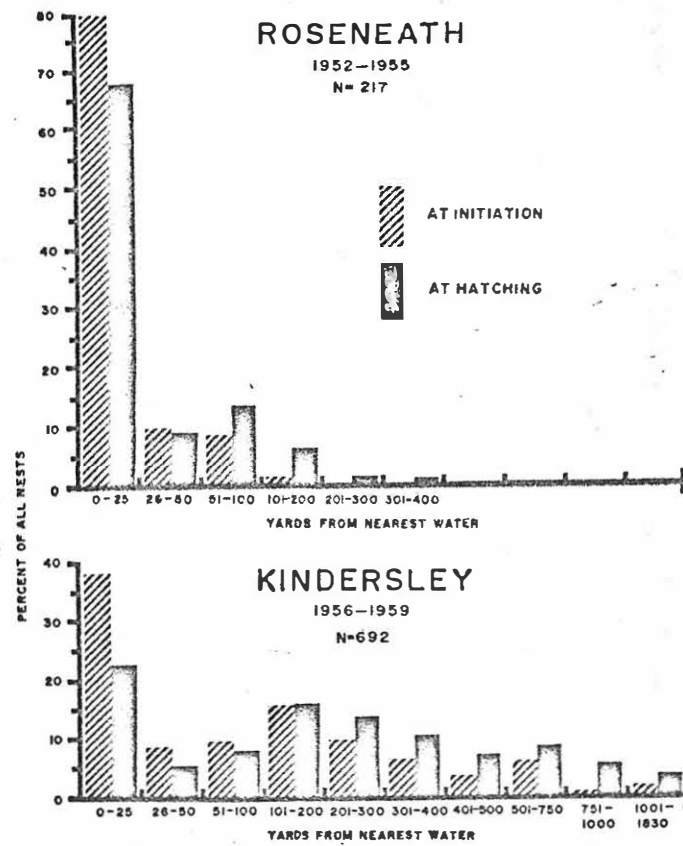


Fig. 4. Per cent distribution of Mallard nests from nearest water.

Table 1. Comparison of the climatic and edaphic factors on the two study areas.

	Roseneath	Kindersley
Habitat type	Aspen parkland	Grassland
Location	9 mi. (14.5 km) S Minnedosa, Man.	12 mi. (19.3 km) SW Kindersley, Sask.
Latitude and longitude	50°08' x 99°51'	51°19' x 109°25'
Topography	Knob and kettle	Gently undulating
Study block, acres (ha)	895 (362)	6,720 (2,720)
Portion in cereal crops, %	60	75
Portion in water, %	15	10
Portion uncultivated, %	25	15
Number of pothole basins	181	114
Basins < 1.0 acre (0.4 ha)	141 (78%)	84 (74%)
Range basin sizes, acres (ha)	0.01-10.5 (0.004-4.25)	0.03-226.2 (0.012-91.5)
Avg. basin size, acres (ha)	0.7 (0.3)	5.7 (2.3)
Soil zone	Black	Brown
Major grass forms	<u>Bromus-Agropyron</u>	<u>Stipa-Bouteloua</u>
Major tree forms	<u>Populus-Quercus</u>	<u>Salix</u>
Climatic region (Köppen)	Humid continental	Middle latitude steppe
Avg. annual ppt., in. (cm)	17.8 (45.2)	11.5 (29.2)
Avg. annual snowfall, in. (cm)	45.0 (114.3)	25.3 (64.3)
Avg. annual water deficiency, in. (cm)	4 (10.2)	8 (20.3)
Frost-free period, days	96	100
Degree-days above 42°F(8.3°C)	2,500 (1,389)	2,700 (1,500)
Mean date last snow cover	20 April	10 April

Table 2. Median distances of Mallard nests from nearest water.

Roseneath					Kindersley								
All nests					Early nests				Late nests				
	N	Median distance yards (m)		Range yards (m)	N	Median distance yards (m)		Range yards (m)	N	Median distance yards (m)		Range yards (m)	
		At initiation	At hatching	At hatching		At initiation	At hatching	At hatching		At initiation	At hatching	At hatching	
1952	52	4.5 (4.1)	55 (50)	1-325 (1-297)	1956	157	15 (14)	50 (46)	1- 650 (1- 594)	26	65 (59)	127.5 (116.6)	3- 545 (3- 498)
1953	67	5 (5)	5 (5)	1-200 (1-183)	1957	249	30 (27)	187.5 (171.4)	2-1270 (2-1161)	33	220 (201)	255 (233)	6-1740 (5-1591)
1954	56	4 (4)	5 (5)	1-110 (1-101)	1958	112	125 (114)	210 (192)	4- 780 (4- 713)	33	185 (169)	260 (238)	4- 855 (4- 782)
1955	42	4 (4)	4 (4)	1-130 (1-119)	1959	66	290 (265)	850 (777)	4-1830 (4-1673)	16	220 (201)	695 (636)	5-1140 (5-1042)
Total 217 median		4.5 (4.1)	6 (5)		584		50 (46)	190 (174)		108	162.5 (148.6)	255 (233)	
Biased mean		16 (15)	33 (30)				137 (125)	275 (251)			298 (272)	351 (321)	

Table 3 . Fate of mallard nests, Roseneath, 1952-55.

	Early nests					Late nests				
	1952	1953	1954	1955	Totals	1952	1953	1954	1955	Totals
Inactive	7	8	13	3	31	1	5	4	4	14
destroyed	6	7	11	3	27	1	4	3	3	11
hatched	1	-	-	-	1	-	1	-	-	1
deserted	-	1	2	-	3	-	-	1	1	2
Active	36	48	31	30	145	16	19	21	12	68
hatched	14	17	12	16	59	8	10	8	6	32
abandoned	2	2	3	1	8	1	-	1	-	2
destroyed	20	29	16	13	78	7	9	12	6	34
avian predator	7	18	4	6	35	2	4	4	4	14
mamm. "	5	8	6	4	23	3	4	7	2	16
unk. - other	4	1	2	-	7	1	-	-	-	1
flooding	-	-	4	-	4	-	-	1	-	1
hen killed	1	1	-	1	3	-	-	-	-	-
agric. - man	3	1	-	2	6	1	1	-	-	2
Total nests	43	56	44	33	176	17	23	25	16	81
Total successful	15	17	12	16	60	8	11	8	6	33
Percent hatched	35.	30.	27.	48.	34.1	47.	48.	32.	38.	41.

Table 4. Fate of Mallard nests, Kindersley, 1956-58.

	Early nests				Late nests*			
	1956	1957	1958	Totals	1956	1957	1958	Totals
Inactive	15	17	39	71	11	2	14	27
destroyed	13	17	37	67	9	2	13	24
hatched	-	-	2	2	2	-	1	3
deserted	2	-	-	2	-	-	-	-
Active	153	249	113	515	31	33	32	96
hatched	121	208	80	409	25	21	17	63
abandoned	6	8	2	16	1	2	1	4
destroyed	26	33	31	90	5	10	14	29
avian predator	5	5	4	14	-	-	1	1
mamm. "	11	15	19	45	4	9	13	26
unknown - other	4	2	2	8	-	-	-	-
hen killed	4	7	5	16	1	1	-	-
agric. - man	2	4	1	7	-	-	-	-
.....								
Rejected								
Fate unknown	6	3	5	14	-	-	2	2
.....	20	21	23	64	5	6	4	15

Table 4 Concluded.

	Early nests				Late nests*			
	1956	1957	1958	Totals	1956	1957	1958	Totals
Total nests	168	266	152	586	42	35	46	123
Total successful	121	208	82	411	27	21	18	66
Per cent hatched	72.0	78.2	53.9	70.1	64	60	39	53.7

* May include influx of immigrant hens.

Table 5. Early and late clutch and brood sizes for Mallards at Roseneath, Manitoba.

Year	Clutch sizes*						Brood sizes*					
	All completed clutches		Successful clutches				Class Ia		Class II		Class III	
			Incubating		Hatching							
<u>EARLY SEASON</u>												
1952	9.2	(31)**	9.5	(14)	9.0	(14)	6.6	(32)	7.6	(24)	5.9	(18)
1953	8.6	(37)	8.6	(17)	7.9	(17)	6.2	(23)	6.3	(9)	6.3	(12)
1954	7.7	(23)	8.1	(12)	6.2	(12)	5.4	(31)	4.7	(21)	4.9	(17)
1955	8.3	(20)	8.8	(16)	8.5	(16)	6.9	(53)	6.4	(38)	6.6	(44)
Sample, S.D.	111	1.7	59	1.9	59	2.1	139	2.2	92	2.2	91	1.7
Mean \pm S.E.	8.55 \pm 0.16		8.8 \pm 0.2		8.0 \pm 0.3		6.40 \pm 0.19		6.3 \pm 0.2		6.1 \pm 0.2	
<u>LATE SEASON</u>												
1952	7.2	(14)	7.6	(8)	7.3	(28)	6.4	(21)	6.2	(11)	6.6	(9)
1953	7.3	(13)	7.1	(10)	6.6	(10)	5.5	(13)	5.8	(8)	5.6	(7)
1954	7.1	(18)	6.8	(8)	6.5	(8)	5.6	(14)	5.0	(12)	5.9	(16)
1955	7.4	(10)	7.5	(6)	7.2	(6)	6.6	(13)	6.0	(9)	6.5	(24)
Sample, S.D.	55	1.5	32	1.2	32	1.2	61	1.9	40	1.8	56	1.7
Mean \pm S.E.	7.2 \pm 0.2		7.2 \pm 0.2		6.8 \pm 0.2		6.1 \pm 0.2		5.8 \pm 0.3		6.2 \pm 0.2	

*Mean with sample size in parentheses.

**Only those active nests (Table 3) which contained completed clutches used.

Table 6. Early and late clutch and brood sizes for Mallards at Kindersley, Saskatchewan.

Year	Clutch sizes*			Brood sizes*		
	All completed clutches	Successful clutches		Class Ia	Class II	Class III
		Incubating	Hatching			
<u>EARLY SEASON</u>						
1956	8.7±.15 (159)	9.1±.13 (121)	8.0±.14 (121)	6.3±.3 (84)	5.5±.3 (43)	5.1±.3 (41)
1957	9.3±.10 (252)	9.5±.10 (208)	8.8±.11 (208)	6.4±.26 (111)	5.7±.2 (60)	5.2±.3 (38)
1958	9.4±.15 (118)	9.5±.2 (80)	8.8±.2 (80)	5.8±.2 (69)	5.5±.2 (76)	4.9±.2 (52)
.....
1959	7.7±.25 (68)	Incomplete		5.2±.29 (64)	4.7±.30 (46)	4.8±.35 (42)
Sample, S.D.	529 1.7	409 1.5	409 1.7	264 2.4	179 1.8	131 1.8
56-58 only						
Mean ± S.E.	9.12±0.07	9.36±0.07	8.55±0.08	6.21±0.15	5.54±0.14	5.06±0.16
<u>LATE SEASON</u>						
1956	7.5±.2 (31)	7.6±.3 (25)	7.3±.2 (25)	5.4±.3 (23)	5.0±.2 (70)	4.7±.3 (48)
1957	8.0±.3 (33)	8.3±.4 (21)	8.1±.4 (21)	5.3±.3 (34)	5.5±.3 (46)	4.7±.4 (23)
1958	7.7±.2 (34)	7.9±.3 (17)	7.7±.4 (17)	5.4±.4 (24)	5.3±.3 (45)	4.8±.3 (28)
.....
1959	6.8±.4 (19)	Incomplete		4.5±.5 (17)	5.1±.3 (32)	4.2±.3 (24)
Sample, S.D.	98 1.5	63 1.5	63 1.6	81 1.8	161 1.8	99 1.9
56-58 only						
Mean ± S.E.	7.7 ± 0.2	7.9 ± 0.2	7.7 ± 0.2	5.4 ± 0.2	5.24±0.2	4.7 ± 0.2

Table 7. Index of pond density and distances between ponds during the brood period.

Year	Number ponds on July 1	Average number ponds per mi ² (km ²)	Mean nearest neighbor distance to yards (m)				Mean number of ponds within	
			1st pond	2nd pond	3rd pond	4th pond	440 yds* (402 m)	880 yds** (805 m)
<u>ROSENEATH</u>								
1952	88	63 (24)	59±4.6 (54±4.2)	96±5.4 (88±4.9)	138±5.4 (126±4.9)	180±5.3 (165±4.8)	14.8±0.4	50.5±0.9
Range			5-120 (5-110)	5-240 (5-219)	60-280 (55-256)	100-300 (91-274)	8-23	31-66
<u>KINDERSLEY</u>								
1956	49	4.7 (1.8)	245±29 (224±27)	400±45 (366±41)	524±44 (479±40)	636±49 (582±45)	2.5±0.2	3.0±0.4
Range			15-1216 (14-1112)	96-1856 (88-1697)	160-1856 (146-1697)	224-2304 (205-2107)	0-6	0-12
1957	7	0.7 (0.3)	938 (858)	1670 (1527)	2041 (1866)	2414 (2207)	.3	.7
1958	8	0.8 (0.3)	910 (832)	1602 (1465)	2140 (1957)	2433 (2225)	0	.8
1959	4	0.4 (0.2)	1280 (1170)	1785 (1632)	2240 (2048)	3230 (2954)	0	0

* Enclosing an area of 126 acres (51 ha)

** Enclosing an area of 503 acres (204 ha)

Table 8. Comparison of calculated and measured autumn mallard populations at Roseneath.

Year	Calculated production							Measured production						
	Censuses spring breeding pairs ¹		Clutches hatched ²	Average young per fledged brood ³	Estimated no. of hens re ⁴ nesting	Clutches hatched ²	Average young per fledged brood ³	Adults dying from April to June		Theo- retical September population ⁵ Ad:Imm	Hens success- ful in fledging broods		Average young per fledged brood ³	September popu- lation ⁵ Ad:Imm
♂	♀	♂						♀	N		%	Ad:Imm		
1952	60	54	19	5.9	10	5	6.6	3	4	105:138	20	37	6.1	105:116
1953	55	49	15	6.3	18	9	5.6	3	3	95:138	25	51	6.0	95:142
1954	46	41	11	4.9	21	7	5.9	2	3	80:90	9	22	5.4	80:46
1955	37	33	16	6.6	8	3	6.5	1	3	64:109	17	52	6.5	64:104
4-yr aver.	50	44	15	6.1	14	6	6.2	2	3	86:119 1:1.4	18	40	6.1	86:102 1:1.2

¹ Assuming a sex ratio of 112:100 (Dzubin, 1969b:188).

² Hatching success, early and late nestings from Table 3.

³ Average young per fledged brood from Table 5.

⁴ Mid- to late-June pair census, approximately 50% of hens losing primary clutch, reneest.

⁵ Minus April to June mortality of adults and assuming a further 3% loss in adult ♂♂ and ♀♀, plus a 5% loss in fledged broods during July and August.

Table 9. Comparison of calculated and measured autumn Mallard populations at Kindersley.

Year	Calculated production							Measured production						
	Censuses spring breeding pairs ¹		Clutches hatched ²	Average young per fledged brood ³	Esti- mated no. of hens re- nesting ⁴	Clutches hatched ²	Average young per fledged brood ³	Adults dying from April 1 to June		Theo- retical September popu- lation ⁵ Ad:Imm	Hens success- ful in fledging broods		Average young per fledged brood ³	September popu- lation ⁵ Ad:Imm
♂	♀	♂						♀	N		%			
1956	278	248	179	5.1	21	13	4	13	494:926	77	31	4.9	494:356	
1957	401	358	280	5.2	23	14	7	19	711:1448	40	11	5.0	711:190	
1958	194	173	93	4.9	24	9	8	10	339:474	48	27	4.9	339:223	
3-yr avg.	291	260	183	5.1	23	12	6	14	515:940 1:1.8	55	21	4.9	515:256 1:.5	

¹Assuming a sex ratio of 112:100 (Dzubin, 1969b:188).

²Hatching success, early and late nestings from Table 4.

³Average young per fledged brood from Table 6.

⁴Estimate 30% of hens losing primary clutches re-nest (Gollop and Fyfe, 1956:75).

⁵Minus April to June mortality of adults and assuming further 3% loss in adult ♂♂ and ♀♀, plus 5% in fledged broods during July and August.

Table 10. Summary of production data for 100 Mallard pairs, April through August.

	ROSENEATH (4 yr. avg.)			KINDERSLEY (3 yr. avg.)		
	%	N	% Loss	%	N	% Loss
A. Breeding pairs, drakes:hens		112:100			112:100	
<u>Primary nesting</u>						
B. Clutches hatching	34	34		70	70	
C. Clutch size, succ. nest incubating		8.8			9.4	
D. Clutch size, hatching		8.0			8.6	
E. Brood size, fledging		6.1	33		5.1	84*
F. Hens reaching water	100	34		49	34	
G. Hens successful in fledging broods	33	33		20	20	
<u>Renesting</u>						
H. Hens renesting	48	32		30	9	
I. Clutches hatching	40	13		54	5	
J. Clutch size, succ. nest incubating		7.2			7.9	
K. Clutch size, hatching		6.8			7.7	
L. Brood size, fledging		6.2	14		4.7	88*
M. Hens reaching water		13			2	
N. Hens successful in fledging broods		13			1	
<u>Production</u>						
O. Total succ. hens - brood size	46	46-6.1		21	21-4.9	
P. Drakes minus April to June mortality		108	4		110	2
Q. Hens minus April to June mortality		93	7		95	5

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Table 10 Concluded.

	ROSENEATH (4 yr. avg.)			KINDERSLEY (3 yr. avg.)		
	%	N	% Loss	%	N	% Loss
R. Total adults - end August minus mortality, July-August		196	3		199	3
S. Total immatures - end August minus post-fledging mortality		267	5		106	5
T. Mean immatures/adults		1.4			.5	
U. Implied mortality rates operative Ad 50 Imm 70				48**		61
V. Production to balance mortality rate immatures/adults		1.7			1.2	
W. Population status		Fluctuating, decline			Immigration, decline	
X. Number of ponds		Fairly stable			Decreasing, drought	

* Derived from
$$\left[1 - \frac{(\text{Brood size fledging}) (\text{Hens successful})}{(\text{Clutch size incubating}) (\text{Clutches hatching})} \right] \times 100$$

** After Gollop, 1965b.