

# A SIMULATION ANALYSIS OF MALLARD REPRODUCTIVE BEHAVIOR IN RELATION TO BREEDING HABITAT

By

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### ABSTRACT

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A computer simulation was designed to relate experimental measures of innate mallard breeding behavior to breeding habitat quality and quantity as measured by numbers of pairs, nesting chronology, and duckling production. Weather and predation were simulated as exogeneous variables modifying reproductive performance. The results of the simulations were compared with 3 years each of field data near Kindersley, Saskatchewan and in the Aspen Parkland Life Area near Edmonton, Alberta. In all simulations, the number of pairs calculated as needed to produce a nesting chronology and duckling production similar to those reported in the field studies was less than the number of indicated pairs reported in the field studies. Weather and predation as simulated by the model did not account for the difference. However, in 3 of 5 simulations where weather data from field studies was simulated, the resulting nesting chronology was statistically similar to the reported nesting

chronology. Predation rates used in the simulation that resulted in nesting chronologies and duckling production similar to those reported if the field studies were identical to or slightly higher than those reported in the field studies. In all but one simulation, the estimate of ducklings fledged was within the range estimated in the field studies or differed by no more than 39 percent.

The model simulated the difference in mallard reproductive performance between grassland and parkland breeding habitats. However, breeding habitat quality and quality and reported from field studies in terms of pond numbers and change in pond numbers in the same habitat did not correspond with the simulated measures of pair use and duckling production per pond. Explanations of these differences include mallard spacing mechanisms and changes in winter and breeding habitat quality that were not incorporated in the model.

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## INTRODUCTION

Evaluations of the reproductive effort and success of a population of mallards (<u>Anas platyrhynchos</u>) breeding in a given area have always been inexact because of the difficulties of measuring actual breeding pairs, nests, and broods. These population estimators are further confounded by weather, predation, asynchronous breeding period, brood movements, and the fact that the nest site and rearing area for broods are not necessarily located within the defended portion of the breeding space of a given pair. However, an experimental study of captive mallards by Batt and Prince (1978, 1979) produced quantitative measures of many endogenous factors regulating mallard reproduction, making it possible to compare experimental data to field data and thereby better evaluate field data and mallard reproductive performance.

Because of the availability of the quantitative measures by Batt and Prince of mallard breeding behavior in captivity and the strong relationship of those data to mallards breeding naturally, it was assumed that a model could further clarify the relationships among mallard

breeding behavior, habitat quality and quantity and the exogenous variables of weather and predation. Specifically, it was hypothesized that innate mallard breeding behavior, modified by climatic factors, regulates habitat use, and if the effects of predation could be reasonably accounted for, it could be demonstrated that the results of mallard spatial and temporal behavior as measured by nesting chronology and duckling production are a indication of habitat quantity and quality. It was further hypothesized that if a general expression of habitat quantity could be developed, changes in habitat quality could be measured.

This study examined through computer modeling the interactions of endogenous factors (numbers of pairs, nest initiation rates, renesting rate, egg production, hatching rate and brood survival) and exogenous factors (date, weather, number of ponds, acres of wetlands and pond quality, and predation) that may effect breeding strategy and reproductive success on a specific site. Comparisons between the predictions of the model and the results of field studies are made to evaluate both the model and the field data and to quantitatively relate reproductive strategy to habitat parameters in reference to current theory.

### LITERATURE REVIEW

Most mallards move to traditional wetland areas in April or May already paired (Hochbaum, 1944; Sowls, 1955; Weller, 1965). A pair establishes a territory as the female begins egg formation and nest establishment (Dzubin, 1955 McKinney, 1965). Territories are variable in size. especially between geographic regions, and probably reflect the relative distribution of the physical resources of food and cover necessary for successful reproduction (Bellrose, 1976). Because these territories may include several ponds, may not include the actual nesting site, and are not defended by the drake after the onset of incubation, they are not mutually exclusive in either time or space and do not fit the classic definition of territory as defined by Further, Dzubin (1969) cites evidences that Lack (1966). mallard drakes may defend larger breeding spaces when pair densities are low and smaller areas when pair densities are high.

Numerous studies have attempted to relate amounts of wetland habitats and productivity of mallard breeding habitat to mallard reproduction, but a complex interaction of several factors tend to confound such attempts. Breeding

habitats of the same type vary in productivity from area to area (Dzubin, 1969). Stewart and Kantrud (1974) in a statewide study of waterfowl use of wetland habitats in North Dakota found that seasonal and semi-permanent ponds and lakes (Classes III and IV) were used most heavily by mallards and other dabbling ducks, but that use of these types varied considerably from region to region. Similar results were obtained by March et al. (1973) in a study of duck populations and habitat in Wisconsin.

Waterfowl productivity also varies with time within wetland type. Semi-permanent wetlands increase in productivity when flooded if the flooding is preceded by drying due to drought or regulated drawdown. Production gradually decreases if higher water levels exist for more than 5 to 6 years (Weller and Fredrickson, 1974; Weller, 1978; Bishop et al. 1979). Periodic change of water levels produces the best amounts and distribution of drowned vegetation, submersed and emergent vegetation, open water, and associated invertebrate populations needed by mallards for food and cover for reproduction. Experimental manipulations of marsh habitat to simulate the ideal conditions of the semi-permanent marsh by Kaminski and Prince (1981) and Murkin et al. (1982) revealed that a 50% interspersion of emergent vegetation and open water over drowned growth of the previous year were most heavily utilized by mallard pairs.

Productivity appears to vary with the density of ponds in that the greatest productivity occurs in areas where wetlands are the most numerous (Stoudt, 1969; Steward and Kantrud, 1973; Krapu et al. 1983). Within any given area, wetland density varies from year to year because many wetlands are emphermal, temporary, or seasonal. Density of wetlands (number of ponds) varies directly with precipitation (Pospahala et al. 1974).

Productivity of a given area is difficult to evaluate because mallards hens may not place the nest within the utilized wetlands and may move their broods over a long distance and numerous wetlands. Nests located long distances from water (over 1,700 meters), high nest densities in dense upland vegetation or on islands, high nest densities in maintained wetlands during drought, and brood movements well outside habitat used for courtship and nesting are well documented (Keith, 1961; McKinney, 1965; Dzubin and Gallop, 1969; Johnson et al. 1978; Trauger and Stoudt, 1978; Giroux, 1981; Lokemoen et al. 1984).

Productivity of wetlands varies with size. Cowardin and Johnson (1983) demonstrated that semi-permanent, seasonal, permanent, and temporary wetlands increased in productivity with size. Semi-permanent and seasonal are the most productive if greater than approximately 5 ha. Semipermanent and permanent wetlands, however, are the most productive at smaller sizes. The authors acknowledge,

however, that the predictive equations left considerable variation unexplained, probably because of the interactions of the relationships just described.

Several attempts have been made to relate wetland numbers to productivity. Crissey (1969) found that breeding populations in the spring correlate well (r = 0.89) with July ponds the previous summer in the southern prairie provinces from 1954 to 1965. However, in 1957, the number of ponds had been declining and was average, but favorable breeding season weather and a high breeding populations produced the largest production during the mid 1950 period. Cooch (1969) attempted to relate May-July pond ratios to production, but encountered similar abnormalities. Hammach and Brown (1974) tried to relate May ponds and July ponds to production, but also found abnormalities in 1957 using July ponds and in 1964 using May ponds. Finally Heitmeyer and Fredrickson (1983) found through regression analysis that neither May or July ponds, or May and July ponds correlated well with mallard age ratios in the fall harvest, but that May and July ponds and departure from normal precipitation the preceding winter correlated well with the age ratio (R2= 0.92) for more recent years (1969-70, 1979-80). The authors suggest that poor winter habitat may not allow mallards to accumulate the needed reserves of lipids and proteins to successfully reproduce, despite favorable conditions in breeding habitat.

Nest initiation occurs for approximately 2 months. Pairs not ready to initiate a nest, pairs unable to establish territories, and unpaired birds, mostly males, move from one body of water to another, and act as a reserve waiting for an opportunity to reproduce (Aldrich, 1973; Humberg et al. 1976; Jackson et al. 1983).

It is difficult to count actual breeding pairs at any one point in time or in total because of the difficulty in determining the reproductive status of observed birds (Dzubin, 1969). Johnson and Sargent (1977) found that lone drakes may not represent a pair. In addition to lone pairs, lone drakes, flocked males, and flocked pairs have been used to estimate pairs, but Jackson et al. (1985) demonstrated that under drought conditions up to 85% of the lone drakes may not represent a pair.

The date of nest initiation is an individual characteristic of the hen (Batt and Prince, 1979). Once the female is ready to initiate a nest, a breeding territory is established and defended by the drake. The hen lays one egg a day until the clutch, usually 11 eggs, is completed (Bellrose 1976). Batt and Prince (1978) established that the decreasing clutch size of captive mallards overtime is a function of the date of nest initiation.

If the eggs are destroyed during laying, the hen will renest. Sowls (1955) found that with bluewinged teal (<u>Anas discors</u>) and shoveller (Spatula clypeta)

hens, loss of a nest during laying was followed the next day by renesting, leading him to believe there is no renesting interval when a nest is lost during laying. In captive mallards, Prince et al. (1970) report a mean renesting interval of 6.0 +3.6 days when eggs were collected on the second day after the last egg was laid.

The effect of cold weather and precipitation on laying is not well defined. Sowls (1955), Dane (1966), Dane and Pearson (1971), Sorensen (1978) and Batt and Prince (1979) report that sub-freezing temperatures and heavy precipitation will delay the onset of nesting. Gollop (1954), Sowls (1955), Keith (1961), Hunt et al. (1968) and Dzubin and Gollop (1969) all report a reduction of duck nesting during periods of inclement weather. Hunt et al. (1968) reported that a 20-25% decrease in egg production from hand reared mallards during "periods of heavy or prolonged rainfall, or when below freezing temperatures prevailed for the greater part of a 24-hour period."

Within a given locality, not all paired hens initiate nests at the same time. In a confined experimental population provided an ad libitum balanced diet and nesting sites for each pair, Batt and Prince (1979) found significant differences between hens in nest initiation dates and that nest initiation dates are consistent with an individual hen year to year. Batt and Prince (1979) also noted that weather conditions delay initiation. No first

nest attempt was initiated after June 21 in the experiment by Batt and Prince (1979), but several field studies report a few nests, probably renests, begun after that date but no later than June 26 (Keith, 1951; Dzubin and Gollop, 1969; Sorensen, 1978).

During the laying period, the drake accompanies the hen as in courtship and defends the territory (Dzubin, 1955). If the hen is forced to abandon her nest during laying, she usually renests with her original mate (Humberg, 1976). When the hen begins to incubate the clutch, the drake gradually loses interest and leaves the hen and the defended area (Lebret, 1961). Drakes assemble in small groups, usually on larger waters and are available for hens attempting to renest. Large groups of drakes may make it difficult for a pair to re-mate and may relentlessly pursue and rape hens seeking a mate, perhaps even disrupting breeding attempts (Aldrich, 1973). During incubation the space occupied by the pair is no longer defended and may be occupied by a waiting pair, or by a pair attempting to renest.

If the nest is lost during incubation, the hen goes through a recycling period as her reproductive system readjusts to produce more eggs. The recycling period will be a minimum of 6-10 days (Prince et al. 1970; Batt and Prince, 1979). If the nest is lost after 8 days of incubation, however, the recycling time increases with each

succeeding day beyond the eighth day (Batt and Prince, 1979). Sowls (1955) reports a linear relationship between the number of days into incubation and the renesting interval.

Incubation lasts for approximately 26 days, but Prince et al. (1969) found that the incubation time of artificially incubated eggs varied from 23 to 30 days depending on temperature and humidity. Prince and Batt (1979) found that there was no significant difference in the hatchability of eggs from first nests of adult and novice hens during their first year in captivity. They detected a decline in hatchability of eggs from second, third, and fourth nests, but attributed the effect to captivity, probably because of declining viability of the eggs. The average hatchability of artificially incubated eggs from Manitoba birds for first nests was approximately 75%.

After brooding the newly hatched chicks for several hours, the hen leads the brood to water. Considerable loss of both individual ducklings and entire broods may occur during this period. Distances from nest to water, weather, dense vegetation, parasitism and predation are factors relating to mortality of Class I broods (ducklings 1-18 days of age as judged from size and development). Dzubin and Gollop (1969) and Sorenson (1978) both report heavy Class I brood loss due to exposure to cold and rain, and at the Kindersley study site, high brood mortality was correlated

with the distance from nest to water, especially through dense upland vegetation. Gilmer et al. (1975) found a similar relationship in northern Minnesota (r = -0.39). Stoudt (1971) noted that brood mortality increases in drought years and Pospahala et al. (1974) were able to correlate brood size to July ponds for several areas (r =0.90, 0.47, 0.44). They were not able to correlate brood mortality from Class II (ducklings 19-45 days old) to Class III (ducklings 46-55 days old) broods with the number of July ponds (r < 0.10) using data from a study by Stoudt (1971).

Predation on adults, nests and broods has been difficult to measure and relate to environmental factors. It varies among habitats, being higher (50-60%) in prairieparklands and lower (20-40%) in mixed grasslands (Dzubin and Gollop, 1969). Keith (1961) estimated summer mortality rate of 2% for male mallards and 8% for females in southern Alberta, while Dzubin and Gollop (1969) estimated a 4% mortality for drakes and a 5% mortality for hens in grassland and 7% in parklands during the breeding season. Anderson (1975) derived a 9% mortality for drakes and a 16-18% mortality for hens from May to August. Johnson and Sargent (1977) found similar mortality rates in a predation study for grassland habitat.

Habitat factors associated with breeding sites, but not necessarily a part of the wetlands utilized, also effect

predation rates. Nests on mammal free islands and in dense upland vegetation experience less predation (Keith, 1961; Duebbert, 1969; Klett et al. 1984).

Predation also varies with the species of predators present. Common predators in parklands include crows (<u>Corvus brachyrhynchos</u>), magpies (<u>Pica pica</u>), skunks (<u>Mephitis mephitis</u>), and ground squirrels (<u>Spermophilus</u> <u>franklini</u>), while the common predators of grasslands include skunks, badgers (<u>Taxidea taxus</u>), mink (<u>Mustela vison</u>), weasels (<u>M. rixosa, M. erminea</u>), coyotes (<u>Canis latrans</u>) and certain raptors (Dzubin and Gollop, 1969; Johnson and Sargent, 1977). Predator species also change over time. Foxes (<u>Vulpes fulva</u>) and raccoons (<u>Procyon lotor</u>) for example, have become more numerous in recent years in many areas (Sargent et al. 1979).

Another problem exists in evaluating nest predation losses and is dependent on sampling procedures and calculation techniques. Miller and Johnson (1978) point out that the fewer the search intervals, the more likely unsuccessful nest will be missed, thus underestimating losses. If a greater proportion of successful nests are found than unsuccessful nests, then mortality will be overestimated. The authors recommend the Mayfield method (Mayfield, 1960) of calculation, which assumes a constant success (mortality) rate and is calculated by relating the age of nests at hatching to the age of nests when found. By

evaluating data collected and analyzed by Green (1977), the authors found some daily variation but no significant difference between the daily success rates of nests during laying and nests during incubation.

#### MATERIALS AND METHODS

# The Model

The model is organized to simulate the daily events in mallard reproductive behavior during the breeding season (Fig. 1). The program begins by pairing drakes and hens and assigning them a breeding status. Then, for each day in a simulation, all nesting events are tallied - potential nest initiation, first nests, renests, total daily nests, nests hatched by mature hens, nests by juvenile hens, total nests hatched, and hens killed. At the end of the nesting season, all categories are summed. The eggs and young produced by each category hen and the number of hens that fail to nest successfully are also summed. In addition, ducklings surviving to fledging are calculated. The program is written in Fortran 5 and all computations were done on the Michigan State University 750 Cyber computer.

Mallard nest initiation frequencies were calculated from original data from Batt and Prince (1979) using information from Manitoba adult and novice birds taken from wild populations.



Figure 1. Organization of the model used to simulate the interaction of mallard reproductive behavior with habitat parameters.

The frequencies were plotted and found to have a Poisson distribution over a period of 52 days. The following equation for a generalized Poisson distribution was used to generate daily frequencies of nest initiation:

$$DF = f(x, a, b, c, d) = \left[ \left( \frac{b-x}{b-a} \right)^{c} e^{\left( \frac{c}{d} \right)} \left[ 1 - \left( \frac{b-x}{b-a} \right)^{d} \right] \right]$$

where DF= daily frequencies x = days into breeding season a = value of x where f(x) is maximal b = value of x where f(x) = 0 for x<b c = parameter for curve shape subsequent to a d = parameter for curve shape prior to a

A program was written to calculate the daily frequencies and through iteration was used to determine the values for the variables that produced daily frequencies approximating the experimental data (Fig. 2). Because of the Poisson distribution, small sample size, and the comparison of data frequencies, the Kolmogorov-Smirnov one sample test was used to determine which combination of values produced the frequencies which best fit the frequencies of the data (a=13, b=60, c=13, d=3,  $\alpha < 0.01$ ). In the simulation model, the daily number of potential nest initiations is calculated as follows:



Figure 2. Comparison of the first nest initiation frequences of captive mallards housed in outdoor pens in Manitoba to a simulated frequency. (Data from Batt and Prince, 1979).

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Within the simulation program, the weather parameter and available breeding spaces limit nest initiation. If weather is bad or no breeding space is available, the appropriate number of pairs are stored as ready to initiate a nest, and are allowed to initiate a nest only when weather is good or when breeding space is available. Mature hens are initiated first, thus simulating a natural sequence and at the same time simulating lesser reproductive effort by juvenile hens, since hens laying later in the season produce fewer eggs.

Breeding spaces are set by input data and are initially estimated as the maximum number of pairs per week or nest per week from field data. Within the model, nesting is spatially simulated, as recommended by Holling (1978), by an array for laying birds and an array for incubating birds. The size of the laying array is equal to the number of breeding spaces, thus simulating defended space. The incubation array is limited to the total number of birds in a simulation, thus accommodating any possible number of birds.

The laying array contains the following information: age of the hen (mature or juvenile), the number of eggs she has laid (one per day), consecutive and total bad days, and the number of eggs she will lay (clutch size). One day of

bad weather terminates laying and 2 consecutive days or 3 total days of bad weather eliminates all eggs (nest abandonment) unless the hen has laid 75% of her clutch. As soon as weather is good, laying is resumed by the addition of eggs, one per day. If a nest is calculated to be lost to predation during laying, eggs are set equal to zero, and eggs are added, one per day on the next day of good weather. When the first egg is added, the nest is counted as a renest. The clutch size is determined by the equation from Batt and Prince (1979), clutch size = 26.80 - 0.19x + (0.0005)x2, where x=day of year.

When the number of eggs laid equals clutch size, the hen, her status, number of eggs, and the day of the year plus 26 are transferred to the incubation array. When the day of the year equals the date assigned plus 26, the nest is counted as hatched. Hatch rate is 75% of clutch size. Although the hatching rate for eggs in nests in the wild approaches 95%, the lower rate is used to account for early duckling mortality.

If a nest is calculated to be lost to predation during incubation then the hen is held in another array for 10 days. If she was 9 or more days into incubation, she is held in the array for a number of days determined by the equation x=4.44 - .644x, where x=days into incubation when the nest was lost Sowls (1955). When a hen or hens are again ready to lay, if there are drakes available for

pairing, the frequency of re-nesting is 1 if the day of the year is less than 129. If not, the frequency of renesting is calculated by the equation N = number of pairs available for renesting x (2.55-0.012x) where N = renesting pairs and x=day of year (Batt and Prince, 1978).

Rates of predation are derived from field data. Predation rates reported in field data are often for early in the nesting season and late in the nesting season, so the model was designed to utilize two rates, with the late predation rate being applied to all nests after the second nest to hatch. The predation rate is divided by the number of days the hen will lay and incubate and is assigned to the predation array on the day laying begins. The daily predation rate is then summed for all hens each day to determine the daily predation rate. The total number of nests lost each day is the product of the total number of nests and the daily predation rate. Nests are selected from either the laying or incubation arrays according to their relative abundance. For each ten nests lost, one hen is recorded as killed and removed from the appropriate array. The actual nests selected to be depredated is done randomly through the use of a random number generation routine.

No mathematic expression was found in the literature to relate duckling mortality to habitat change, so several were developed and tested. Although weather, predators and other factors can be important mortality factors in any given

20.

year, much duckling mortality occurs when nests are a long distance from water or when water areas dry up in late spring and summer. The only relationship that was consistently reported was water loss in May and through July. The percent deviation of the number of May ponds from a known maximum of May ponds was combined with the percent loss of ponds May through July and regressed against duckling mortality. Data were used from a 14 year study by Stoudt (1971) which was not evaluated in the simulations As a check, a similar equation was developed (Fig. 3). from data combined from 3 other investigations and was similar in slope, intercept, and means of the dependent and independent variables. Statistical significance of the differences were not evaluated. The equation used in the model is as follows: y = 0.167 + (0.53 x) where y = percentduckling mortality and x = percent combined water loss.

# The Simulations

Two studies, one from Kindersley, Saskatchewan and the other from Edmonton, Alberta, Aspen Parklands Life Area (Dzubin and Gollop, 1969; Sorensen, 1971) provided sufficient data for model operation and hypothesis testing. Three years of data were available in each of the investigations. In the initial computer run for the first year of the study, the data entered was that given in the



Figure 3. Mallard duckling mortality as a function of variation in the number of May ponds from a known maximum and the percent pond loss from May to June. (Data from Stoudt, 1971).

investigation except for the number of breeding spaces which was estimated. If the number of nests per week and the final nest and egg production predicted by the model were different from the results of the field investigation, the data entered on subsequent runs was varied to determine which input values and combinations of values resulted in a nesting sequence and final production values most similar to the results of the field investigations.

All possible variations were not used, but only those that had meaning in a an ecological context. For example, if all the results of the computer simulation were lower than the field study values, predation rates were not increased, since this could only serve to lower simulation results, further increasing discrepancy. Bad weather data was never added where none was reported in the field studies. Breeding spaces were not increased beyond the point of no effect, nor were they decreased when any further decrease resulted in limiting nest initiations.

The procedure used for varying data inputs was as follows. The first number of pairs used was all indicated pairs (lone pairs + lone drakes + flocked pairs) and, if both nesting data and production data were high, as was always the case, predation rates were increased. If this failed to produce results similar to the field results, predation rates were reset to the initial values and the number of breeding spaces was increased or decreased until

the pattern of the nest hatching sequence resembled the pattern of the results in the field study. Predation rates were then increased or decreased in a direction that would produce production values similar to the values reported in the field study. If this failed, the number of pairs was reduced to lone pairs and lone drakes, and then breeding spaces and predation were varied accordingly. This process was reiterated until the final results approximated the results of the field study.

In cases where bad weather was involved, the exact dates from the field study were used, if given. If weather was reported in a general way (e.g. a cold snap during the week of ...) dates were varied but only with the week reported. Final nest hatching sequences generated by the computer that closely resembled the results of the field study were statistically compared with the results of the field studies using the Walsh test as described by Seigel (1956). This method was chosen because of the Poisson or non-normal distribution of the nesting sequences, small sample size, and the power of the test in detecting differences in symmetry in distributions.

The number of breeding spaces and pairs used to calculate the results finally accepted as most closely approximating the field study results were used to calculate, where possible, pairs per breeding space, pairs per pond, ponds per breeding space, and acres per breeding

space. These results, along with the results for weather, predation and final production were then compared qualitatively, since statistical comparisons were not possible.

### RESULTS

Whenever the estimated number of breeding spaces was too low to accommodate all of the pairs calculated as ready to initiate nests within the number of days required to complete a clutch, no nests could be calculated as initiated. This resulted in nest initiations in excess of the number of breeding spaces being delayed until the estimated number of breeding spaces was high enough to accommodate all of the pairs calculated as ready to initiate at the time plus those previously delayed.

Consequently, the greater the discrepancy between the number of breeding spaces estimated and the number required, the greater was the difference between the actual nesting sequence and the one generated by the model. For example, in the 1957 Kindersley simulation, when the number of breeding spaces was increased from 105 to 205 with subsequent iterations, the pattern of the simulated sequences began to resemble the pattern of the actual sequence (Fig. 4), but the number of nests in the simulation was greater than in the field data (349 vs. 229) and the nesting sequences were significantly different ( $\ll$  < 0.10). The number of pairs used in generating Fig. 4 was the



Figure 4. The effect of varying breeding spaces on the number and sequence of mallard nests hatching per week. (Data from Dzubin and Gollop, 1969).

maximum number of indicated pairs in the field study as estimated from counts of lone pairs, lone drakes, and flocked pairs. Whenever the estimated number of breeding spaces was too low to accommodate the number of indicated pairs, an increase or decrease of the predation rate resulted in little or no agreement in either the pattern of the simulated nest sequence or in the numbers of nests in the sequence with the patterns and numbers of nests in the sequences from the field data.

Whenever the number of breeding spaces was adjusted so as to be just sufficient for the number of indicated pairs from the field investigations as in the 1957 Kindersley simulation, the resulting production of ducklings as calculated by the model (2991) was far greater than the results from the field studies (2000) (Table 1). When this discrepancy occurred, predation rates were increased in an attempt to lower calculated production.

Increases in early and late predation rates (Fig. 5) and in just the early rate (Fig. 6) lowered calculated productivity, but the frequency of nest initiations as calculated by the model differed significantly from the results of the field studies. For example, in the 1970 Alberta Parklands simulation, 70 pairs when used with a predation rate of 85% produced 409 ducklings versus 492 with 53% predation (Table 2). This number is larger than the number reported in the field study (183) and the nest
Ares	Date	Number of indicated pairs	Actual duckling production	First estimate of breeding space	Resulting simulated production	Second estimate of breeding space	Resulting simulated production	Final estimate of breeding space	Resulting simulated production
Kindersley	1956	248	1183	134	1332	100	1332	95	1332
	1957	358	<b>20</b> 00	105	2911	150	2954	205	2991
	1958	173	860	71	1156	63	1156	57	1156
Alberta	1968	89	185	13	676	17	681	18	685
rarkiand	1969	70	238	37	676	*	<b>*</b>	25	676
	1970	101	183	42	786	*	*	27	768

Table 1. Response of mallard duckling production to amounts of breeding space waried hefore varving weather in order to simulate field observations. (Data from Dzubin and Collon, 1969 and Serensen, 1978).

\*Not simulated

Table 2. Response of mailard ducking production to predation rates varied to simulate field observations. (Data from Drubin and Gollop, 1969 and Sorensen, 1978).

	2	-	Duck1 ing	Preda	t lon	1	Preda	t lon		Preda	tion		Preda	t Ion	
Area	ate o	umber of pairs	reported	early	late	broduct for	ear ly	late	production	early	late	product ion	early	late	product for
Kindersley	1957	358	2000	6	27	1991	15	30	2912	35	35	2725	35	20	2717
Alberta Parkland	1970	70	183	53	53	492	60	90	462	75	75	413	85	85	605

.



Figure 5. The effect of increasing constant simulated predation rates on numbers and sequence of mallard nests hatched (Data from Sorensen, 1978).



Figure 6. The effect of increasing varied early and late predation rates on numbers and sequence of mallard nests hatching per week (Data from Sorensen, 1978).

hatching sequence differed significantly from the reported one,  $\ll > 0.109$ .

When weather affecting nesting was described as adverse "during the week of...", an entire week of bad weather was entered into the simulation. This procedure resulting in limiting laying and nest initiation far longer than actually occurred producing a larger response in good weather than actually occurred (Fig. 7). Further iterations in which bad weather was reduced by one day per iteration revealed that 3 days bad weather reduced nesting slightly too much, and 2 days or less bad weather had too little effect. Thereafter, 3 days bad weather was used, but location within the designated week proved important (Fig. 7). The simulated production of ducklings without bad weather was greater than the simulated production of ducklings with the appropriate bad weather (Table 3).

When data from the 1956 Kindersley study was used in the simulation, the total numbers of indicated pairs was too high a value to produce a nesting sequence similar to the actual data, but the number of lone pairs permitted a closer simulation (Table 5 and Fig. 8). The initial estimate of 134 breeding spaces ultimately proved too high. The predation rates of 13% on active nests in the study when used in the simulation resulted in the closest simulation, $\prec$ = 0.012. When 178 pairs were tested with predation rates of 23%, the nesting sequence was less similar,  $\prec$  < 0.012.

Figure 7. The effect of the number of days and dates of simulated bad weather on mallard nest hatching numbers and sequence. (Data from Sorensen, 1978)

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Figure 7.

Area	Date	Number of initiated pairs	Actual duckling production	Simulated production no bad weather	Simulated production- bad weather
Kindersley	1956	248	1183	1981	1913
Kindersley	1958	173	860	1427	1337
Alberta Parkland	1969	70	238	342	326
Alberta Parkland	<b>19</b> 70	101	183	494	494

Table 3. Response of mallard duckling production to amounts of breeding space and weather conditions varied to simulate field observations. (Data from Dzubin and Gollop, 1969 and Sorensen, 1978).

Figure 8. Comparison of the number of mallard nests hatching per week to the results of the closest simulation. (Data from Dzubin and Gollop, 1969; Sorensen, 1978).



DAYS OF THE YEAR

Figure 8.

1 H S Vä 5 : ex ca. 19 Wea spa COR prec Prod :esp cer :esų Rody <sup>si</sup>gnj Simulated duckling production (1443) was also higher then the production of the closest simulation (1332) (Table 4).

The number of indicated pairs in the 1957 Kindersley study was also too high and produced values in the nesting sequence and duckling production (2991) (Table 1) far beyond the field data (2000) (Table 5) and beyond what could be reduced by simulated predation rates of 35%-50% (Table 2). However, the number of lone pairs, 267, when used in the simulation produced nesting sequence values and production values below the values reported in the field study. Table 5 shows that the number of May and July ponds in 1956 exceeded the number of May and July ponds in 1957, yet the calculated number of breeding spaces in 1956 is less than in 1957. Note, however, the bad weather in 1956 and no bad weather in 1957.

In contrast with 1956, the estimated number of breeding spaces for 1956 proved too low (Table 1). The first combination of numbers for pairs, breeding spaces and predation that produced values for the nesting sequence and production closely resembling the field data were respectively, 290, 167, and 15%-15% ( $\ll = 0.102$ ) (Fig. 8). When 300 pairs were used, predation rates of 35% also resulted in similar duckling production to the reported production (Table 4) but the nesting sequence was not significantly similar to the reported sequence ( $\ll > 0.102$ ).

Area	Date	Number of pairs	Predation rate	Resulting simulated production	Number of pairs	Predation rate	Resulting simulated production	Actual production
Kinderlsev	1956	168	13	1332	178	23	1443	1183
Anderrøey	1957	290	15	2301	300	35	2309	2000
	1958	-	-	-	-	-	-	-
Alberta	1968	30	53	181	40	60	234	185
Parklands	1969	-	-	-	-	-	-	-
	1970	55	53	268	65	60	318	183

 Table 4. Response of mallard duckling production to pair numbers and predation rates varied to simulate field observations. (Data from Dzubin and Gollop, 1969 and Sorensen, 1979).

		1956		1957		1958
	<b>Field</b> data	Simulation inputs	Field data	Simulation inputs	Field data	Simulation inputs
Bad <b>weather</b> days	117-123	121-123	none	none	123-130	120-122
Number of indicated						
paírs*	248	168	358	290	173	148
Number of May ponds	81	-	43	-	20	-
Number of July ponds	49	-	7	-	8	-
Number of breeding spaces	-	95	-	167	-	53
Combined water loss (%) Predation (%)	-	40	0	129	-	136
Early nests-all	20	-	15	-	40	
-active only	13	13	9	15	22	22
late nests -all	30	-	31	-	58	
-active only	13	13	27	15	44	54
Nest Hatching Chronology	Re	sults	Re	sults	Res	ults
days	Number	Number	Number	Number	Number	Number
126-132	2	2	2	1	4	1
133-139	19	30	41	55	33	30
140-146	34	44	94	91	18	23
147-153	12	0	44	56	10	9
:54-160	68	76	27	34	10	47
161-167	7	6	14	16	8	3
168-174	4	2	5	9	5	19
175-181	2	0	2	5	11	3
182-188	0	2	0	3	1	2
189-195	0	0	0	0	0	2
Total nests hatched	148	162	229	270	100	139
Total nests	210	229	301	346	193	210
Total renests	21	61	23	56	24	62
Mean eggs hatched/clutch	8.1	8.2	8.4	8.5	8.2	8.3
Total ducklings hatched	1183	1332	2000	2301	860	1156
Total ducklings fledged						
Nacourod	356		190		223	
neasureu	J J J U		120			

Table 5. Comparison of field data from Kindersely, Szskatchewan to the most similar simulated response of mallard reproductive parameters to breeding space, weather and predation rate variables. (Data from Sorensen, 1978).

\*Field data derived from a census of lone pairs, flocked pairs, lone males and flocked males corrected for sex ratios.

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As with the previous studies, the number of indicated pairs from the Kindersley 1958 field study proved too high to produce simulation results similar to the nesting sequence reported in the study. However, the estimated number of breeding spaces was only slightly too high. Nonetheless, no combination of bad weather and numbers in the simulation produced results statistically similar to the field results,  $\ll > 0.111$  (Fig. 8). Note, however, the severe drought as indicated by the number of ponds in Table 5 for 1958 and that the simulated nesting sequence for the early part of the season closely approximates the actual sequence. Also note the high late predation rates used in the simulation when compared to the field data. When lower predation rates were used, the simulated nest sequence for the late part of the season had values even greater than indicated in Figure 8 and Table 5.

Simulation of the data from Alberta Parklands 1968 was conducted as with previous simulations, and once again, the number of indicated pairs when used in the simulation resulted in duckling production values that were too high (Table 1). When the maximum number of observed pairs per week (40) was used along with 60%-60% early and late predation rates, the resulting nesting sequence values were statistically similar ( $\ll = 0.047$ ), but duckling production was high (Table 4). However, when the next lowest number of pairs per week (30) was used in the simulation, along with

early and late predation rates of 53%-53% which were estimated by the author of the field study, a closer approximation of the nesting sequence (Fig. 8) was achieved, ( <= 0.016) and duckling production was similar to the field data (Table 6). Note, however, that in Table 6 the values for the numbers of nests and ducklings hatched from the simulation are just slightly lower than the field study data.

It was not possible to produce a simulation that was statistically similar to the data from the Alberta Parklands 1969 data ( $\ll$ > .111) (Fig. 8). However, the author of the investigation reports that unusually cold weather (-6° and -7°C) during the time (June 12-13) when most hens were incubating resulted in "damage to some eggs" and subsequent renesting. The model, however, eliminated these late renests.

Note, however, that the model was able to simulate the decline in nest initiations from a high starting point and a slight increase in nest initiations at the end. These results were achieved by setting bad weather at the beginning of nest initiation as indicated in the field data, and by setting the date for peak nest initiation in the simulation at the date of the high point in the field data. Early nest initiations in the simulation were then delayed until good weather was indicated, thus producing a beginning high point instead of a peak 13 days later as would normally

Sorensen, 1978)	•					
		1968		1969		1970
	Field data	Simulation inputs	Field data	Simulation inputs	Field data	Simulation inputs
Bad weather days	91-111	91-111	<b>91 100</b> 163-164	<b>91-100</b> 163-164	<b>91–111</b> 181–182	91-111 181-182
Number of indicated						
pairs	89	30	70	55	101	55
Number of May ponds	43	-	158	-	150	-
Number of July ponds	20	-	50	-	70	-
Number of breeding spaces	-	18	-	25	_	27
Combined water loss (%)	-	129	-	70	-	59
Predation $(%)^2$						
Early nests	53	53	53	60	53	53
Late nests	53	53	53	50	53	53
Nest Hatching Chronology <sup>3</sup>	Re	sults	Res	ults	Re	sults
Davs	Number	Number	Number	Number	Number	Number
147-153	5	4	7	11	5	3
154-160	7	7	5	10	9	12
161-167	3	5	3	6	9	9
168-174	3	4	4	5	5	6
175-181	3	1	2	2	2	2
182-188	2	2	6	1	2	1
189-195	3	0	7	4	2	1
196-202			1	0		
203-209			0	0		
210-216			1	0		
Total nests hatched	26	23	36	39	34	34
Total nests	-	40	-	67	-	<b>6</b> 0
Total renests ,	-	10	-	22	-	15
Mean eggs hatched/clutch <sup>4</sup>	6.4	7.9	6.4	7.8	6.4	7.8
Total ducklings hatched	185	181	238	304	183	268
Total ducklings fledged	44	27	140	140	104	139

Table 6. Comparison of field data from Edmonton, Alberta Aspen Parkland Life Area to the most similar simulated response of mallard reproductive parameters to breeding space, weather and predation rate variables. (Data from Sorensen, 1978).

<sup>1</sup>Maximum number of indicated pairs per week including lone pairs, flocked pairs, lone males and flocked males

## <sup>2</sup>Estimated by author

<sup>3</sup>Estimated from Class I broods

<sup>4</sup>Estimated from ducklings/Class I broods

be produced by the simulation. The increase in nest initiations at the end of the simulated nesting sequence was achieved by using a number of pairs greater than needed to produce the early part of the sequence, and then raising the reported predation rates of 53%-53% to 60%-60%.

The simulation of the Alberta Parklands 1970 field study was conducted as all previous simulations, and the field observation of a maximum of 55 lone pairs and lone drakes per week and the field study estimate of early and late predation rates of 53%-53% produced the simulation results most closely approximating the field data,  $\ll = 0.047$ (Table 6 and Fig. 8). A higher number of pairs and a higher predation rate resulted in a greater number of ducklings produced (Table 4).

When the numbers of pairs in both the Kindersley field data and simulations are compared with habitat over the 3 year period, the number of ponds decreases with each succeeding year (drought), while the number of pairs/pond and pairs/acre increases in both field and simulations (Table 7). The number of breeding spaces does not vary with the number of ponds, but note in Table 5 that 1957 and 1959 had bad weather during the breeding season. The number of ponds/breeding space and acres/breeding space both decrease with drought. Duckling production, reported or simulated, does not vary with pond numbers.

	19	56	19	57	1958		
	Field	Model	Field	Model	 Field	Model	
Censused pairs	248	-	358	-	173		
Calculated breeding pairs (nests-renests)	-	101	-	214	-	77	
May ponds	81	-	43	-	20	-	
Total wetland acres	642	-	573	-	176	-	
Pairs/pond	3.1	1.2	8.3	5.0	8.6	3.8	
Number of breeding spaces	-	95	-	167	-	53	
Pairs/breeding space	-	1.1	-	1.4	-	1.4	
Ponds/breeding space	-	0.9	-	0.3	-	0.4	
Acres/breeding space	-	6.4	-	3.4	-	3.3	
Duckling production	1183	1332	2000	2301	860	1156	
- per pond	14.6	16.4	46.5	53.5	43.0	57.8	
- per breeding space	-	14.0	-	37.7		21.8	

Table 7. Comparison of actual and simulated mallard pair and duckling production response to habitat at Kindersley, Saskatchewan. (Data from Dzubin and Gollop, 1969).

When the number of pairs in both the Alberta Parklands field data and simulations are compared with habitat over the 3 year period, the number of ponds increases abruptly in 1969 and 1970, while the number of pairs per pond in both field and simulations generally decreased (Table 8). The number of breeding spaces does not vary with the number of ponds, but note in Table 6 the bad weather during the 1969 breeding season. The number of pairs/breeding space remains constant while the number of ponds/breeding spaces increases. Duckling production does not vary with pond numbers.

In Table 5, the number of simulated nests hatched exceeds the measured hatch in all cases, and the authors of the field study report that not all nests were found in nest searches. Correspondingly, the simulated number of ducklings hatched proportionally exceeds the measured hatch. This is not the case for 1969 and 1970 in Table 6. Although the number of nests hatched differ between the field data and the simulation by 3 and 0, in both cases the simulated number of ducklings fledged is much larger than the number from the field data. During both of the years, the author reports severe weather in June that he believes destroyed many late nests and Class I broods.

Note that the simulated numbers of ducklings fledged in Tables 5 and 6 are very close to or falls within range of the numbers of ducklings estimated and/or measured in the

	19	968	19	969	19	970
	Field	Model	Field	Model	Field	Model
Maximum number of indicated pairs/week	62	_	89	-	101	-
Calculated pairs (nests-renests)	-	13	-	17	-	19
May ponds	43	-	158	-	150	-
Pairs/pond	1.4	0.3	0.6	0.1	0.8	0.1
Number of breeding spaces	-	18	-	25	-	27
Pairs/breeding space	-	0.7	-	0.7	-	0.7
Ponds/breeding space	-	2.4	_	6.3	-	5.6
Duckling production	185	181	238	304	183	268
- per pond	4.3	4.2	1.5	1.9	1.2	1.7
- per breeding space	-	10.0	-	12.2	-	9.9

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Table 8. Comparison of actual and simulated mallard pair and duckling production response to habitat at Edmonton, Alberta Aspen Parkland Life Area. (Data from Sorensen, 1978). field studies in 4 of the 6 years simulated. However, in Kindersley 1959 and Alberta Parklands 1968, the duckling mortality between hatching and fledging is overestimated. Although the mortality in Alberta Parklands 1970 appears to be underestimated, the simulated number of ducklings hatched is higher than the number reported for probable reasons previously discussed.

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## DISCUSSION

If the model is in fact a reasonably accurate simulation of mallard breeding biology, it demonstrates how a phenotypic expression of a genetic trait can be used to better evaluate the performance of a species within its habitat, and the relative suitability of the habitat. In this case, the individual genetic trait is the time of nest initiation of individual hens and the resulting distribution of nesting frequencies of the local population. Exogenous variables, however, can greatly alter the response and must be considered.

The importance of knowing the actual number of breeding pairs is one of the most obvious results of this study. In the Kindersley study, the number of indicated pairs in 1956 and 1958 were approximately twice the number of pairs estimated by the model, and in the Alberta Parklands study, the number of indicated pairs was approximately 5 times the number of predicted pairs. The model indicates that had all indicated pairs actually nested, the resulting nesting sequence would have been similar in pattern, but with double or up to five-fold the number of nests.

It has been established that the number of indicated mallard pairs includes birds not actually paired, especially during drought (Johnson and Sargent, 1977; Jackson et al., 1985). Although this relationship offers a partial explanation for why the simulations estimated fewer nesting paris than the number of indicated pairs, it does not explain the range of differences from year to year. The percent of indicated pairs simulated as nesting pairs increased from 68 to 86% in the Kindersley area during increasing drought, yet the percent of indicated pairs simulated as nesting pairs varied independently with increasing water levels in the Alberta Parkland area.

It can be argued that the indicated pairs did nest, but that many of the nests were destroyed by predators. Were this the case, then the field estimates of predation were greatly underestimated. It is entirely probable that the predation rates were underestimated as suggested by Miller and Johnson (1978), but the predation rates required by the model to produce statistically comparable nesting sequences would have been more than three times greater than the field estimates. For example, in the 1957 Kindersley study the number of pairs predicted by the model was 290, but the number of indicated pairs reported in the field data was 358. When 358 pairs was used in a simulation, it required an 85% predation rate to reduce the resulting duckling production to a value approaching that reported in the field

data. That rate also produced a nest hatching sequence statistically different than the reported sequence ( $\ll$  0.11).

It could also be argued that in the field studies not all nests were found and not all broods counted, thus underestimating production. This is definitely true, but in most of the simulations, the closest simulation estimated a greater number of nests and ducklings than reported in the field studies. Thus, the number of nests and ducklings hatched predicted by the simulation may be closer to the actual production than that reported by the field studies.

It was not possible, however, to estimate a somewhat larger number of breeding pairs and then achieve a nesting sequence and duckling production comparable to the reported production by increasing predation. For example, in simulations of the 1957 Kindersley study, 290 pairs and predation rates of 15% produced a nesting sequence more statistically similar to the reported sequence ( $\ll = 0.102$ ) than when 300 pairs were used with predation rates of 20% ( $\ll$ >0.102).

The model does not indicate that bad weather alone could account for why some the lack of nesting by indicated pairs. In the 1957 Kindersley study, there were 43 May ponds in which the model predicted 290 of 358 indicated pairs produced 2301 ducklings, as compared to the reported production of 2000. Therefore, the 81 ponds in May of 1956

should have provided habitat enough for all of the 248 indicated pairs that year. This was not the case because the field study reported fewer nests (148 vs. 229) and less duckling production (1183 vs. 2000) than in the 1957 investigation. The model predicted that only 168 of the 248 indicated pairs nested to produce 1332 ducklings.

When 248 pairs was used in simulation with and without bad weather, the simulated bad weather reduced duckling production from 1981 to 1913, but this result is much greater than the 1183 ducklings reported in the field study. Thus, while the model produced a similar number of ducklings and a nest hatching sequence to those reported when bad weather and 168 pairs was used, this does not explain why only 168 pairs nested. These same relations can be seen in the Alberta Parklands study where the number of ponds nearly quadrupled between 1968 and 1969, yet indicated pairs actually decreased in 1969 and the number of nests increased from 24 in 1968 to only 36 in 1969 and 34 in 1970. Again, weather was involved, but the model does not indicate that the weather was as limiting as the number of pairs and duckling production would indicate (Table 3).

The effect of weather, however, is not satisfactorily simulated by this model in all cases. Although the effect of bad weather was simulated reasonably well in the 1956 Kindersley study, it was not satisfactorily simulated in either the 1958 Kindersley study or in the 1969 Alberta

Parklands study. It cannot be determined at this time if the model simulates the effect of weather imprecisely or if the imprecise reporting of weather is the cause of the discrepancies, or some combination of both.

Although the model does not indicate that spring weather in the Alberta Parklands 1969 and 1970 studies was responsible for the lack of nestings and production, it still may have been a determining factor. The author of the Alberta Parklands counted broods and calculated nest hatching from those data. If the severe weather killed broods that went undetected, then the number of calculated nests would be lower than actual. The model would simulate this by correspondingly reducing the number of breeding pairs.

Another possible explanation for why so few of the indicated pairs nested in the Alberta Parklands study is that the pairs arriving in the spring were not physiologically ready to breed because of poor water conditions in the wintering areas. The regression equations of Heitmeyer and Fredrickson (1983) utilizing water condition in wintering areas, May ponds and July ponds show that water conditions on the wintering areas in 1969 and 1970 account for almost half (R2 = 0.496) of the variation in the equation predicting mallard age ratios for those years. The R2 for the entire equation was 0.922.

Mallard spacing behavior could have restricted nesting. In the Kindersley studies and simulations, the calculated number of pairs per pond increases with drought, while ponds and acres per breeding space decrease with drought (Table 7). In the Alberta Parklands studies and simulations, the reverse is true. With increasing wetlands numbers, pairs per pond decrease while ponds per breeding space increases (Table 8).

These relationships suggest that a pair of mallards occupy smaller areas when there is less wetland habitat and larger areas when there is more wetland habitat. Weather certainly had an effect on these values, but not their relative relationship. For example, had the weather at Kindersley been good in 1956 and 1958 the pairs/pond, pairs/ acre, and acres/breeding space all would have been higher for both years (Table 7). Further, since the number of pairs/breeding space calculated from the simulation changes little in relation to the other habitat parameters, then the size of the breeding space must expand with increasing wetland habitat and decrease with decreasing wetland habitat.

Although the results of this investigation do not suggest how large a breeding space can be, the acres/ breeding space in Table 9 for Kindersley 1956 indicate 6.4 acres. Obviously, the size could be larger.

Since 1958 was an extremely dry year at Kindersley, the number of acres/breeding space that year, 3.3 acres, (Table 1) may approach the minimum size. Unfortunately that year was poorly simulated and the number of breeding spaces is probably over-estimated. Nevertheless, that estimate is close to the minimum size of a wetland required to support a mallard pair, estimated at 3.0 acres by Dzubin (1969), approximately 4.9 acres for semi-permanent wetlands, by Cowardin and Johnson (1983), and 1.1 acres for experimentally manipulated marsh by Kaminski and Prince (1981).

No evidence was discovered in this investigation of the crowding of large numbers of indicated pairs on less habitat resulting in lowered production. The converse was true, because in the 1957 Kindersely study the largest number of pairs produced the greatest number of young in a period of declining numbers of ponds and wetland acres. However, high densities of mallards nesting on artificial structures, islands, and in dense upland vegetation should not necessarily be accepted as evidence of mallard breeding in extremely small areas. As indicated in the literature review, mallard hens may nest a long distance from the defended wetland area necessary to provide the food needed to sustain reproduction (Lokemoen et al. 1984). The model, however, did not simulate such conditions.

A final possible explanation as to why more of the indicated pairs did not nest may be that the model was simulating full utilization of available breeding habitat and that the necessary resources for reproduction were not available for all indicated pairs. As noted by Weller and Fredrickson (1974), avian use of a marsh is less when there are few pools, possibly resulting from drought, or when there are large pools consisting mainly of open water, possibly resulting from several years of high water levels. Obviously, the number of pools may not indicate the existence of the 50% interspersion of open water and aquatic vegetation in a marsh that results in the greatest number of pairs breeding in the marsh.

Although there were more ponds in the Kindersley area in 1956, the seven preceeding years were years of increasingly abundant precipitation (Pospahala et al. 1974), which may have produced a large number of ponds consisting primarily of open water that had relatively lower pair use. The ensuing drought reduced the number of ponds in 1957, but may have created in the remaining ponds the temporary hemimarsh conditions most abundantly used by mallard pairs. As the drought worsened in 1958, the ponds may have become too few in number and contained too small a percent water to maintain the high pair use. If such were the case, then the model may have successfully simulated full utilization of the available resources.

The same relation may have also occurred in the Alberta Parklands study. Neither indicated pairs nor simulated pairs increased proportionally with the increase in ponds, but the large and sudden increase in ponds in 1969 that was maintained in 1970 may not have permitted the development of the hemi-marsh that would have supported increased pair use.

The model successfully simulated the difference in productivity between grassland and parkland habitat. Both the field data and the simulations show greater pair use and duckling productivity per pond in grassland than in parkland habitat. Dzubin (1969) found the same relationship when comparing data from Roseneath, Alberta and Kindersley, Saskatchewan and attributed the difference to the difference in average pond size of the two areas. The average pond size in the grassland of Saskatchewan was 5.7 acres, but in the parkland of Alberta was only 0.7 acres. This also agrees with the prediction and qualification of Cowardin and Johnson (1983) concerning pond size, pond conditions, and pair use.

The failure of the model to successfully simulate the 1958 Kindersley study not only points out a weakness in the model, but perhaps best illustrates how the mallard nesting sequence is a measure of habitat. The model closely simulates the nesting sequence and the effects of bad weather early in the nesting season (Fig. 8), but when the bad weather variable is removed, the model predicts an

increased response in nesting and subsequent nest hatching in the same way it did in the 1956 Kindersley simulation (Fig. 8). Yet there was not a subsequent increase in nesting and nest hatching in 1959.

The number of May and July ponds in Table 5 show 1959 to be a year of severe drought, starting dry in May and getting dryer through the nesting season. Note that there were more ponds in July 1956 than in May of 1958. Thus the reason that nesting did not increase after bad weather in 1958 as it did in 1956 appears to be because the habitat was not available in 1958 to allow nesting. Unfortunately, the model measures the productive capacity of wetlands as a constant number, the number of breeding spaces. Obviously, this factor should have been treated as a series of functions instead of a constant.

Note that the predation rates in the Kindersley 1958 study are not equal and higher than in previous years in both the field data and the simulation. The rates in the simulation are unequal and high because they somewhat reduced the high simulated nesting sequence values, thus making the simulation more closely resemble the actual sequence and are probably artificially high, especially the late predation rate. Predation rates from the field study may have also been too high, because a simulation using a lower early predation rate (18%) produced a early portion of nesting sequence more closely resembling the actual early

portion, but was rejected because no rationale could be determined for using early predation rates lower than field estimates since predation rates estimated when many hens are laying are usually underestimated.

One obvious constant discrepancy between field data and model simulations is with renests estimated in the field studies and the simulated renests. Only late nests in the field study were counted as renests, and since renesting probably occurs throughout the season as simulated by the model, the field estimates of renesting are probably low.

The equation estimating duckling survival did not consistently predict survival for all years (Tables 5 and 6). One obvious reason is that the equation did not account for severe weather that can destroy ducklings, especially those in Class I broods. It also may not apply to all areas equally well, since it was developed from the data from one specific location. Another explanation is that the departure of pond numbers from the maximum number of May ponds is a poor measure of distance of the nest from water, the actual determining factor. A multiple regression of mean distance of nest from water and percent pond loss May-July may prove more reliable, but this equation was not developed because of lack of sufficient number of years of estimates for the distance factor.

In all successful simulations, predation rates for early and late nesting seasons were equal (Tables 7 and 8).

The unequal rates in the unsuccessful simulations are, as previously discussed, compensating for some other effect not simulated. The constant rate of predation agrees with the estimates of constant daily nest survival by Green (1977) and Miller and Johnson (1978), but in all cases, the rates were equal to or just slightly greater than the field estimates. This is in opposition to the methods developed by Mayfield (1960) and modified by Miller and Johnson that show field measures of predation are usually underestimates. No reason can be suggested for this discrepancy.
## CONCLUSIONS

- The mallard nesting sequence, a phenotypic expression of a distribution of mallard genotypes, can be used to evaluate mallard reproductive performance if adjusted for weather and predation.
- Weather is an important variable controlling mallard productivity and appears to be directly related to habitat suitability.
- 3) The mallard nesting sequence can be used to evaluate relative habitat suitability.
- 4) Mallard breeding pairs will crowd to a density of 1 pair per 3-5 acres of wetland habitat, but how this is related to mallard spacing mechanism and the limits of habitat productivity remains undetermined.
- 5) When wetlands are abundant as expressed by breeding space, the mallard spacing behavior seems to produce less than maximum utilization of habitat, even when weather is taken into account.

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## LITERATURE CITED

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APPENDIX

## Program Listing

	<pre>FROGELM Fac INPLICIT INTEGEF(A=7) REAL POISST.MEX.MINEHT.LFTSHP.RHTSHP.FUNCTN.SUM FEAL POISST.MEX.MINEHT.LFTSHP.RHTSHP.FUNCTN.SUM FEAL A.F.C.C.S.FFL.F.F.C.S.U.F.F.C.AT.LTPREF.LUPFFD.MEPOUND.HCCCEV CH4RLCTEF+10 MCCS.VETHEP DIMENSION NFAPS.C.C.C.J.C.C.C.C.D.J.NCHAT(650.3).LAYING(AFFC.F) DIMENSION NFAPS.C.C.C.J.C.C.C.C.D.J.NCHAT(650.3).LAYING(AFFC.F) LIMENSION NFAPS.C.C.C.J.C.C.C.C.D.J.NCHAT(500.1.S.NPPLM(570.5) CIMENSION SEPPIN(500.1.N.C.C.C.S.D.S.NPPLM(570.5) CIMENSION SEPPIN(500.1.S.C.C.S.C.S.S.S.PPLM(570.5) CIMENSION SEPPIN(500.1.S.C.C.S.C.S.S.S.PPLM(570.5) FUNCTN(X)=2.F5-C.C.12.C.FFL(X) FGGS(X)=7.FC.C.F.FL(X)/(F-A))+D)+(EXF((D/C)+(1 HOISSN(A.F.C.F.F.))/(F-A))+D)+(EXF((D/C)+(1 HOISSN(A.F.C.F.F.))/(F-A)))/(F-A))/SUM</pre>
c	FEAD AND INITIALIZE VARIAME AND ARRAYS         FROMEO.         FROMESUED.         FREDATEC.         CDPNTED         NPRSKPTED         SRPPTTO         NPRSKPTED         SRPPTTO         SRPPTTO         NPRSKPTED         SRPPTTO         NPRSKPTED         SRPPTTO         NPRSKPTED         SDSMPTTO         NVCTTO         NVEGGED         TOTTAKEO         NVCTTEC         TONNTSED         TONTSHED         RENSTSET         READ(* I) MOTE
10 20	FOFWAT(4(13,3x)+F3+;+7x+14) KEAL(++10)MCURAH,NOMTH(+HONVHN+NOBDSP+F2CDEV+ACTKIL PEAD(++20)(AYF(N+#X)AY FOFWAT(C(13,3x))
<b>3</b> 0	FEAD(**30)#TCTOF*KVCTCF FORMAT(2(13*3*)) FFAD(**40)#(******)
<b>6</b> 40	CALCULATE PAIRS AND SUFFLUS BIRDS FORMAT(4(F4.1.1X),F10.8,1X,2(F2.2.1V))
	CALL PAIR (NODRAR, NORTHE, FOR VHN, NEARSKOPE SPICALRSKOPE SPICE) • SPOSTNOSEPPIMOSEPPIMOSEPPIMOSEPPIMOSEPPIMO TOTAL=PRSKFI+NFRSPI DAY=DAYPEN-1 DAY=DAYPEN-1
50	
	CYCL (1, 0, 0) = 094 CYCHED=1000 DO 60 I=1+T0TAL+1 INCBAT(I+1)=I+1 INCB1T(I+0)=0
60	CONTINUE TNCFAT(TOTAL,1)=C INCFED=1
	ECDATA=>CHCSF+1 CC 7C J=1+CCCSF+1 LAYING(I+1)=C+1

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LAYING(1.0)=
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FORMAT(A10)
   76
75
C 80
  85
CCCCC
                     DAILY CALCULATIONS

CALCULATF EGG FFODUCTION BY DATE AND WEATHEP

DO 90 J=100DATA1

IF(LAYING(1,1))LE,-1)THEN

MAXEGGENINT(.75)LAYING(1,5))

TF(LAYING(1,2))LT.MAXEGDTHEN

IF(LEYING(1,2))LT.1)THEN

IF(LAYING(1,2))LT.1)THEN

IF(LAYING(1,2))LT.1)THEN

LAYING(1,2)=LAYING(1,2)+1

LAYING(1,2)=LAYING(1,2)+1

LAYING(1,3)=0

LAYING(1,3)=0

LAYING(1,3)=CGS(0AY)

FEVSTS=RENSTS+1

ELSF

LAYING(1,1)=1

LAYING(1,1)=1
                                                                                  LLSE
LAYING(I+1)=I
FAILNT=FAILNT+1
END IF
ELSF
                                                                                    LAY ING(1,2)=LAYING(1,2)+1
LAYING(1,3)=0
END I=
                                                                        FLOD
                                                                                   CE

LAYJNG(1,2)=LAYING(1,3)+1

JF(LAYING(1,2)+GE+1)THEN

IF(LAYING(1,3)+GT+1+EN

LAYING(1,3)+GT+1+CK+LAYING(1+4)+FG+2)THFN

LAYING(1+2)=0

LAYING(1+3)=0

ELSF

ELSF

LAYING(1+4)=0
                                                                      FNI IF

FLSE

IF(LAYING(1,2)+LT+LAYING(1,5))THEN

LAYING(1,2)+LAYING(1,2)+LAYING(1,2)+LAYING(1,2)

CALL PUSH(SPRSTK,SRSKPT+LAYING(1,1))

CALL SET(CAY,INCEAT+INCHED+I+LAYING+LAYHED)

FNR IF

FNR IF
                                              ELSE
ENG IF
90
                                   CONTINUE
CCCC
                     CALCULATE FGG HATCH

[0 150 ]=1+TOTAL+1

IF(INCHAT(I+1)+LF+-1)THEN

TF(INCHAT(I+1)+G+CAT)THEN

IF(INCHAT(I+1)+G+CAT+EN

MFCFTF=MFCFTE+1

NTE(G=MTFGG+NINT(+75+INCHAT(I+2))
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INCHER:

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INCHER:

INCEAT(I,2)=INCHER

INCEAT(I,2)=INCHER

INCEAT(I,2)=INCHER

INCEAT(I,2)=0

INCEAT
 100
C
C
C
C
                                                           CALCULATE PAIRS FROM SURPLUS BIRDS

IF(DAY.LF.MTCTFF)THEN

REPEAT

CONTINUE

IF(SDSKFT.GE.1)THEN

CALL POP(SPPSTK.SDSKPT.MATE)

CALL POP(SPFFLM,SRPPTM,MATRON)

CALL PUSH(PAIRSK.PPSKPT.MATRON)

CALL PUSH(PAIRSK.PPSKPT.MATRON)

TNU IF

END IF

IF(SDSKFT.GE.1.AMC.SRPPTM.GE.1)G0 TO 110

UNTIL(
ç
110
 с
с
                                                                                       IF (DAY+LE+NVCTOF)THEN

REPEAT

CONTIFLE

IF (SD5+PT+GE+1)THEN

CALL POP(SPDSTK,SDSKPT+MATE)

CALL POP(SPDSTK,SDSKPT+MATE)

CALL POP(SPPFLN+SRPPTN+NOVICE)

CALL PUSH(NPARSK+NPRSPT,NOVICE)

ENC IF

IF (SDSKPT+GE+1+AND+SRPPTN+GE+1)60 TO 120

UNTIL(

END IF
C
120
 С
                                                           END IF
 CCC
                                                          CALCULATE REST INITIATION FROBABILITY
INITATES
IF(DAY.LF.MTCTOF)THEN
PFOR=FEAL(TOTAL)+POISSN(MAX,MINPHT.LETSHP.RHTSHP.(2Y)
P10BSU=PFOPSU+PPC=
IF(DAY.EG.MTCTOF)THEN
INITATENINT(PFOHSU)
END IF
IF(PROPSU-GE.1.)THEN
REFEAT
Ċ
                                           -APPI

-NINT(PEDHSU)

IF(PROPSU.GE.1.)THEN

REFFAT

CONTINUE

INITAT=INITAT+1

PROBSU=PROPSU-1.

IF(PROFSU.SF.1.)GO TO 125

ELSE

END IF

ELSF

END IF
C
125
 С
 CCCC
                                                            CALCULATE FECYCLED HENS
IF(DAY.LE.MICTOF)THEN
FINDERRE
                                                           HOLD=1(00+NOFDEF
REPEAT
CONTINUE
FIND=FIND+1
C
130
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IF (CYCLE(FJ)))+LE+GAY)THEM

JF(CCCHET+GE+I))+EN

YCLE(FIND)=CYCHED

CYCHEDEFIND

C4LL PCF(SEDSTK+SDSKPT+MATE)

C4LL PCF(SEDSTK+SDSKPT+MATE)

END IF

END IF

TF(SUSYFT+GE+1+AND+FIND+LE+H0LD)30 TO 130

TL
С
                    UNTILC
END IF
C
C
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C
                    CALCULATE RENEST PPOBALILITY

IF(WETHER.FG. 'GCOD')THEN

IF(DAY.LE.MTCTOF)THEN

IF(DAY.GE.129)THEN

NUMEROENINT(REAL(COPNT)+FUNCTN(DAY))

FLO
                               FLSE NUMSNO=COFNT
                   END IF
END IF
ELS<u>F</u>
                    END IF
CCC
                    CALCULATE SECOND NESTS

SNICNTED

JF(NUMSND, GE+1)THEN

JF(L2YTHG(LAYMEE+1)+GF+1)THEY

JF(CLPT-GE+1)THEN

FEFET

CONTINUE

CALL POE (CYCLED+CDPNT+MATPON)

CALL LAY(LAY+LAYING+LAYHED+MATPON)

CALL LAY(LAY+LAYING+LAYHED+1)+GE+1+AND+SNCCHT+IT+

SECCL=SECND+1

SNDCHT=SECND+1

SECCL=5ECND+1

SFFCDPNT+CE+2+AND+LAYING(LAYHED+1)+GE+1+AND+SNCCHT+IT+

NUMSNDJGC TO 140
C
140
                   END IF
С
CCCC
                    CALCULATE NESTING OF RESERVE MATRON PAIRS
IF(DAY.LE.MTCTCF)THEN
IF(WETHEF.ED.+GODD+)THEN
IF(LAYING(LAYHED,1).GE.1)THEN
С
                                                   IF (FMDLT.GE.1)THEN

PEPEAT

CONTINUE

CALL POF(FEDMAT.FMFNT.MATPON)

CALL LAY(CAY.LAYING.LAYHED.MATRON)

MATF.MATF.N1

IF(LAYING(LAYHED.1).GE.1.AND.RMPNT.GE.1)GO TO 150

HNTTL
150
                             UNTIL
FND IF
FND IF
J IF
С
                    END IF
CCCC
                    CALCULATE NEGTING OF RESERVE NOVICE PAIRS

IF(FAVLE-NVCTOF)THEN

IF(L2YT)G(L4YDED+)THEN

IF(L2YT)G(L4YDED+)).GE+1)THEN

IF(FXFTEGE+1)THEN

FFFEAT

CONTINUE

CALL FOF(FEDNOV-RNPNT,NOVICE)

CALL LAY(DAY+LAYING+LAYHED,NOVICE)
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WRITE(**435)NVCPTE

FORMAT(* **TOTNOVNTSHCH=**16)

WRITE(**436)MPCPTE*NVCFTE

FORMAT(* **TOTNESTE=**16)
425
435
430
             445
455
456
465
465
С
             CALL LOKATE (CYCLE + CYCHEN + DAY)
٢
             WPITF(+.475)CYCHEN+MTFNT+NVPNT+CDPNT+FAILNT
FORMAT(+ *,*FAILED TO RENEST=*,16)
475
C
C
             CALCULATE DUCKLING PRODUCTION
CALL DUKLINGMTEGG,NVEGG,MZODEV,JDUCKS,HDUKLN)
ç
            CALCULATE POPULATION FOR FALL
CALL NEWPOPINCOPAK,NOMTHP,NOMVHN, DEDHEN,JDUCKS,ACTKJL,DIFKIL,
+BRDPOP,FALFOP,ALOKIL,AGEFAT,SEXFAT).
             WP JTE (+.4=5) HDUKLN
FORMAT(' ','DUKLINHCH=',I6)
WR ITE (+.4=5) JDUCKS
FORMAT(' ','DUKLINFLDG=',I6)
WR ITE (+.515) FRCPCP
FORMAT(' ','FALLPOP=',I6)
WR ITE (+.535) FALPCP
FORMAT(' ','FALLPOP=',I6)
WR ITE (+.535) ALCKIL
FORMAT(' ','CIFKIL=',I6)
WR ITE (+.555) AGERAT
FORMAT(' ','AGERATIO=',F6.2)
WR ITE (+.555) SEXPAT
С
465
495
515
525
535
545
555
             WRITE(+.565)SEXPAT
FORMAT(* * * *FALSEXRATIO=* *F6.2)
END_IF
565
                          STOP
             END
      .
```

CUBEOUTINE FAIR(NGDEAR.NOMTHN,NONVHN,NFAFSK,NPRSPT,PEJFCK,FRSFFT, SDSKPT,SPDSTK,SRPPTM,SRFFTN,SURFLM,SNFPLN) CALCULATE FAIRC AND SUFFLUG BIRDS INPLICIT INTEGER (A-2) DIMENSICH NEASH (E00),PAJPSK(500),SPDSTK(500),SPPPLM(EU0),SRFFLM ٠ C 1.7 E D0 4C I=1,NONVHN,1 CALL PUSH(NPARSK,NPRSPT,-3) CONTINUE D0 50 I=1,SUPPLD,1 CALL PUSH(SPDSTK,SDSKPT,-2) CONTINUE IF 30 40 50 ELSE DO 60 J=1.NONVHN,1 CALL PUSH (NPARSK,NPRSPT,-3) CONTINUE ELSE DO 70. J=1.NONVHN-1 61 ÖG 70 J=1•NONVHN•1 CALL FUCH (CJAFLN•SRPPTN•−3) CONTINU: 7 2 CONTINUE FND IF ELSE SURPMHENCHTHM-NODPAN DF F2 I=1,NODRAN,1 CALL PUSH(F4IRSK,PFSKPT,-2) CONTINUE DC 90 I=1,SURPMH,1 CALL FUSH(SURPLM,SPPPTM,-2) CONTINUE DC 1CCI=1,NONVHN,1 CALL PUSH(SURPLN,SRPPTN,-3) CONTINUE END IF 80 9,1 100 END IF SURFOUTING FUGH(STACK, FCINTH, ENTPY) AUD VAFIAFLE TO APFAY IMPLJCIT INTEGEF(A-2) FIMFNSION STACK(SCO) FCINTR=FOINTF+1 STACK(POINTR)=ELTPY PETUFN С

SUBROUTINE POP(ETLCK, POINTE, PETURN) DELETE VARIAGLE FROM AFFLY IMPLICIT TATEGEP(A-2) LIMERSION STACK(FOO) PETUPNESTACK(FOINTE) STACK(POINTE)=C FOINTE=POINTE)=C FOINTE=POINTE-1 PETUPN FND

E ND

С

SUBPOUTINE SET(LAY+IACLAT+INCHED+POH+LAYING+LAYHED) CALCULATE FGG HATCH MPEICIT I'TEGE(A-2) LIMENSION INCEAT(EC,3)+LAYING(FED+5) SAVF=INCPAT(INCHED+1) ''CTAT(I'NCHED+1)=LAYING(FCH+1) INCEAT(I'NCHED+1)=LAYING(FCH+2) INCBAT(IACHED+3)=DAY+25 INCHFD=SAVF DO IC J=2+5+1 LAYING(FOH+1)=LAYHED CANTINUF LAYHED=ROW RETUPN END -C 10 SUPPOUTINE LAY(CAY+LAYING+LAYHED,PAIR) CALCULATE FCC PFODUCTION THELICIT TEGEF(A-Z) FEAL EGCC DIMENSION LAYING(650,5) FGGS(X)=26.45-.15+(A)+((.05+.01)+(X++2)) CAVE=LAYING(LAYHED,1)=PAIR LAYING(LAYHED,1)=PAIR LAYING(LAYHED,3)=C LAYING(LAYHED,3)=C LAYING(LAYHED,5)=EGGS(DAY) LAYHED=SAVE RETUPN END С END SURFOUTINC ACCULT (NORDSF,LAYING,INCBAT, FENLAY, HENING) CALCULATE HENS LAYING AND INCUBATING IMPLIGIT INTEGET (A-2) DIMENSICK LAYING(F50,5),INCBAT(650,3) HENINC= NODE=0 REPEAT С NODE=0 PEPEAT CONTINUE NODE=NODE+1 IF(LAYING(NODE,1).LE.-1)THEN HENLAY=HENLAY+1 END IF IF(NODE.LT.NOPDSP)G0 TO 10 UNTIL NODE=0 REPEAT CONTINUE NODE=NODE+1 IF(INCBAT(NODE,1).LE.-1)THEN HENINC=HENINC+1 END IF IF(NODE.LT.NOBDSP)G0 TO 20 UNTIL RETUPN END **S**10 С **C** 20 С

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SUBROUTINT PPFY(LAYING,LAYHED, INCBAT, INCHED, HENLAY, HENING, DEFHE, +CYCLE, CYCHED, HT4CN, NVICE, MIFNT, NVPNT, MTCTOF, NVCTOF, DAY, NOPDE, +PFEDAT, MAXDAY, DAYCNT, FILL, TCTTAK, K&OUND, INITAT, CHNGKL, HENSTS) CALCULATE FHEDATION JMPLICIT INTEGEP(4-2) FFAL PROPOF, PREVAT, HCLC, Y, KILL, TODAKL, KHCUND, PARTKL DIMENSION LAYING (650, 5), INCPAT(650, 3), CYCLE(1000:150), MTFON(F0), +NVICE(500), FILL(FO:220, FC:220) HOLC(X)=4,4+0.644, \*X EGGS(E)=26,60-,10+(E)+((.05+.01)+(E++2)) PARTKL=(INITAT+PREDAT)/(26.0+EGGS(DAY)) С С TODAKL=0 LROUND=0 IROUND=0 IROUND=0 ADJKIL=0 INCKIL=0 LAYKIL=0 TAKEN=0 IF(DAY,LT.MTCTOF)THEN HCHDAY=DAY+26+EGGS(CAY) FISE IF (DAY\_LT.MTCTOF)THEN HCHDAY=DAY+26+EGGS(DAY) ELSE HCHDAY=220 END IF D0 17 I=DAY,HCHDAY,1 J=DAY WILL(I.J)=PARTKL CONTINUE FSTDAY=CAY-DAYCNT D0 11 L=FSTDAY.MAXTAY.1 K=DAY TODAKL=TODAKL+KILL(K.L) CONTINUE DAYCNT=CAYCNT+1 KROUND=KROUND+TCDAKL IF (DAY.GT.MTCTOF)THEN ADJKIL=NINT(KKOUND) IF (ADJKIL.GE.1)THEN KROUND=0 FND IF END IF END IF 10 11 END IF END IF IF(DAY.LE.MTCTOF)THEN IF(KROUNC.GE.1.)THEN REPEAT CONTINUE ADJKIL=ADJKIL+1 KPOUND=KROUND-1 IF(KROUND.GE.1.) GO TO 12 UNTIL(KPOUND.LT.1.) ELSE END IF END IF C 12 C С IF(ADJKIL.GE.1.)THEN IF(HENLAY.GT.G.OR.HENINC.GT.O.)THEN PROPOR=REAL(HENLAY)/(REAL(HENLAY)+PEAL(HENINC)) IF(PROFOR.LT..GGG01)THEN LAYKIL=0 INCKIL=ADJKIL ELSĒ IF (PROPOP.EG.1.) THEN LAYKIL = ADJKIL INCKIL=C ELSE IF(CHNGKL +EQ + 1)THEN LAYKIL = ADJKIL CHNGKL = CHNGKL + 1 END IF

```
END IF
C
                                                   IF (LAYKIL.GF.1)THEN

STRTKL=NINT(FANF()+KEAL(NOBDSF-1))+1

NOUE=STRTKL

REPEAT

CONTINUE

IF (LAYING(NODE,1)+LE+1)THEN

TAKEN=TAKEN+1

TOTIAK=TOTTAK+1

IF (TOTTAK-E3.10)THEN

LAYING (NODE+1)=LAYHED

LAYING (NODE+1)=LAYHED

LAYING (NODE+2)=0

LAYING (NODE+3)=0

LAYING (NODE+5)=0

LAYING (NODE+5)=0
ç
30
                                                                                                                                                                                                                                                                                                                                                                                                                                                                                  ٠
                                                                                                                                               FLSE
LAYING (NODE +2)=0
LAYING (NODE +3)=0
LAYING (NODE +4)=0
                                                                                                                   END IF.

END IF

IF(NODE+LT+NOBDSP)THEN

NODE=NODE+1
                                                                                                                ELSE
NODE=1
END IF
IF (NODE •NE •STPTKL •AND •TAKEN•LT•LAYKIL) GO TO 30
                                                       UNTIL
END IF
 С
   С
                                                        IF (INCK IL .GE .1)THEN

STRTKL =NINT(RANF() + FEAL (NOBDSP-1))+1

NODE = STFTKL

REPEAT

CONTINUE

IF (INCRAT(NODE, 1).LE.-1)THEN

TAKEN=TAKEN+1

TOTTAK=TOTTAK+1

IF (TOTTAK.E0.10)THEN

DEDHEN=DEDHEN+1

TOTTAK=0

FLSE
 Ç,
                                                                                                                                           DEDHEN=DEDHEN+1

TOTTAK=0

ELSE

IF((INCBAT(NCDF,+1)+EQ+-1)+OR+(INCBAT(NODE+1)+FQ+-2))

THEN

IF(DAY+LE+MTCTOF)THEN

IF(DAY+LE+MTCTOF)THEN

IF(TIME=DAY+(INCBAT(NODE+3)-25)

SAVE=CYCLE(CYCHED)=NINT(DAY+HOLD(REAL(TIMF)))

ELSE

CYCLE(CYCHED)=DAY+10

ELSE

CALL PUSH(MTRON+MTPNT+INCBAT(NODE+1))

ELSE

IF(INCBAT(NODE+1)+EQ+-3)THEN

IF(DAY+LE+NVCTOF)THEN

IF(DAY+LE+NVCTOF)THEN

IF(IME=DAY-(INCBAT(NODE+3)-25)

SAVE=CYCLE(CYCHED)=NINT(DAY+HOLD(REAL(TIMF)))

ELSE

CYCLE(CYCHED)=NINT(DAY+HOLD(REAL(TIMF)))

ELSE

CYCLE(CYCHED)=DAY+10

FND IF
                                                                                                                                                                                                                                                                     ELSE
CYCLE (CYCHED)=DAY+10
ENC IF
                                                                                                                                                                                                                                                                         CYCHED=SAVE
                                                                                                                                                                                                                                          ELSE
CALL PUSH(NVICE,NVPNT,-3)
                                                                                                                                                                                                                                          ENDIF
                                                                                                                                                                                                             END
```

```
END IF

FND IF

II.CRAT(NODE+1)=INCHED

INCHAT(NODE+2)=0

INCHAT(NODE+3)=0

I*CHED=NODE

END IF

IF(NODE+LT.NOPDSF)THEN

NODE=100E+1

ELSE

NODE=1

IF(NCDE+NE-STKTKL.AND.TAKEN.LT.INCKIL) GO TO 40

UNTIL

END IF

RETURN

END
         С
                                                                                     •
                                SUBPOUTINE LOKATE(CYCLE+CYCHEN+DAY)
CALCULATE HENS FFING RECYCLED
IMPLJCIT INTEGEF (A-7)
DIMENSION CYCLE(1000:150r)
CYCHEN=
NODE=999
REPEAT
     С
     С
                               REPEAT
CONTINUE
NODE=NOUE+1
IF(CYCLF(NODE).LE.DAY)THEN
CYCHEN=CYCHEN+1
END IF
IF(NODE.LT.1500)G0 T0 10
UNTIL
RETURN
END
     10
   С
                               SURPOUTINE DUKLIN(MTEGG+NVEGG+H20DEV+JEUCKS+HDUKLN)
CALCULATE DUCKLING PROLUCTION
IMPLICIT INTEGEP(A-2)
REAL H2CDEV,DUKLMT
HDUKLN=MTEGG+NVEGG
DUKLMT=0.167+(C.530+H20DEV)
JDUCKS=NINT(REAL(HCUKLN)-(REAL(HDUKLN)+EVKLMT))
RETURN
END
    С
                                                                                                                                                                                                                                                      .
                       SUPROUTINE NEWPOF(NODPAK+NOMTHN+NONVHN+DEDHEN+JDUCKS+ACTKIL+DIF*IL

+BRDPOP+FALPOF+LOKIL+AGERAT,SEXPAT)

CALCULATE POPULATION FCF FALL

IMPLICIT INTEGFF(A-2)

REAL AGEPAT-SEYPAT

HRDPOP=NODRAK+NOMTHN+NONVHN

FALPOP=HPPTPOP+JDUCKS-DEDHEN

ALOKIL=NINT(((1:0-(0.95+REAL(BRDPOP)/REAL(FALPOP)))-0.344)/0.5-)+

REAL(FALPOP)

DIFKIL=ALOKIL-ACTKIL

AGEPAT=REAL(JNUCKS)/(REAL(BRDPOP)-REAL(DEDHEN))

SEXPAT=PEAL(NODPAK)/(FEAL(NOMTHN)+REAL(NONVHN)-REAL(DEDHEN))

RETURN

FND
С
```

