

PART 4

Assessing breeding populations of ducks by ground counts

Alex Dzubin

Contents

- Introduction, 179
- Study areas, 179
 - Roseneath Study Area, 179
 - Kindersley Study Area, 179
- Census methods, 183
 - Roseneath Study Area, 183
 - Dabbling ducks, 183
 - Diving ducks, 183
 - Coding of population components—
Kindersley, 184
 - Kindersley Study Area, 185
 - Analyses of census results, 186
 - Definitions, 186
- Migration, inventory, and population components, 187
 - Spring arrival dates, 187
 - Sex ratios, 187
 - Differential sex ratios and migration, 189
 - Species composition—Roseneath, 190
 - Species composition—Kindersley, 191
 - Indicated pairs and nonbreeding in divers, 191
 - Nonbreeding in dabblers, 192
 - Breeding season dynamics of dabblers—1958, 193
 - Mallard, 195
 - Pintail, 197
 - Widgeon, 197
 - Shoveler, 197
 - Gadwall, 198
 - Blue-winged teal, 198
 - Optimum census periods, 198
 - Estimates based on different components, 199
 - Daily change in population components, 200
 - Seasonal variability of walking and vehicle census, 201
 - Walking census, 201
 - Vehicle census, 203
 - Time of day and variability of estimates, 204
 - Pond numbers and breeding pair populations, 205
 - Duck census techniques, 207
 - Components counted as indicated pairs: a review, 208
 - European census methods, 210
 - Appraisal of factors influencing inventories, 211
 - Unmated males and the census, 211
 - Sex ratio correction factors, 212
 - Late influxes of pairs, 212
 - GFAC, ARF, and TBF and the census, 213
 - Pair bond duration and the census, 213
 - Grouped drakes and the census, 214
 - Optimum census periods, 215
 - Number of seasonal counts required, 216
 - Time of day for counts, 216
 - Duck and pond distribution, 217
 - Recommendations for block study area census, 218
 - Grassland, 218
 - Parkland, 221
 - Behaviour and census, 222
 - Supplementary data required, 223
 - Summary, 224
 - Acknowledgements, 225
 - Literature cited, 226

Introduction

Waterfowl inventories taken during the breeding season are recognized as a basic technique in assessing the number of ducks per unit area. That waterfowl censusing is still an inexact technology leading to divergent interpretations of results is also recognized. The inexactness stems from a wide spectrum of factors that include weather, breeding phenology, asynchronous nesting periods, vegetative growth, species present and their daily activity, previous field experience of personnel, plus others (Stewart *et al.*, 1958; Diem and Lu, 1960; Crissey, 1963a). In spite of the possible errors, accurate estimates are necessary to our understanding of production rates of all North American breeding waterfowl. Statistically adequate censuses of breeding pairs and accurate predictions of young produced per pair still remain as two of the primary statistics in determining yearly recruitment rate of species breeding in particular units of pond habitats. Without precise breeding pair and production data, the problems involved in describing the reproductive potential of any species and its environmental or density-dependent limiting factors cannot be adequately resolved.

The purposes of this paper are to (1) describe methods used to estimate yearly breeding pair abundance on two study areas, one in Manitoba and the other in Saskatchewan; (2) assess the relative consistency, precision, and accuracy of pair counts as related to the breeding biology of duck species; and (3) recommend census methods that can more closely approximate absolute populations breeding in parkland and grassland habitats.

Scientific names of each duck species are from the A.O.U. Check-list (1957) except that both American widgeon and shoveler are considered species of *Anas* after Johnsgard (1965). Widgeon is used synonymously with American widgeon.

Study areas

The comparative study of census methods in relation to waterfowl ecology and behaviour was made on two partially cultivated blocks of pond habitat: one, the Roseneath Study Area in the parkland of Manitoba, 9 miles south of Minnedosa; and the other, the Kindersley Study Area in the grassland of Saskatchewan, 12 miles southwest of Kindersley. Field work was conducted in Manitoba from 1952 through 1955 and in Saskatchewan from 1956 through 1959.

Roseneath Study Area

This 895-acre block is part of the characteristic 4,000-square-mile pothole country of southern Manitoba. The topography is of a knob-and-kettle type with sloughs, ponds, or potholes located in the depressions (Fig. 1).

One hundred and eighty-one basins were located on the area, varying in size from 0.03 to 10.5 acres. The average basin size was 0.70 acre. Of the total basins, 141 (78 per cent) were less than 1 acre in size (Table 1). The emergent vegetation of potholes varied with land use and previous water levels; the dominant plants were white-top (*Scolochloa festucacea*), sedge (*Carex* spp.), cattail (*Typha latifolia*), and bulrush (*Scirpus acutus*, *S. validus*, *S. paludosus*). The uncultivated upland areas contained clumps of aspen (*Populus tremuloides*) and bur oak (*Quercus macrocarpa*). The shrub layer was primarily snowberry (*Symphoricarpos occidentalis*) and wolfberry (*Elaeagnus commutata*). Willow clumps (*Salix* spp.) of various heights were common around the shore lines of some 20 ponds. Brome grass (*Bromus inermis*) was common on all road edges.

The soils were predominantly northern black earth. Precipitation was variable, an average of 18 inches falling annually, much of it during the summer growing season. The frost-free period was usually less than 100 days. Approximately 60 per cent of the total block was cultivated to cereal crops, 15 per cent was made up of water areas, and the remainder was in permanent pasture, fence rows, farm yards, aspen-oak bluffs, and unutilized pond edges. More complete descriptions of the Manitoba parkland and study area, in particular, are given by Kiel (1949), Evans (1949), Evans, Hawkins, and Marshall (1952), Dzubin (1954), and Bird (1961).

Kindersley Study Area

This area of 6,720 acres of partially cultivated, grassland-pothole habitat formed part of a delineated waterfowl survey block, Stratum A-west (Crissey, 1957, 1963a). The area lies between the pure grain-farming regions of central Saskatchewan and the mixed grain farm - grassland regions of the drier western habitat, near the Alberta-Saskatchewan border. Surface geology is a complex of glacial lacustrine clays, silt and sand deposits, and re-sorted till deposits. The topographic features are gently to moderately rolling with the low areas filling with spring snow-melt waters.

Figure 1 Pond-basin distribution on the Roseneath Study Area.

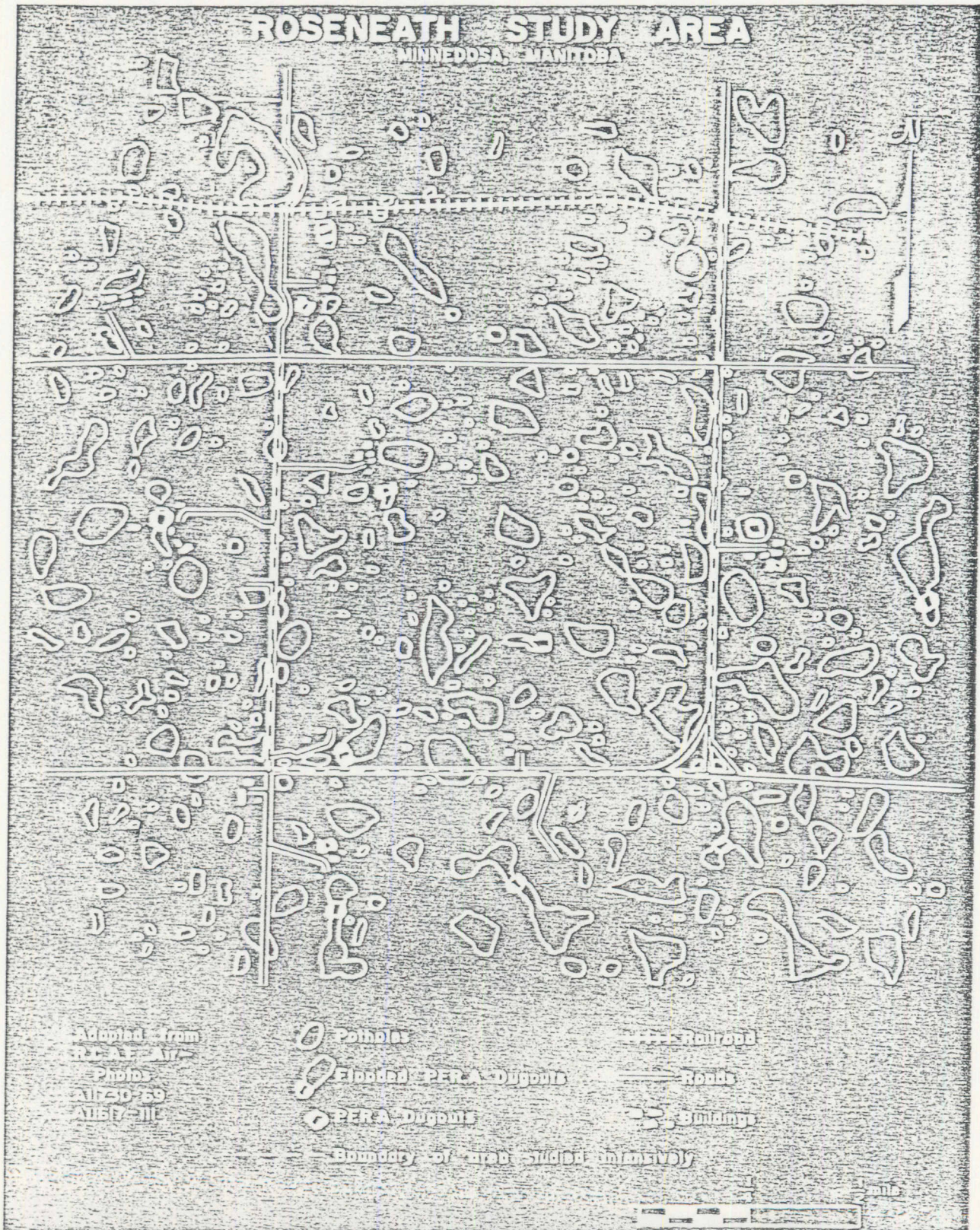
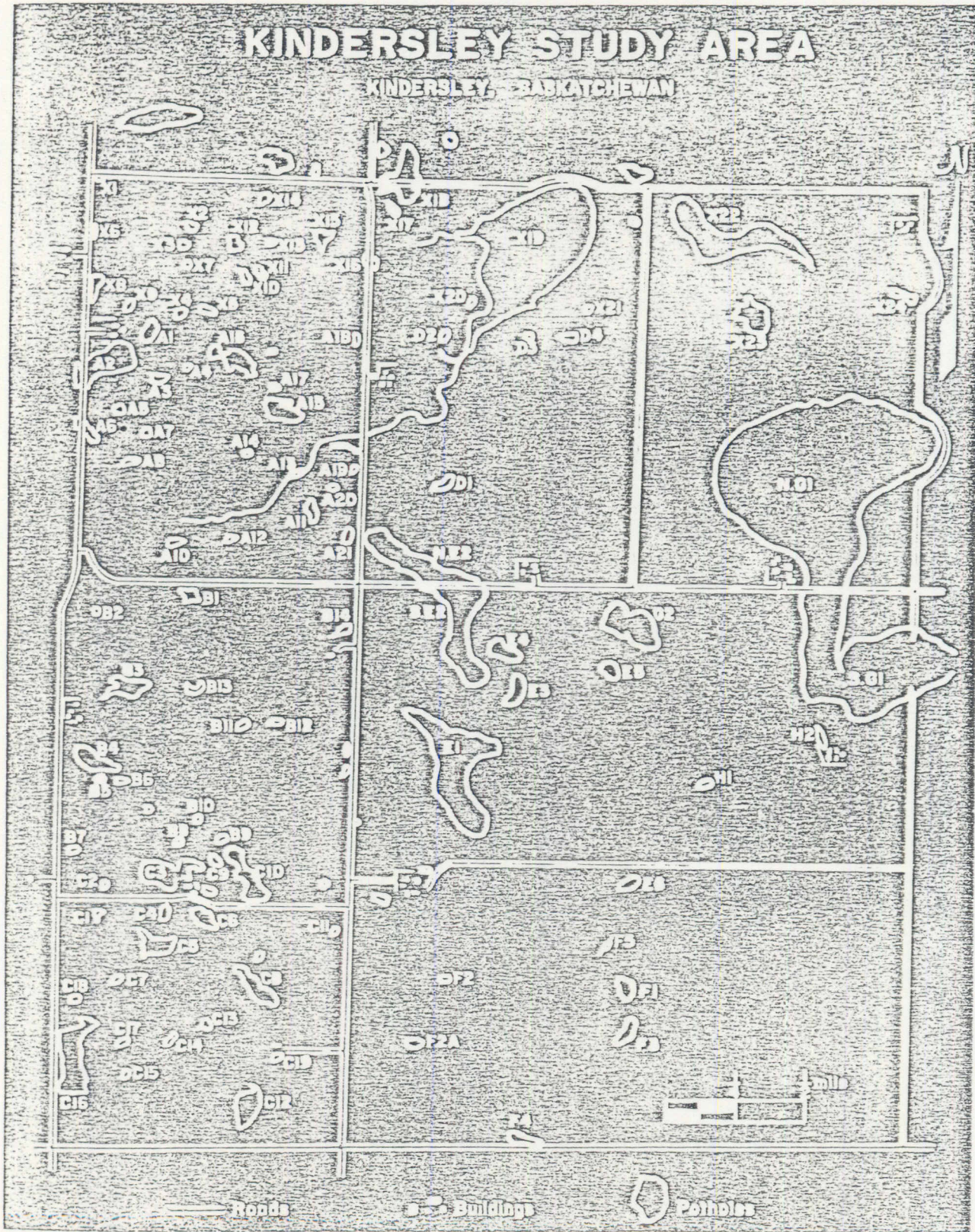


Figure 2 Pond-basin distribution on the Kindersley Study Area.



detailed descriptions see Mitchell, Moss, and Clayton (1944), Coupland (1950, 1961), Boughner, Longley, and Thomas (1956), and Gollop (1965).

Census methods

Because of poor visibility of pairs in the heavily vegetated parkland ponds, and because of the relatively large (10.5 square miles) study block in the grassland, two different census methods were adopted to assess the abundance of breeding pairs.

Roseneath Study Area

Dabbling ducks

Each pond on the 895-acre study block was visited a minimum of four times during a 7- to 10-day period when most of the early nesting pairs of mallards and pintails were in the laying or early incubation stages. Because of yearly variations in phenology, the census period varied, but was usually between May 5 and May 25. The exact locations on ponds of pairs, lone drakes, and groups of five or less drakes were plotted on a base map. If a pair or lone drake was observed on or near the same pond on three out of the four counts, a breeding pair of that species was "assigned" to that area. This method was similar to the one proposed by Evans and Black (1956) to test "constancy" of pond use. It is also similar to a method in use by Kirsch (*in litt.*) on the Woodward Study Area, North Dakota. Counts were conducted in morning and late evening hours when many hens were off their nests for recess periods. A comparable census was conducted 2 to 3 weeks later when most of the late nesting dabbling species—widgeon, gadwall, blue-winged teal, shoveler, and green-winged teal—were also in the laying or early incubation stages. Again pairs were assigned to a particular pond or localized area. Where the number and species of pairs breeding in a locality was doubtful, 2 to 3 hours of observation on 4 or 5 consecutive days helped resolve the questionable count. In short, the accuracy of the census depended on an intimate seasonal knowledge of the pairs continually utilizing a localized area and on the assessment of these birds as indicated breeders. Because the study block was small and home ranges of many pairs would encompass all or parts of it (Sowls, 1955; Dzubin, 1955), I also periodically censused pairs in the quarter-sections surrounding the study area to determine populations. Pairs were arbitrarily assigned to the study area only if the

drake's or pair's waiting area (Hochbaum, 1944; Sowls, 1955; Dzubin, 1955) was located within its boundary. Censuses of a small block-type area, such as the 895-acre Roseneath Study Area, do not lend themselves to close approximations of breeding pair numbers as the ponds, upland and even pair populations form an integral part of a much larger complex of habitat surrounding the block. As such, the assigned population is an estimate of the pairs utilizing ponds on the study block as waiting areas and does not include the pairs breeding in its immediate environs and using the study area ponds periodically.

Diving ducks

Early in the study I concluded that ground census of diving ducks—canvasback, redhead, lesser scaup, and ruddy ducks—utilizing various ponds would not adequately estimate breeding members. Diver pairs, except ruddy ducks, tended to aggregate on particularly deep ponds that I named "primary waiting areas" (Dzubin, 1955), and to fly to surrounding smaller ponds for nesting, feeding, and loafing. On the study area, two such congregating ponds served 15 to 25 pairs that nested on the block and ponds surrounding it. A census of pairs and lone, unmated drakes on such primary waiting ponds could not be used to estimate pairs actually breeding on the block. Canvasback and redheads have maximum home range sizes of 2 to 4 square miles. Such mobile species with large ranges do not lend themselves to adequate census on a small block. Lesser scaup are not as mobile while ruddy ducks tend to be sedentary. Some redhead hens were semi-parasitic, some were completely parasitic, while others laid normal clutches (see Weller, 1959). The distorted sex ratio in all divers and especially scaup (Bellrose *et al.*, 1961) made counts of diver lone males to indicate pairs, meaningless. The secretive habits of ruddy ducks also made analysis of observational data difficult. Therefore, diver populations were censused through a nesting study, wherein all emergent cover was periodically searched for over-water nests. The maximum number of viable, destroyed, and deserted nests found during the peak breeding period was used to estimate the breeding population on the study block.

Several basic assumptions were made in arbitrarily assigning breeding pair numbers to the study block:

1. That lone drakes or pairs of dabbling ducks localize their breeding activity to one or more ponds and are consistent in their use of waiting areas. Previous studies on marked birds had shown that all breeding pairs restrict their activity during the prenesting, laying, and early incubation periods (Sowls, 1955; Dzubin, pers. obs.). However, much individual variation in activity localization within any species occurs, and species differ in hourly and daily mobility and home range sizes (Sowls, 1955; Dzubin, 1955; Evans and Black, 1956). Sowls (1955: 54-57) has reported that on a ditch near a marsh much interchange of pairs between the same waiting site occurred through the day. I noted more interchange of waiting sites under dense pair populations of the grassland than under less dense populations of the parkland.

2. That any ingress of pairs onto the block was counterbalanced by a similar egress of the same number and species of pairs out of the study area. This is the most difficult assumption to assess, in the light of the wide home range size of pintails, mallards, and divers. However, under the low population levels with which I worked, assumption (1), above, was considered to be valid.

3. That all pairs counted on the block remained there to nest and that all species present bred. I noted that pairs were occasionally displaced by other pairs or remained on the study area for 1 to 2 weeks without any nesting attempt. This was especially true of a small number of late nesting gadwall and widgeon pairs that tended to move off the area as soon as the nest site was chosen away from the study block. There was no evidence of nonbreeding pairs of any species in the parkland, except in the case of parasitic redheads.

4. That turnover of pairs was minimal. Hochbaum (1944: 158) and Smith and Hawkins (1948) discussed the possibility of late nesting pairs moving into an area and not being enumerated by a census conducted during one interval. Almost yearly I noted an influx of five or six mallard pairs in late May or early June. Drakes of such pairs were brightly plumaged, unlike the drab males that had been seen in the area for the previous 2 weeks. These pairs appeared to be late breeders, nesting for the first time. In the population assessment, they were not considered to be breeding pairs over and above those cen-

sused in mid-May. As I could not determine if they were new breeders or reneesters, I again assumed that an equal number of reneesting mallards left the area to breed elsewhere. Acceptance of this assumption probably led to underestimation of seasonal population sizes each year.

5. That all diver nests were located in the emergent vegetation of study area ponds. This assumption was considered valid as all emergent vegetation was checked for nests at 2-week intervals. Any diver pairs that utilized the study area as a part of their home range, and nested on a pond immediately off the area, were not counted.

At best, estimates taken from direct ground counts of pair numbers breeding on a small block of parkland habitat should be considered relatively imprecise approximations of seasonal breeding pair populations. The estimation of absolute breeding pair numbers per unit area remains an inexact technique, subject to many vagaries of species behaviour, visibility, mobility, and seasonal nesting chronology.

Coding of population components—Kindersley

All data were coded by a system adopted after a U.S. Bureau of Sport Fisheries and Wildlife ground-census code, i.e., 1/0 = pair, 0/1 = lone male, 3/2 = 3 pairs and 2 lone males, 3:0 = 3 grouped males, 5:5 = 5 grouped pairs, 0/F = lone female, 0:4 = 4 grouped females (W.H. Kiel, *in litt.*).

Although Hochbaum (1944: 85) recommended that only territorial pairs and lone, waiting drakes be censused as breeding birds, he described seven categories of ducks found in a breeding marsh from April to early July: (1) unmated ducks not yet courting, (2) unmated ducks in prenuptial courtship, (3) mated pairs, (4) novice drakes, (5) sexually active unmated males, (6) summering drakes, and (7) unsuccessful or nonbreeding females.

For counts of dabbling species on the potholes of the Kindersley Study Area the following 10 categories were adapted for use after Hochbaum's components:

1. *Resident pairs*—lone pairs on ponds, or pairs spaced over 15 feet apart along sections of shore line. These were apparently settled, dispersed nonmigratory birds.

2. *Grouped pairs and drakes*—aggregated pairs or pairs and drakes that behaved as flocks and were not spaced. They were apparently migrating individuals, not yet settled or dispersed.

3. *Breeding-season groups*—aggregations of 2 to 20+ males and one hen on ponds. Birds were assigned to either (a) "group flights associated with courtship" (GFAC), in April and early May, if males were giving displays and hens were "inciting", i.e., "spring courting flight" of Dzubin (1957); or (b) "attempted rape flights" (ARF), if drakes harassed lone hens which gave the repulsion call (Dzubin, 1957; Raitasuo, 1964; McKinney, 1965). In mallards and pintails these latter flights were seen after May 5, at a time hens start to incubate. For other species they were generally recorded after May 25. Birds in "three-bird flights" (TBF), i.e., territorial pursuits, were also noted. If the pursuing drake returned to the pond under observation, he was recorded as a lone drake. If the chased pair landed in an already censused pond, it was also recorded.

4. *Postbreeding-season groups*—aggregations of males and two or more hens which behaved as a unit. These groups were usually observed after June 15. Such flocks of drakes and pairs were considered to be in postbreeding condition and not part of the breeding population.

5. *Lone drakes*—drakes that were spaced over 15 feet from other drakes on waiting stations. These drakes were generally observed through the laying and early incubation periods. The distance separating drakes varied with phenology of season and the species.

6. *Grouped drakes, five or less*—drakes associated with other drakes in small, cohesive aggregations of two, three, four, or five. These groups were observed in mallards and pintails from late in the laying period through the mid-incubation period, April 24 through June. In other dabblers they were seen from mid- to late incubation, beginning May 20 through June. Small groups of unmated drakes, two to five in number, of all species, were occasionally recorded through April and early May.

7. *Grouped drakes, more than five*—aggregations of more than five drakes. They were usually observed in the late incubation or postbreeding periods.

8. *Lone hens*—hens not associated with drakes. This category included hens that had just left their nests, after laying or during incubation recesses, and had not yet rejoined their drakes. They made up less than 4 per cent of any population count in May and early June but were

more common in late June after drakes had left for the moulting grounds.

9. *Grouped hens*—two or more hens in aggregations that behaved as units. They were observed in the postbreeding period after June 15 and to July 10. They included hens that had either lost clutches or had abandoned near-flying broods. Rarely would two or more incubating hens on recess from the nest be seen together. They were not considered pairs, even though their drakes may have already abandoned the home range.

10. *Drake-hen ratios*—where divers, and occasionally migrating dabblers, were associated in loose aggregations, and pairs and lone drakes could not be separated, counts were lumped and recorded as a ratio of drakes to hens, e.g., 12:9.

Kindersley Study Area
Direct counts of all ducks were used to estimate population levels on the grassland study block. Because of staggered breeding seasons and differential times of migration and nesting of each species, a number of counts were conducted through April, May, and June. Few breeding pairs or lone drakes of any species were recorded after July 15.

In 1956, the 10.5-square-mile study area was divided into three sections. All of the "indicated" pairs on the ponds of each section were counted by two men who walked together to each pond. Although an attempt was made not to flush pairs, it was unavoidable on small, open ponds where some pairs tended to flush as far as 200 to 300 yards away. Pair counts made on ponds in the western third of the study area showed that from 20 to 45 per cent of the pairs were flushed. Pairs or drakes seen to land in a pond not already tallied were subtracted from the pond totals. However, some censusing of previously counted pairs undoubtedly occurred. The magnitude of the duplication error was unknown and variable. However, the consistency of counts taken in mid-May was high, and comparison with nests found, especially for the major breeding species (i.e., mallard), showed no wide discrepancies. Counts were conducted from 0530 to 1100 hours, M.S.T., at approximately 7-day intervals from May 3 to June 11.

From 1957 to 1959, inclusive, breeding pair counts were made with binoculars or a 20× telescope from a vehicle that was driven to a point overlooking each pond. Fewer than 5 per cent of all ducks were flushed. Approximately 22 miles

were driven during the census of the 10.5-square-mile block. Censuses were generally conducted on bright days when wind velocities were below 15 mph. Two censusers working together were able to survey all wet ponds between 0800 and 1200 hours. I had determined that pairs of most species were least mobile during this period. Fewer than 15 of the 114 pond basins contained dense stands of dried emergents (*Carex*, *Scirpus*, *Beckmannia*, or *Glyceria*) in which pairs could secrete themselves. It was generally after May 20 when emergent vegetation grew to a 6- to 8-inch height, and therefore no attempt was made to "beat-out" ponds. Near emergent-rimmed ponds, the slamming of the car door or sounding of a horn was sufficient to alert the birds enough to make them visible for censusing. Again counts were made at 5- to 10-day intervals from early April to mid-June.

As on the Roseneath Study Area, census of pair and drake divers was not considered an adequate measure of the number of pairs breeding on the study block. Therefore, data on breeding divers were obtained from an associated nesting study. A viable, hatched, or predator-destroyed nest was considered evidence of a breeding pair.

To ensure that dabbling censuses were conducted at an optimum period, a similar nesting study was simultaneously conducted to determine breeding season chronology. Census dates were arbitrarily chosen to ensure coverage during optimum breeding periods for early nesters, mallards and pintails; intermediate nesters, widgeon and shovelers; and late nesters, blue-winged teal and gadwall.

Analyses of census results

Census results from each survey made during the optimum breeding interval for each species (i.e., when the greatest proportion of hens of pairs were laying, incubating, or in reneating breeding phases) were lumped and an average breeding pair figure calculated. All mallard and pintail pairs, lone drakes, grouped drakes, and grouped drakes in group flights associated with courtship and attempted rape flights, counted before May 20, were considered breeding pairs. For widgeon and shoveler, all of the above categories were considered breeding pairs if censused before June 5, while for blue-winged teal and gadwall all of the above categories were considered breeding pairs if noted before June 10. Lone hens were not added to the population

counts as I assumed all hens to be paired to one of the lone or grouped drakes already enumerated on the study block. Since fewer than four lone hens of any species, or less than 4 per cent of the indicated pairs counted from 1956 to 1959, were ever encountered on any census, any error in deleting this component would be small. The average number of pairs was termed the "mean indicated breeding population".

Sex ratio data from Bellrose *et al.* (1961) had shown that among most dabbling species there is a preponderance of drakes immediately prior to the breeding season. I collected similar data during the prenesting interval. To ensure that pair census data were not weighted with the unmated-male segment, a correction factor using the average prelaying drake-to-hen ratio for each species was applied to the indicated population. The breeding-pair population figure was then termed the "sex-ratio corrected population". Sex ratio corrections were applied only to dabbling figures as diver populations were assessed from nesting studies. Murdy (1962) has more recently applied such corrections to spring censuses of lesser scaup and ring-necked ducks at Yellowknife, N.W.T.

In 1956 and 1959, in order to test stability of population and reproducibility of census counts, four or five censuses were made during the period when the greatest proportion of pairs were in the prenesting, laying, or incubation periods. In 1959, periodic censuses were conducted three times a day on May 11, 15, and 16 to determine daily variability in the census and percentages of pairs, lone males, and grouped males during any one time interval.

Definitions

To clarify further what population components were used in breeding-pair counts, the following definitions will be followed throughout this paper:

Assigned breeding population—The dabbling breeding population assigned to a unit of habitat, usually 160 acres. The population was determined by plotting the location of pairs and lone drakes on a map during four or five censuses. If a pair or lone drake of any species was seen on a particular pond three or four times, it was assigned to that pond or quarter-section.

Indicated breeding population—The population estimated from counts of various components.

1. Mallards and pintails: Prior to May 20, all

lone males, pairs, all grouped males, and males in aerial flights temporarily on ponds censused were considered pairs. Thereafter, all lone males, pairs, grouped drakes of five or less, and aerial flights temporarily on ponds were considered evidence of breeding pairs. After May 20, groups of six or more males were considered postbreeding birds.

2. Widgeon and shoveler: Prior to June 5, all lone males, pairs, all grouped males, and all males in aerial flights on ponds censused were considered pairs. Thereafter, only grouped males of five or less in number, lone drakes, drakes in aerial flights, and pairs were considered breeding pairs. Groups of mated males, usually in two's and three's, were rarely observed until mid- or late incubation. Groups of unmated males were, however, more common.

3. Gadwall and blue-winged teal: Same as widgeon and shoveler except cut-off date of June 10 was used. Again, associations of mated males were uncommon until mid-incubation.

4. Divers: All viable, hatched, destroyed, or deserted nests found, which were initiated prior to June 15, were considered evidence of a breeding pair unless field observation indicated a nest to be a re-nest. With ruddy ducks the cut-off date was extended to June 20.

Sex-ratio corrected population—This was the mean indicated breeding population taken during four or five censuses, during the time most breeding pairs were in the prelaying, re-nesting, laying, or incubation stages, to which a sex-ratio correction factor as found in Table 3 was applied. The correction factor was determined from spring counts of the sex ratio of each species before the first eggs were found. It reduced the indicated pair population by the proportion of unmated drakes found in the species. The sex-ratio corrected population was considered to be the best estimate of the absolute breeding population of a study area.

Migration, inventory, and population components

Spring arrival dates

Most dabbling species arrived at both the Rose-neath and Kindersley districts before the diving ducks (Table 2). Of the dabblers, pintails were the first species noted, usually by the last week in March. They were followed by mallards, widgeon, green-winged teal, shoveler, gadwall,

and blue-winged teal during the first to third week of April. Redheads and canvasback arrived at about the same time as green-winged teal, and shovelers were usually observed 1 to 4 days before lesser scaup. Ruddy ducks and white-winged scoters, which rarely nested at Kindersley, were the latest species to migrate. The first migrant pairs of pintails and mallards were associated with the first appearance of snow-water pools in fields. Arrival dates were about 1 week earlier at Kindersley than at Roseneath. Migrants arrived at Roseneath 1 to 2 weeks later than dates given for southern Alberta by Keith (1961: 42) and for Delta, Manitoba, by Sowls (1955: 12). The species sequence is about the same for all areas. Arrival dates of all species given by Ellig (1955: 11) for Montana are generally 1 to 2 weeks earlier than the Kindersley arrivals. Keith's arrival dates for all species in 1956 are 5 to 8 days earlier than dates from Kindersley.

Peak influxes of all species were generally 1 to 2 weeks later than first arrivals. Major migrations were associated with favourable weather, i.e., southerly winds and temperatures above 30°F. Prolonged April cold periods tended to dampen movements until early May. In the cold spring of 1954, Gollop and Lynch (1954: 47) recorded flocked mallards and pintails as late as May 10, after which they dispersed. Gollop (1954: 65) has also described the delaying effect of a mid-April cold snap on migration and nesting in the Kindersley district. Except for exceptionally warm springs with few intervening cold snaps when migrants moved into the study areas, en masse, over 7 to 10 days, e.g., 1955, two or three influxes of migrants occurred over a 3-week period. Few migrants were recorded as late as 30 days after the first arrivals were noted. At Kindersley from 1956 to 1959, most mallards and pintail pairs were settled by May 5 whereas all other species, except lesser scaup and ruddies, terminated migration by May 20. At Roseneath, a few migrating mallard flocks were recorded as late as May 12. The last migrant gadwall and blue-winged teal were noted by May 25 while a small number of lesser scaup moved through until early June.

Sex ratios

Sex ratios taken on the Kindersley Study Area before the first clutches were found showed only superficial differences among all dabbling species

(Table 3). Utilizing the binomial probability distribution (Steele and Torrie, 1960), I found no significant difference ($p = >0.05$) in the sex ratio means among all seven dabblers. Similarly, no significant difference existed among the four diver sex ratio means. Yearly comparisons were not particularly valid because of small sample sizes. However, there was a significant difference ($p = <0.05$) between years for lumped samples of lesser scaup, i.e., 1956 plus 1957 vs. 1958 plus 1959; the percentage of males ± 95 per cent confidence interval was 56.8 ± 2.6 and 63.3 ± 1.6 . For all species (Table 3), the sex ratios do not differ significantly ($p = >0.05$) from those shown for Manitoba by Bellrose *et al.* (1961: 416). I also found no significant difference ($p = >0.05$) for all species between the sex ratios gathered at Kindersley and those presented by Bellrose *et al.* (1961: 428) for the mid-continent breeding grounds, except for lesser

scaup, i.e., 61.1 ± 1.4 vs. 66.1 ± 2.1 , and assuming sample sizes in Bellrose *et al.* were in the order of 2,000.

On an Alberta grassland breeding ground, sex ratios for five late nesting species (Keith, 1961: 43) were slightly higher for gadwall (113:100), blue-winged teal (144:100), lesser scaup (163:100) and ruddy duck (203:100) but lower for redhead (127:100) than comparable data in Table 3. None of these ratios was significantly different ($p = >0.05$) from those taken at Kindersley.

All dabblers including mallards and pintails, the most common breeders at Kindersley, did not show any significant departure ($p = >0.05$) from a 50:50 ratio. Yet, Bellrose *et al.* (1961) showed a consistent preponderance of drakes in spring counts taken of these two species throughout North America. Other authors have also shown consistent deviations favouring males. Sex

TABLE 2 Recorded spring arrival dates of first duck pairs, 1953 to 1959

Species	Rosenearth District				Kindersley District				Range in days
	*1953	1954	1955	Range in days	1956	1957	1958	1959	
Pintail	Mar. 29	Apr. 8	Apr. 1	10	Apr. 1	Mar. 25	Mar. 29	Mar. 20	12
Mallard	Mar. 31	Apr. 8	Apr. 2	8	Apr. 4	Mar. 25	Mar. 29	Mar. 23	12
Widgeon	Apr. 23	Apr. 12	Apr. 14	11	Apr. 10	Apr. 3	Apr. 4	Mar. 31	10
Green-winged teal	Apr. 21	Apr. 16	Apr. 10	11	Apr. 17	Apr. 18	Apr. 6	Apr. 8	12
Showeler	Apr. 28	Apr. 18	Apr. 20	10	Apr. 12	Apr. 14	Apr. 4	Apr. 14	10
Gadwall	Apr. 27	Apr. 25	Apr. 17	10	Apr. 21	Apr. 15	Apr. 18	Apr. 11	10
Blue-winged teal	Apr. 29	Apr. 25	Apr. 17	12	May 3	Apr. 25	Apr. 24	Apr. 21	12
Canvasback	Apr. 21	Apr. 19	Apr. 12	9	Apr. 16	Apr. 15	Apr. 12	Apr. 11	5
Redhead	Apr. 27	Apr. 18	Apr. 17	10	Apr. 18	Apr. 15	Apr. 10	Apr. 10	8
Lesser scaup	Apr. 24	Apr. 19	Apr. 13	11	Apr. 16	Apr. 15	Apr. 10	Apr. 15	6
Ruddy duck	May 5	Apr. 13	Apr. 25	18	May 14	May 12	Apr. 29	Apr. 21	23

* In 1952 all species were present prior to May 9, except ruddy ducks which were first seen on May 12.

TABLE 3 Sex ratios of ducks, 1956 to 1959, Kindersley Study Area. From counts taken of spaced birds (not migrating flocks) before the first clutches were found

Year	Mallard	Pintail	Widgeon	Gadwall	Showeler	Blue-winged teal	Green-winged teal	Canvasback	Redhead	Lesser scaup	Ruddy duck
	% No. male	% No. male	% No. male	% No. male	% No. male	% No. male	% No. male	% No. male	% No. male	% No. male	% No. male
1956	364 54	— —	179 50	319 53	35 —	113 52	94 51	15 —	98 51	807 55	59 58
1957	— —	— —	312 51	98 51	196 56	225 56	100 57	72 68	139 66	785 59	— —
1958	310 52	393 55	550 53	181 53	148 53	80 54	352 54	24 —	171 57	1133 63.5	97 53
1959	358 53	235 53	493 52	175 51	184 54	104 54	135 55	65 55	370 56	2003 63.2	435 66
Total	1032 52.8	628 54	1534 51.9	773 52	563 54	522 55	681 54	176 61	778 57	4728 61.1	591 63
95% con. int.	± 3.0	± 4	± 2.6	± 4	± 5	± 5	± 4	± 7	± 4	± 1.4	± 4
Mean ratio M:F this study	112:100	117:100	108:100	110:100	119:100	120:100	110:100	159:100	134:100	157:100	172:100
Bellrose <i>et al.</i> * (1961:428)	105:100	119:100	129:100	112:100	123:100	133:100	121:100	174:100	127:100	195:100	211:100
Bellrose <i>et al.</i> † (1961:416)	117:100	142:100	116:100	121:100	139:100	117:100	115:100	132:100	111:100	154:100	—

* Recalculated from Table 34, for Saskatchewan, Minnesota, Manitoba, and North Dakota.

† Recalculated from Table 27, for Manitoba, April 21 to 25 or April 29 to May 7.

ratio means for mallards and pintails from Kindersley are close to those given for Delta, Manitoba, by Hochbaum (1944), i.e., 102:100 for mallards and 109:100 for pintails. For Montana, Ellig (1955: 12) gave ratios of 127:100 for mallards and 107:100 for pintails, in birds censused prior to April 14, 1952. Sowls (1955: 24), summarizing early spring mallard and pintail sex ratios from Delta, gave a mean ratio of 108:100 in favour of males for both species. Counts made by Bue (in Bellrose *et al.*, 1961: 418) in eastern South Dakota prior to April 15, 1950 and 1951 show percentages of mallard drakes of about 53 per cent (113:100) and pintails of 57 per cent (132:100).

Spring sex ratios for dabblers and divers have been published by a number of other authors. Comparisons of published figures with the data shown in Table 3 are not particularly meaningful as published ratios were taken through the spring migration period and are not confined to the breeding grounds. Sex ratio data for many waterfowl species were presented in Bennett (1938), Furniss (1938), Erickson (1943), Hochbaum (1944), Beer (1945), Low (1945), Sowls (1955), Ellig (1955), Johnsgard and Buss (1956), and Moyle (1964). A discussion of the errors involved in gathering and comparing "piece-meal" sex ratio counts is given by Bellrose *et al.* (1961). The Kindersley data, which were gathered in a localized area of the vast breeding grounds, tend to substantiate the views

of many workers that in spring populations of most waterfowl species there is a preponderance of unmated males which I suggest can be counted erroneously as indicated pairs.

Differential sex ratios and migration

Bellrose *et al.* (1961: 412-416) discussed changes in sex ratio related to times of northward migration in many species. Sex ratios are generally more unbalanced in favour of drakes in late spring than in early spring. In the present study with its small samples no such marked seasonal changes in prebreeding sex ratios were noted with any species except lesser scaup. In 1958 when only three lesser scaup nested on the Kindersley area and in 1959 when no breeding was observed, sex ratios taken before May 15 were significantly different (chi square, $p = < 0.05$) from those collected in late May and through June (Table 4). The data, although not affected by increasing number of hens nesting, show an increase in proportion of migrant drakes through early and mid-June. The change may reflect an increasing number of drakes abandoning early nesting hens away from the study block or may suggest that unmated males migrated later, perhaps remaining farther south than mated males.

Changes in sex ratios in favour of males as spring migration progresses have been reported for widgeon and shoveler by Erickson (1943), for green-winged teal by Beer (1945), and for pintail and lesser scaup by Hammond (in Bell-

TABLE 4 Seasonal changes in sex ratios of migrating lesser scaup, 1958 and 1959, Kindersley Study Area

Dates	Migration and prebreeding period				Breeding and postbreeding period			
	April 19 to May 3		May 10 to 15		May 24 to June 6		June 12 to 26	
Year	Number	% drakes	Number	% drakes	Number	% drakes	Number	% drakes
1958*	870	63	346	63	315	73	393	86
(95% con. int.)		(± 3)		(± 5)		(± 5)		(± 3)
Dates	April 21 to May 8		May 11 to 15		May 28 to June 4		June 12 to 17	
Year	Number	% drakes	Number	% drakes	Number	% drakes	Number	% drakes
1959*	861	67	1,142	60.1	439	71	270	84
(95% con. int.)		(± 3)		(± 2.9)		(± 5)		(± 5)

* Sex ratio sig. diff. $p = < .05$. Both periods chi square, 1958 = 25.3, 1959 = 24.5, 1 d.f.

rose *et al.*, 1961: 402). In Manitoba, Hochbaum (1944: 16) noted that although April sex ratios were nearly balanced in mallards and pintails there was an influx of unmated drakes into the marsh in early May, as evidenced by large numbers of "courting parties". In Illinois, Bellrose *et al.* (1961: 414) report that sex ratios were heavily weighted to drakes in mallard, pintail, canvasback, and ring-necked ducks in late February but that the preponderance of drakes declined in March and April. Lesser scaup sex ratio counts given for Manitoba by Kiel (in Bellrose *et al.*, 1961: 416) do not show an upward swing in drakes through June as noted in the present study. However, local differences in sex ratios determined from small samples may not reflect similar changes in the population as a whole over the entire migration or breeding habitat.

Species composition—Roseneath

Mallard, blue-winged teal, and widgeon were the predominant dabbling species, making up an average of 82 per cent of the 105 breeding pairs (Table 5). Ruddy ducks and canvasbacks were the major diving duck species nesting on the area, comprising an average of 75 per cent of the 28 breeding diver pairs. Green-winged teal, gadwall,

and lesser scaup were the least numerous breeding species. Mallards dropped from 54 to 33 pairs over the 4-year span of the study, while blue-winged teal and pintails showed somewhat erratic yearly fluctuations. Major increases in numbers were noted for ruddy ducks, with a recorded increase from 4 breeding pairs in 1952 to 15 pairs in 1955. The ring-necked duck was an uncommon breeder in the area; one pair established a nest in 1954. Species composition of the study area and pairs observed per square mile are similar to those given for the same block by Evans, Hawkins, and Marshall (1952: 38) for the 1951 breeding season. In their study, of the 88 breeding pairs recorded per square mile, mallard, blue-winged teal, and canvasback were again the most common species. For the entire Newdale-Erickson district of west-central Manitoba, Kiel (1951: 56) showed the blue-winged teal, mallard, and lesser scaup as the three most numerous breeding species. For the same area, Pospichal, Cram, and Parsons (1954: 86, 87) showed that from 1949 to 1954, mallard was the predominant breeder followed by blue-winged teal, lesser scaup, and pintail.

TABLE 5 Breeding pair estimates and species composition, Roseneath Study Area, 1952 to 1955

Species	Assigned breeding pairs				4-year average	% species composition	Mean pairs/square mile
	1952	1953	1954*	1955			
Dabblers:							
Mallard	54	49	41	33	44	33.1	31.5
Blue-winged teal	31	27	35	24	29	21.8	20.7
Widgeon	12	13	15	12	13	9.8	9.3
Pintail	11	6	12	7	9	6.8	6.4
Shoveler	4	3	5	3	4	3.0	2.9
Green-winged teal	5	3	5	0	3	2.3	2.1
Gadwall	3	3	2	3	3	2.3	2.1
Subtotal	120	104	115	82	105	79.1	75.0
Divers:							
Canvasback	12	10	10	8	10	7.5	7.1
Redhead	4	10	6	5	6	4.5	4.3
Lesser scaup	1	2	2	0	1	0.7	0.7
Ruddy duck	4	10	14	15	11	8.2	7.9
Subtotal	21	32	32	28	28	20.9	20.0
Total	141	136	147	110	133	100.0	95.0

* Plus one pair of nesting ring-necked ducks.

Species composition—Kindersley

On the grassland study block, mallard and pintail were the predominant breeding species (Table 6). They made up 72 per cent of the mean breeding population for the 4-year period. Dabblers made up 97 per cent of the entire population while divers, chiefly lesser scaup, made up the remainder. No ruddy ducks were found breeding on the area, while one nesting pair of white-winged scoters was recorded in 1958. This area contained an average of 52 breeding pairs per square mile, in contrast to the average of 95 pairs per square mile at the Roseneath study area (Table 5). Although 2 to 12 pairs of white-winged scoters were regularly censused on a 90-acre pond in late May and early June 1956 through 1959, only one pair was recorded nesting near this pond in June 1958.

Major yearly fluctuations in pair numbers occurred with all species. Peak numbers of mallard and pintail pairs (358 and 269, respectively) were found on the area in 1957, a year of drought which probably forced many pairs onto the relatively well-watered study block from the surrounding drought-stricken regions. While mallards and pintails increased in abundance in 1957,

other breeding species decreased. Decreases in breeding pair numbers occurred generally in all species in 1958 and 1959, associated with continuing drought and poor production of young.

Gollop (1954: 71) conducted pair surveys on a sample of 20.5 square miles in the Kindersley-Eston district and determined indicated breeding populations of 75 pairs per square mile in 1952 and 40 pairs per square mile in 1953. Pintails, mallards, shovelers, and blue-winged teal were the predominant dabbler species recorded, while lesser scaup and canvasback made up the greatest portion of divers.

Indicated pairs and nonbreeding in divers

As previously discussed, there is some difficulty in assigning diver pairs to a study area as indicated breeding pairs from ground census. Also, there is no way to differentiate migrating pairs from residents and nonbreeding from breeding pairs (Smith and Hawkins, 1948; Ellig, 1955). A comparison of the mean indicated population with numbers of nesting pairs found on the 10.5-square-mile block showed that only 48 per cent of the indicated population of diver pairs nested in 1956, 38 per cent in 1957, 39 per cent in 1958, and 3 per cent in 1959 (Table 7). Most of

TABLE 6 Breeding pair estimates and species composition, Kindersley Study Area, 1956 to 1959

Species	1956	1957	1958	1959	4-year average	% species composition	Mean pairs/square mile
Sex ratio corrected breeding dabbler pairs							
Mallard	248	358	173	149	232	42.8	22.1
Pintail	182	269	143	43	159	29.3	15.1
Widgeon	75	40	41	35	48	8.9	4.6
Gadwall	44	19	25	23	28	5.1	2.7
Shoveler	30	29	29	23	28	5.1	2.7
Blue-winged teal	38	25	27	16	26	4.8	2.4
Green-winged teal	5	7	3	4	5	1.0	0.5
Subtotal	622	747	441	293	526	97.0	50.1
Nesting diver pairs							
Canvasback	1	0	0	0	<1	<0.1	Tr.
Redhead	4	2	0	0	2	0.4	0.2
Lesser scaup	26	15	12	3	14	2.6	1.3
White-winged scoter	0	0	1	0	<1	<0.1	Tr.
Subtotal	31	17	13	3	16	3.0	1.5
Total	653	764	454	296	542	100.0	51.6

TABLE 7 Comparison of indicated pairs of diving ducks from ground census and observed nesting population, May 20 to June 5, Kindersley Study Area, 1956 to 1959

Species	1956			1957			1958			1959		
	Mean pairs	Nest population	% breeding	Mean pairs	Nest population	% breeding	Mean pairs	Nest population	% breeding	Mean pairs	Nest population	% breeding
Lesser scaup	57	26	46	29	15	52	27	12	44	70	3	4
Canvasback	1	1	100	7	0	0	1	0	0	2	0	0
Redhead	5	4	80	7	2	29	1	0	0	15	0	0
Ruddy	1	0	0	2	0	0	2	0	0	27	0	0
Total	64	31	48	45	17	38	31	12	39	114	3	3

the breeders were lesser scaup. Only one canvasback and six redhead pairs nested, while no ruddy duck nests were found. I concluded that indicated pair populations taken only from pair counts (i.e., omitting all lone or grouped males) during the period when divers should be nesting do not adequately approximate pair numbers actually nesting. Some of the indicated pairs were undoubtedly late migrants, especially ruddy ducks, but observations showed that many pairs of lesser scaup, and to a lesser extent, canvasback and redhead, remained on the area through late June without making any attempt to nest.

Some of the lesser scaup censused may have been nonbreeding yearlings, although McKnight and Buss (1962), after histologically examining 16 ovaries, concluded that most, but not all, yearlings are physiologically capable of breeding. In Manitoba nonbreeding in lesser scaup has been associated with deteriorating habitat conditions and nonflooding of nesting cover (Rogers, 1964). Rogers (1963) also noted that the proportion of hen scaup nesting around four intensively studied potholes decreased from 64 per cent in 1958 to 8 per cent in 1959. In 1960 with a recovery of water levels, 60 per cent of the resident pairs nested. Each year some of the hens failed to nest. In Montana, Smith (1953: 286) also noted an absence of lesser scaup broods in late summer even though pairs were present earlier on his study reservoirs. Similarly, in British Columbia, Munro (1941) suspected that a proportion of the lesser scaup population did not breed but retained their bright breeding plumage into mid-summer. I suggest that, owing to poor habitat conditions, deteriorating water levels, and decrease in pothole numbers, many divers also

became nonbreeders in the Kindersley area from 1957 through 1959, with the lowest ratio of nesting pairs to indicated pairs in 1959.

Nonbreeding in dabblers

Nonbreeding in mallards and pintails has been reported for Alberta by Smith (1961) who concluded that pairs did not breed under deteriorating water conditions due to "physiological and psychological shock". I obtained no direct evidence for nonbreeding of dabbler species because of the difficulty in separating breeders from nonbreeders. However, in 1957, of some 358 indicated mallard pairs censused on the Kindersley Study Area, only 300 nests were located during two complete "beat-outs" of the upland nesting cover. Approximately 20 more nests were estimated to be in stubble fields and fence rows. Either the coverage of nesting habitat was less than 100 per cent efficient, or some pairs nested at over 1 mile from the study block, or 35 to 40 of the immigrant pairs failed to nest. Also, in 1959, a periodic census of gadwall and widgeon pairs indicated that as many as 20 of the 35 widgeon pairs and 14 of the 23 gadwall pairs failed to nest. Loose aggregations of these pairs were seen on two ponds through late May and early June with no evidence of dispersion or laying. Six gadwall hens were collected from flocked pairs outside the study area on June 5. On internal examination four of the hens' ovaries showed ova in various stages of atresia, with no evidence of ovulated follicles present. The other two had apparently attempted to lay, as regressed follicles were noted. The mechanisms involved in nonbreeding under conditions of poor quality habitat and high pair densities are not known.

Breeding season dynamics of dabblers—1958
 Periodic censuses conducted from 0800 to 1200 hours on the Kindersley Study Area throughout the 1958 breeding season showed wide changes in pair, lone drake, and grouped drake categories of each dabbler species (Tables 8a to 8f). A nesting study conducted concurrently gave known reference points for start of nesting, peak laying, first broods, and peak of hatching. The major difference between the early nesting mallard and

pintail population components (Tables 8a and 8b, respectively) and later nesting widgeon (Table 8c), shoveler (Table 8d), gadwall (Table 8e), and blue-winged teal (Table 8f) is the near absence of a grouped drake component in the last four species until the mid- or late incubation period. Also, no major posthatching influxes of the last nesting species were recorded.

A graphic comparison of one example of an early nester, mallard, with an intermediate nester,

TABLE 8a Seasonal census of mallards on Kindersley Study Area, 1958

Date	Pairs	Lone drake	Group sizes of drakes Number of groups						Other ^a	Drakes as % all birds	Indicated population
			2	3	4	5	6-10	10+			
Apr. 4	33	2	1						52	37	
Apr. 12	116	6	1						52	124	
Apr. 19	135	17	0	1					53	155	
Apr. 24	96	62	6	4					66	182	
Apr. 29	71	69	13	1	3				73	187	
May 3	49	64	24	6	1	3		1(6) ^c	80	198 ^b	
May 10	35	55	19	11	2	3		1(7)	85	191	
May 21	52	49	27	13	2	2		1(9)	81	212	
May 24	48	72	21	17	3	1	1(8)		3:1	83 hp ^d	230
May 31	24	47	14	7	3	3	5(35)	4(109)	9:9	90	147
June 6	31	18	6	5	0	1	6(47)	2(39)	19:19	87	81
June 12	12	10	6	1	0	0	2(13)	3(70)	19:19	82	37
June 20	4	3	0	0	0	1	1(6)	1(15)	9:17	67	12
June 26	1	4	1	0	1	0	2(15)	1(14)	10:24	67	11

For all tables, 8a to 8f.

^aBreeding birds in attempted rape flights or postbreeding groups given as a ratio, drakes:hens.

^bOptimum census period, i.e., when population reaches a plateau and is fairly stable.

^cFigures in brackets give exact number of grouped birds.

^dhp = hatching peak.

TABLE 8b Seasonal census of pintails on Kindersley Study Area, 1958

Date	Pairs	Lone drake	Group sizes of drakes Number of groups						Other	Drakes as % all birds	Indicated population
			2	3	4	5	6-10	10+			
Apr. 4	63	8	1	1					55	76	
Apr. 12	84	17	1						55	103	
Apr. 19	112	21							54	133	
Apr. 24	89	46	2	0	1	1	1(6)		20:4	65	174
Apr. 29	49	76	6	5	1	1	1(6)		5:1	78	172
May 3	53	55	13	4	0	2			25:3	76	181
May 10	36	45	11	8	3	2	1(7)		6:1	81	162
May 21	37	39	11	4	5	4	1(9)		3:1	81	150
May 24	36	43	10	10	4	3			7:2	82 hp	160
May 31	21	22	7	6	4	2	4(32)	4(97)	18:13	88	101
June 6	20	14	2	0	1	0	1(6)	2(53)	28:9	82	42
June 12			1				1(8)	1(11)	3:3	89	2
June 20			1	0	1	0			—	—	6
June 26				1			3(20)		100	100	3

TABLE 8c Seasonal census of widgeon on Kindersley Study Area, 1958

Date	Pairs	Lone drake	Group sizes of drakes Number of groups						Other	Drakes as % all birds	Indicated population
			2	3	4	5	6-10	10+			
Apr. 4	1									—	1
Apr. 12	15	2		1						57	20
Apr. 19	43	7								54	50
Apr. 24	62	5							7:1	54	74
Apr. 29	62	2								52	64
May 3	76	5								52	81
May 10	31	4								53	35
May 21	37	18								60	55
May 24	31	25								64	56
May 31	16	25								72	41
June 6	17	15								65	32
											hp
June 12	8	12	1	1	1					78	29
June 20	4	2	0	1				1(11)		83	9
June 26	0	0	1	1			1(6)		4:1	—	5

TABLE 8d Seasonal census of shoveler on Kindersley Study Area, 1958

Date	Pairs	Lone drake	Group sizes of drakes Number of groups						Other	Drakes as % all birds	Indicated population
			2	3	4	5	6-10	10+			
Apr. 4	1									—	1
Apr. 12	0									—	0
Apr. 19	10	2								55	12
Apr. 24	32	3							4:1	54	39
Apr. 29	25	2								52	27
May 3	29	8								56	37
May 10	27	8								56	35
May 21	24	16								63	40
May 24	13	13		1			1(6)			73	35
May 31	7	23								81	30
June 6	6	16	1	2					3:1	75	30
											hp
June 12	1	15	1	1						95	21
June 20	5	5					1(7)			77	10
June 26	0	0							5:1	—	0

TABLE 8e Seasonal census of gadwall on Kindersley Study Area, 1958

Date	Pairs	Lone drake	Group sizes of drakes Number of groups						Other	Drakes as % all birds	Indicated population
			2	3	4	5	6-10	10+			
Apr. 4	—										
Apr. 12	—										
Apr. 19	3									—	3
Apr. 24	9	1								53	10
Apr. 29	6									50	6
May 3	17	1								51	18
May 10	24	1								51	25
May 21	36	6								54	42
May 24	22	4								54	26
May 31	8	16								75	24
June 6	15	12								64	27
June 12	10	6	1	1						68	21
											hp
June 20	4	5	1	1						78	14
June 26				1	1		1(10)		2:2	90	7

TABLE 8f Seasonal census of blue-winged teal on Kindersley Study Area, 1958

Date	Pairs	Lone drake	Group sizes of drakes Number of groups						Other	Drakes as % all birds	Indicated population
			2	3	4	5	6-10	10+			
Apr. 4	—										
Apr. 12	—										
Apr. 19	—										
Apr. 24	3	1							—	4	
Apr. 29	—										
May 3	7	1							53	8	
May 10	27	4							53	31	
May 21	12	9	1						66	23	
May 24	14	21							71	35	
May 31	13	17			1			10:4	71	34	
June 6	5	27	6						90	44	
June 12	6	14	1						79	22	
									hp		
June 20	3	6							75	9	
June 26	2	4		1	2				89	17	

widgeon, shows the lack of grouped widgeon males until the June 12 count, while mallard groupings are evidenced as early as April 24 (Figure 3). Optimum census periods overlapped in the two species during mid-May.

Mallard

Even before the start of egg laying between April 12 and 15, a number of lone and grouped drake mallards were observed (Table 8a). These were probably unmated males. On April 29 the ratio of pairs to lone males was about 1:1, but thereafter pair numbers tended to decrease and lone males increased until a ratio of 1:1.5 was recorded at the hatching peak, about May 21. The grouped drake component increased during this 22-day interval as more hens started to incubate.

During the peak laying interval of April 24 to 29, most grouped drakes were found in aggregations of two. As the incubation period continued, more groups of three to five were observed. During early May when first nesters were incubating, few aggregations of more than five drakes were seen. Before May 21 only three groups of more than five males were observed, one each on April 29, May 10 and May 21. During the censuses prior to May 24 no group flights associated with courtship or attempted rape flights were recorded, although a number were noted on the area in the afternoons when laying and incubating hens returned to waiting areas.

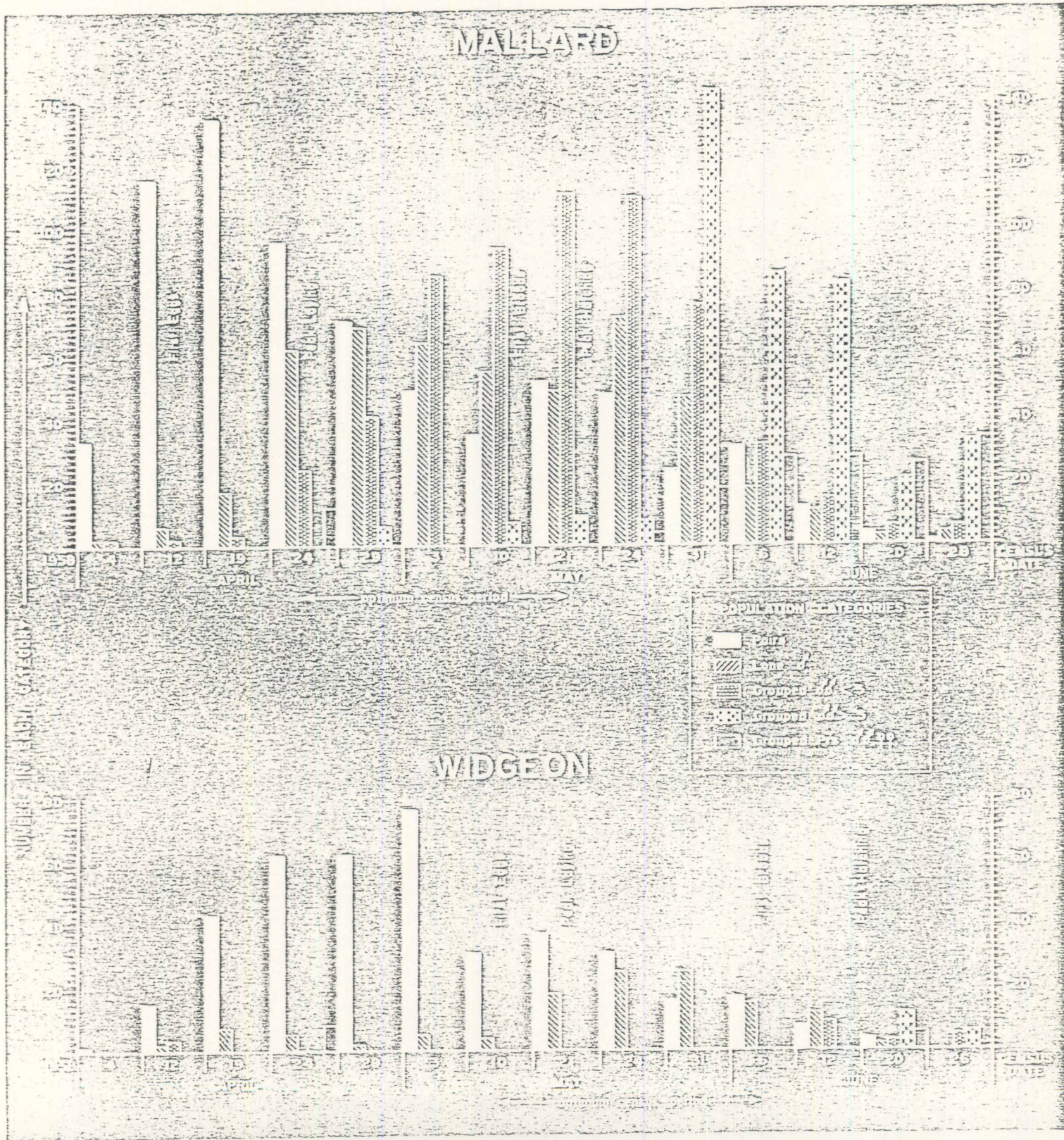
The validity of enumerating the grouped drake component, prior to the main hatching peak, with

the recorded pair and lone male components as indicative of the breeding pair population, was substantiated by the seasonal censuses. Indicated breeding populations, taken from an enumeration of the pair, lone drake, and grouped drake components before the hatching peak, were consistent and varied between 182 and 212 pairs (Table 8a). After the peak of hatching between May 21 and 24, the number of indicated pairs based on grouped drake counts rose and there was no way in which resident grouped males and transient males which had left their breeding home ranges elsewhere could be differentiated. A marked influx of grouped males in aggregations of over 5 and up to 40 was noted after May 31. Such postbreeding aggregations of drakes and hens were recorded until the end of June.

From the present data and complementary data on marked pairs, I concluded that drake mallards congregated while their hens were in the last stages of laying or in the first stages of incubation. Further, they remained on the breeding grounds, although not necessarily on the waiting site, until the second or third week of incubation (first nesting only). Small aggregations of males were associated with the waning of the drake-hen pair bond primarily through the incubation period.

Because some pairs continued to reneest through June, the indicated population, after the first influx of postbreeding groups on May 31, was considered to include the pairs, lone drakes, and only those groups of males five or less in number.

Figure 3 April to June population components from periodic censuses on the Kindersley Study Area, 1958. (Note the lack of grouped male widgeons but the prevalence of grouped male mallards.)



Observations of marked drakes from pairs nesting for the first time had indicated that mated males rarely congregated into groups of five or more before their hens were in the third or fourth week of incubation. Therefore, an arbitrary division was made to include only groups of five or less after the hatching peak. A similar decision was made by Jessen, Lindmeier, and Farnes (1964) and by Hammond (1966).

The lone female component made up less than 3 per cent of the total indicated pair count for all May censuses, i.e., rarely were more than two lone hens recorded per species per census. A few more lone hens were recorded in June after drakes had abandoned their home ranges and left the study area, but the maximum number noted during one census was five pintail. Only five lone mallard hens were recorded, one from each census from May 3 to 31. Smith (1956: 36) reported that lone hens of each species made up less than 4 per cent of the populations on four Alberta study areas. At Kindersley the first small postbreeding groupings of predominantly hens were recorded by June 12. They were usually associated with a number of males. Small flocks of hens from 3 to 38 were periodically noted in the district during the first 2 weeks of July. I assumed these were hens that had lost reneest clutches or abandoned nearly flying young and were retiring to the moulting lakes.

Seasonal sex ratios of mallards recorded on the study area showed a progressive increase in the percentage of drakes, as absences by laying and incubating hens reduced the proportion of visible hens. Ten days after the hatching peak, 90 per cent of the population was made up of drakes. Thereafter, a downward trend in percentage of drakes was noted as more drakes left the breeding grounds and postbreeding groups of hens moved into the region. By examination of sex ratio data from census and a comparison with prebreeding sex ratios, time of laying and incubation can be deduced. The first appearance of lone drakes, i.e., when lone drakes compose over 10 per cent of the indicated pairs, is invariably a good indicator of start of laying by hens, while the first appearance of groups of two or three drakes indicates start of incubation.

Pintail

The seasonal changes in population components paralleled those of mallards (Table 8b). Lone drakes made up a small proportion of the pre-

breeding population prior to April 12, the start of laying, but the number grew as more nests were initiated. Grouping of males was most evident as soon as incubation started, although prebreeding association between mated and unmated males is much more common in this species than in mallards (Smith, 1963). A major difference between the two species is the frequent association of pintail drakes with pairs after April 19, i.e., in groups of three or more males and one hen. These were primarily composed of males harassing females; temporarily on ponds, in attempted rape fights. No pintail pairs were recorded after June 6, indicating an earlier abandonment of home ranges by reneesting individuals than by mallards. As with mallards, a major influx of postbreeding grouped males was noted after May 24. The indicated breeding population based on pairs, lone males, and grouped males from April 24 to May 21 inclusive (the optimum census interval) varied between 150 and 181 pairs.

The percentage of drakes in the breeding population increased to 88 per cent 10 days after the peak of hatching, but did not decrease through June, as in mallards, as no postbreeding groups of hens moved into the area.

Widgeon

The indicated breeding pair population was composed of pair and lone drakes for the greatest portion of the breeding season (Table 8c, Figure 3). The lack of the grouped male category, until after the hatching peak, reflects the stronger pair bond and site attachment in this species than in mallards and pintails.

Two to seven lone drakes were observed on each census prior to the start of egg laying on May 8, and a group of three unmated males was recorded only once on April 12. Lone drakes became more common after May 10 with the peak of laying reached between May 16 and 20. Sex ratios became progressively weighted to males as more hens started laying and initiated incubation. The percentage of drakes reached a maximum of 83 per cent some 10 days after the hatching peak. Few males apparently remained on the study area for more than a week after the hatching period. There was also no major influx of grouped widgeon drakes into the area as was recorded for mallards and pintails.

Shoveler

Most shovelers were observed as either pairs or lone drakes until midway through the incubation

(Table 8d). Eight lone males were observed on May 3, the first indication of laying in species. Groups of males were first recorded on May 24, 2.5 weeks before the hatching peak. Percentage of males increased after May 10, reached a maximum of 95 per cent after the hatching peak.

Seasonal population components are similar to those of widgeon. Only one lone male was observed on each count taken prior to May 21, after the first laying commenced, about May 16, the number of lone males steadily increased (Table 8e). Grouped males were not observed in morning counts until just before the hatching peak, again indicating a strong pair bond and mate attachment in this species. However, neck-banded males were observed to associate with other males, for varying periods of the day, during the third and fourth week of incubation. Sex ratios in favour of drakes increased after laying started and peaked at 90 per cent in males, 7 days after the hatching peak. No influx of postbreeding grouped males was observed in June.

Ringed teal
 Pair and lone drake component made up the major proportion of the indicated pair population until the hatching peak (Table 8f). Seven groups of males, primarily of two, were noted 10 days before the hatching peak. The first nest was observed on May 12 and only one group of two was observed on May 21. Four aggregated groups were seen on May 31. These may have consisted of mated and unmated drakes and unmated drakes only. As with other species, the percentage of males censused in the population progressively increased until a high of 89 per cent males was noted on June 6, 10 days before the hatching peak.

Optimum census periods
 In 1958 counts, plottings of weekly, individual pair populations show wide seasonal variations (Fig. 4). Most dabbling species showed an increasing number of pairs in residence until the beginning of nesting, when a relatively stable number of pair numbers occurred. This plateau was correlated with the initiation of laying and lasted for 3 to 4 weeks while other hens start laying and incubating. Optimum census periods for early nesters, mallard and pintail, overlapped with the intermediate nesters, widgeon and

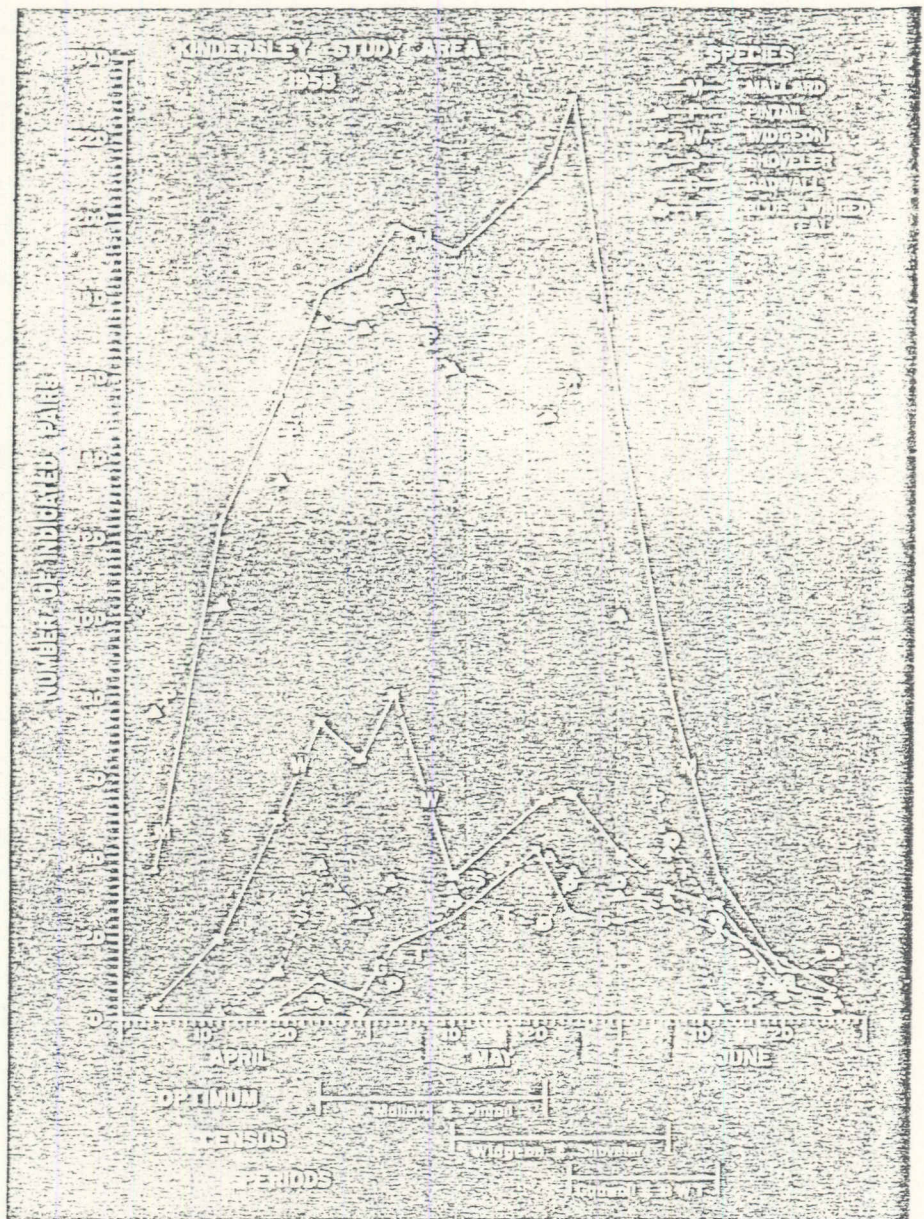


Figure 4 Seasonal indicated pair numbers of six dabbling species. (Note the differences in optimum census periods reflecting variations in time of nesting.)

shoveler, but did not overlap with the late nesters, gadwall and blue-winged teal (Fig. 4). For the 1958 breeding season the optimum census period was April 24 to May 21 for early nesters, May 10 to June 6 for intermediate nesters, and May 24 to June 12 for late nesters.

The optimum census periods can be a week earlier or 2 weeks later than dates given above because of yearly variations in spring break-up, migration of species, and dates of nest initiation. Late April cold periods affect migration and

nest-initiation dates and may lead to double peaks of hatching in late May and early June. Adequate censuses during such years are extremely difficult as mallard and pintail drakes from early nestings have abandoned home ranges when late nestings are only being initiated.

Estimates based on different components

Various authors (Hochbaum, 1944; Sowls, 1947; Williams, 1948; Smith and Hawkins, 1948; and others) have recommended that only the drake and pair components of a censused population be considered indicated breeding pairs. At Kindersley, a wide discrepancy in pair estimates occurred with two species, mallard and pintail, if only these two components were considered (Table 9). A comparison of indicated pair populations of mallards and pintails taken from a single count on May 10 with a mean sex-ratio corrected population (cf. Methods section) taken from five counts suggested that by enumerating lone males and pairs only 52 per cent of the estimated breeding population of mallards and 54 per cent of the pintail pairs were assessed.

Chronology of nesting markedly affects the component parts. During the optimum census period, mallard lone drakes plus pairs made up 158 of the 182 (or 87 per cent) indicated pairs counted on April 24, but had dropped to only 101 of the 212 (or 48 per cent) indicated pairs noted on May 21 (Table 8a). The pintail lone drake plus pair components made up 135 of the 174 (or 78 per cent) indicated pairs on April 24, but had dropped to 76 of 150 (51 per cent) indicated pairs on May 21 (Table 8b).

Breeding population estimates of other dabbling species show less distortion when only pair and lone drake components are considered because few drakes (primarily unmated ones) associate with each other until after mid-incubation. However, at Kindersley, population levels of all other dabbling species, viz., widgeon, shoveler, gadwall, and blue-winged teal, were considerably lower than those recorded for mallard and pintail. Where pair populations occur at densities in excess of five pairs per square mile (Table 5) drakes may associate much earlier in the incuba-

TABLE 9 Comparison of 1958 Kindersley census results utilizing various population components and sex ratio correction factors

	Mallard	Pintail	Widgeon	Shoveler	Gadwall	Blue-winged teal
Census date in May	10	10	21	21	31	31
A. Indicated breeding population from counts including pairs and lone drakes only.	90	81	55	40	24	30
Per cent of estimate D using two components, pairs and lone drakes	(52)	(54)	(134)	(138)	(96)	(111)
B. Indicated breeding population from counts including pairs, lone males, grouped males, GFAC, and ARF	191	161	55	40	24	34
C. Mean indicated breeding population from five census dates (Table 12)	194	168	44	34	28	32
95% confidence interval	±12.9	±13.5	±12.4	±4.6	±7.0	±10.2
D. Mean sex ratio corrected population from C and Table 3	173	149	41	29	25	27

tion period into small groups of two's and three's. Such groups should be enumerated as indicated pairs, and the sex-ratio correction factor applied to delete any groups of unmated males.

Daily change in population components

By hourly observation, I established that variations occur in component parts of a population breeding around a single pond. Censuses conducted during five intervals of the day also showed this variation (Table 10). Counts of indicated mallard pairs conducted after 0530 hours show pairs making up but one-quarter of the population whereas comparable counts started at 0800 hours show 46 per cent pairs, at 1300 hours 57 per cent pairs, at 1530 hours 63 per cent pairs, and at 1800 hours 69 per cent pairs (Table 10). On May 16, only 18 mallard pairs were recorded on the 0530 hour count while 42 were noted on the 0800 hour count. I concluded that most pairs were visiting nesting cover or feeding on upland grain fields in the early morning and were not seen on ponds. Other observations on general daily activity of pairs confirmed this view. At 0530 hours when many hens would be laying, the lone drake component of the population was 30 per cent. It decreased from 23 per cent at the 0800 hour count to 18 per cent at both 1300 and 1530 hours and was only 15 per cent at the 1800 hour count. As the counts were taken between May 11 and 16, when many of the hens

were either laying or incubating, I concluded that there is a simple change of component parts from lone drakes and grouped drakes to pairs progressively throughout the day as more hens return to waiting sites from laying and as more hens take their recesses from incubation in late afternoons.

Mallard hens lay most of their eggs during the morning (Hochbaum, 1944; SOWLS, 1955; Dzubin, MS.). The time spent on the nest per egg is highly variable between successive eggs and among hens. The shortest time I recorded was 2 hours 3 minutes on the nest, while the longest was 13 hours 8 minutes. A few hens may also fly to nest sites in evening and remain on the nest overnight. Incubating hens also vary in the times recesses are taken, but most take an afternoon rest period. Peak recess times occurred between 0300 and 0600 hours and 1500 and 1900 hours (Dzubin MS.). The average length of morning recesses in May was about 47 minutes, (N = 71) while late afternoon recess lengths averaged 89 minutes (N = 200).

After leaving the nest, a laying mallard hen flies to the waiting area of her drake. Hens in early and mid-incubation periods, i.e., up to 18 days, also continue to fly to the activity centre of the home range and rejoin the drake. The exact date drakes leave hens and abandon home ranges varies with the individual pair (McKinney, 1965) and with the phenology of the season.

TABLE 10 Changes in five population components of mallards at five different periods on single days during laying and early incubation, Kindersley Study Area, 1959

	0800 hours					1300 hours					1800 hours				
	Prs.	Lone ♂	Grp. ♂ < 5	Lone ♀	Grp. birds	Prs.	Lone ♂	Grp. ♂ < 5	Lone ♀	Grp. birds	Prs.	Lone ♂	Grp. ♂ < 5	Lone ♀	Grp. birds
May 11	61	53	53	1	9:0	80	35	52			98	35	45		
May 15	42	44	61		4:1	55	45	58		5:1	53	33	28		1
May 16	42	44	66			50	37	56			67	29	19		2
Total	145	141	180	1	14	185	117	166	0	6	218	97	92		3
% all birds	46	23	29	.2	2	56	18	25		1	69	15	15		.5
Ratio	100:	97:	124:	.7:	10	100:	63:	90:		3	100:	44:	42:		1
	0530 hours					1530 hours									
	Prs.	Lone ♂	Grp. ♂ < 5	Lone ♀	Grp. birds	Prs.	Lone ♂	Grp. ♂ < 5	Lone ♀	Grp. birds					
May 16	18	42	64			73	41	44							
% all birds	25	30	45			63	18	19							
Ratio	100:	233:	356			100:	56:	60							

During recesses, after mid-incubation, hens may not return to the activity centre to rejoin the drake but may take recesses elsewhere on the home range. The pair bond may be completely broken at this time. Hens feed alone or, uncommonly, join other hens on recess.

Censuses conducted in the morning, when most hens were laying or incubating, showed a greater preponderance of lone males and grouped males than those taken in the afternoon and evening. As a greater proportion of hens start to incubate, fewer pairs will be observed in morning counts while late afternoon and evening counts will again show a greater percentage of pairs, reflecting the re-establishment of pair bonds by incubating hens with their waiting drakes.

A comparison of ratios of pairs:lone drakes:grouped drakes showed some major changes through the day. Counts made after 0530 hours showed the greatest proportion of grouped drakes with progressively fewer noted at 0800, 1300, and 1530 hours (Table 10). The lowest percentage of grouped drakes was noted in the 1800-hour count. Drake aggregations tend to disperse in late afternoon when incubating hens take their recesses. Drakes return to waiting area sites periodically throughout the day but are more commonly seen as lone drakes in late afternoon hours. The ratio of pairs to lone drakes to grouped drakes noted from periodic counts taken through the day can be used to crudely determine percentages of population laying and incubating. Since the time laying hens spend on nests varies and since mallard hens have one or two recesses a day, precise numbers of hens in each reproductive stage cannot be accurately determined from pair to drake ratios. However, proportions of pairs observed in the 0800- to 1200-hour interval when compared to the 1200- to 1530-hour interval can be used as an index to pairs laying, as most hens lay eggs before noon. In morning counts a large proportion of lone drakes, of the total indicated population, is good evidence of the early laying period for their hens. Associations of two or three drakes may denote late laying and early incubation period while groupings of four, five, or more drakes suggest mid- to late incubation or postbreeding periods. The use of changes in component parts would become more complicated in areas where high nest losses led to

enumeration of many re-nesting pairs throughout the day. The seasonal changes in component parts as assessed from comparable morning counts have been previously shown for mallards (Table 8a and Fig. 3) and other species (Tables 8b to 8f). Daily and seasonal changes in population components of mallards and pintails were similar in that drakes form associations with other drakes during the laying and early incubation periods, while other dabbling males do not show the same degree of association until later in the incubation period. Under the low densities studied most widgeon, shoveler, gadwall, and blue-winged teal drakes were enumerated as lone males until 7 to 10 days before the hatching period.

Seasonal variability of walking and vehicle census *Walking census*

Population estimates of six species taken from a series of four or five walking censuses showed wide variability between each count (Table 11). All estimates were made at a period when the greatest proportion of the mallard and pintail population was known to be in the prebreeding (i.e., pairs spaced and showing activity localization) or breeding period with the remaining species in the migration (i.e., pairs grouped) and postmigration (i.e., pairs spaced but not showing activity localization) period. Estimates of the indicated breeding population of mallards on the Kindersley Study Area were the most consistent, showing a coefficient of variability of 4.8 per cent while shoveler estimates were least consistent with a coefficient of variability of 31 per cent. It should be recognized that consistency need not reflect constancy of population or accuracy of counts. A balance between egress and ingress on the area may be occurring, with the same pairs not being enumerated during each count if turnover is constant. Balanced turnover rates would occur rarely. Biases may also be consistent.

For a breeding duck census period, five conditions are desirable: (1) that the population is resident and not migrating; (2) that no pairs move into the area during the census interval; (3) that approximately the same number of birds are flushed and duplicate counts are minimal; (4) that there is no influx of mated or unmated lone drakes onto the study area; (5) that mortality is not removing part of the population during the census period. Assumption (1) was invalid for all species except mallard and possibly pintail.

Table 11 Mean population estimates of six dabbling species from five census periods in 1956. Kindersley Study Area. Walking census: 0530-1100 hours

Early nesters			
Mallard		Pintail	
Census date	Indicated population	Census date	Indicated population
5/3	265	5/3	278
5/14	274	5/14	193
5/15	264	5/15	200
5/16	298	5/16	202
5/21	289	5/21	194
Mean	278.0 ± 16.7*	Mean	213.4 ± 40.3
Stand. Error	6.0	Stand. Error	14.5
Coef. Var.	4.8%	Coef. Var.	15.2%
Intermediate nesters			
Widgeon		Shoveler	
Census date	Indicated population	Census date	Indicated population
5/14	88	5/14	35
5/15	75	5/15	31
5/16	71	5/16	25
5/21	78	5/21	33
5/28	95	5/28	58
Mean	81.4 ± 10.9	Mean	36.4 ± 14.0
Stand. Error	3.9	Stand. Error	5.1
Coef. Var.	10.8%	Coef. Var.	31.0%
Late nesters			
Gadwall		Blue-winged teal	
Census date	Indicated population	Census date	Indicated population
5/16	49		
5/21	41	5/21	45
5/28	50	5/28	51
6/4	46	6/4	39
6/11	55	6/11	49
Mean	48.2 ± 5.7	Mean	46.0 ± 10.3
Stand. Error	2.1	Stand. Error	3.2
Coef. Var.	9.6%	Coef. Var.	10.0%

*95% confidence interval.

There was no way of assessing assumption (2), but perusal of the data suggested that a portion of the pintails enumerated on May 3 and the shovelers on May 28 were migrants, as the indicated population showed peaks at this time. These peaks tended to increase the variances. Furthermore, mobility and home range size of 202

TABLE 12 Mean population estimates of six dabbling species from five census periods in 1958. Kindersley Study Area. Vehicle census: 0800-1130 hours

Early nesters			
Mallard		Pintail	
Census date	Indicated population	Census date	Indicated population
4/24	182	4/24	174
4/29	187	4/29	172
5/3	198	5/3	181
5/10	191	5/10	161
5/21	212	5/21	150
Mean	194.0 ± 12.9*	Mean	167.6 ± 13.5
Stand. Error	4.7	Stand. Error	4.9
Coef. Var.	5.4%	Coef. Var.	6.5%
Intermediate nesters			
Widgeon		Shoveler	
Census date	Indicated population	Census date	Indicated population
5/10	35	5/10	35
5/21	55	5/21	40
5/24	56	5/24	35
5/31	41	5/31	30
6/6	32	6/6	30
Mean	43.8 ± 12.4	Mean	34.0 ± 4.6
Stand. Error	4.5	Stand. Error	1.7
Coef. Var.	22.8%	Coef. Var.	11.0%
Late nesters			
Gadwall		Blue-winged teal	
Census date	Indicated population	Census date	Indicated population
5/21	42	5/21	23
5/24	26	5/24	35
5/31	24	5/31	34
6/6	27	6/6	44
6/12	21	6/12	22
Mean	28.0 ± 7.0	Mean	31.6 ± 10.2
Stand. Error	2.5	Stand. Error	3.7
Coef. Var.	20.3%	Coef. Var.	26.0%

*95% confidence interval

pintails, their lack of strong site attachment and their erratic long-distance wanderings could have posed a sampling error. There is, however, some consistency of estimates for the mallard, pintail, widgeon, and shoveler taken on 3 successive days. The low densities of widgeon, shoveler, gadwall, and blue-winged teal on the 10.5-square-

TABLE 13 Census of six dabbling species on 3 days of the same week, Kindersley Study Area, 1959

Indicated populations from ground count								
	CST hours	Mallard	Pintail	Widgeon	Shoveler	Gadwall	Blue- winged teal	Total population
May 11	0800	176	58	52	24	21	9	340
	1300	167	41	42	33	29	9	321
	1800	178	45	47	30	18	7	325
May 15	0800	151	47	37	27	16	23	301
	1300	163	30	37	35	23	17	305
	1800	114	30	31	31	20	20	246
May 16	0530	124	33	28	23	16	20	244
	0800	152	48	32	20	17	16	285
	1300	143	45	39	35	25	26	313
	1530	158	59	36	33	18	24	328
	1800	115	31	32	36	18	31	263
Number counts		11	11	11	11	11	11	
Mean		149.2	42.5	37.5	29.7	20.1	18.4	
95% conf. int.		±14.6	±6.8	±4.6	±3.5	±2.6	±4.7	
Stand. error		6.57	3.03	2.07	1.57	1.18	2.13	
Coef. var. %		14.6	23.7	18.3	17.5	19.5	38.3	
May 15 and 16 only—0800, 1300, 1530 hours only								
Number counts		5	5	5	5	5	5	
Mean		153.4	45.8	36.2	30.0	19.8	21.2	
95% conf. int.		±7.3	±11.5	±2.9	±7.2	±4.4	±4.9	
Stand. error		2.62	4.15	1.04	2.59	1.59	1.77	
Coef. var. %		3.8	20.3	6.4	19.3	17.9	18.8	

mile block may have also affected the variability. Under low densities home ranges may be larger. There might be more pairs with home ranges partly off the study area leading to greater variability of counts.

Vehicle census

In 1958, pair counts showed increased precision of estimates for pintail and shoveler but decreased precision of estimates for widgeon, gadwall, and blue-winged teal (Table 12). The coefficient of variability was almost the same in mallards for the two counting methods, viz., 4.8 per cent for walking counts versus 5.4 per cent for vehicle counts. As the same population was not sampled and a 2-year span separated the two series of counts, the data were inconclusive as to what

method of census showed the least variation. Other sources of sampling error may tend to increase variability, masking any differences attributable to the two methods. Factors such as water and vegetation condition, population level, and phase of breeding season were not weighed and they may colour any valid conclusions. Because fewer birds were flushed by the vehicle, one might expect higher rates of precision with this method. The 1958 estimates from vehicle counts for mallards and pintails showed marked consistencies of pair estimates for the April 24 to May 21 interval. The data for these two species tended to substantiate the view that each population reaches a plateau of numbers for a 3- to 4-week period every year. Again, low densities

of the other four species may have affected variability as there was little consistency among counts.

Time of day and variability of estimates

In 1959, population estimates from 11 vehicle counts taken on 3 days of 1 week showed wide variation (Table 13, middle). The coefficient of variability was lowest for mallards, 14.6 per cent, and highest for blue-winged teal, 38.3 per cent. Five mid-day counts arbitrarily chosen from censuses taken after 0800, 1300, and 1530 hours showed lower coefficients of variability for all species except shoveler, when compared to the variation of the 11 counts (Table 13, bottom). I observed that pairs left the census ponds in early morning to fly to nesting cover. Many were not on ponds during the census period. In the evening and to a lesser extent in the morning, a number of mallard, pintail, and widgeon pairs fed in grain-stubble fields and were again not available on ponds for census. Therefore, estimates made from counts between 0800 and 1530 hours were probably more representative of the absolute breeding population than estimates made before or after these times. Population estimates of blue-winged teal were low for May 11 but much higher on May 15 and 16, indicating an influx of birds in this interval. Such migratory influxes naturally increase variance of estimates. For all species except mallard and pintail, the wide variation in counts taken after 0800, 1300, and 1530 hours suggested that all counted pairs were not resident or were nonbreeders with no firm site attachments, moving on and off the study block at various periods of the day and over the 5-day period.

An analysis of variance of dabbling counts for 0800, 1300, and 1800 hours of 3 days in 1959 showed that there was a significant difference ($p = < .01$) in the variances of shoveler and gadwall estimates (Table 14). There was no difference existing between the variances of the morning, mid-day and late afternoon pair estimates of mallard, pintail, widgeon, and blue-winged teal. Even so, the test can be biologically misinterpreted since field observations showed that mallards and pintails, especially, are prone to leave ponds after 1800 hours and be found in wheat-stubble fields. Replication of counts over a longer period would better corroborate whether time of day has an influence on countableness. On two days, May 15 and 16, counts of mallards

TABLE 14 Analysis of variation of dabbling counts taken at three different time intervals, 0800, 1300, and 1800 hours, on 3 days. Data from Table 13

Source of variation	Degrees of freedom	Sum of squares	Mean square	F Value
Mallard				
Total	8	2485		
Time	2	1064	532	
Error	6	1421	236.8	2.25*
Pintail				
Total	8	744		
Time	2	408	204	
Error	6	336	56.0	3.64*
Widgeon				
Total	8	703		
Time	2	412	206	
Error	6	291	48.5	4.24*
Shoveler				
Total	8	290		
Time	2	241	20.5	
Error	6	49	8.2	14.75†
Gadwall				
Total	8	180		
Time	2	144	72	
Error	6	36	6.0	12.00†
Blue-winged teal				
Total	8	1080		
Time	2	548	274	
Error	6	532	88.7	3.09*

For 2 and 6 d.f. $F_{05} = 5.14$, $F_{01} = 10.92$.

*The null hypothesis that no significant difference exists between time means of different time periods is accepted at .05 level.

†The null hypothesis that no significant difference exists between time means of different time periods is rejected at .01 level.

and pintails started at 1800 hours were lower than mid-day counts. The May 11 counts do not show this decrease but point out the need for further extensive series of replicate daily and hourly counts. The present data are too few for valid conclusions.

Counts should be conducted at times when pairs of all species are most regularly found on ponds and not in nesting cover or fields, i.e., between 0800 and 1800 hours. Other supporting data show that wind velocity generally increased in the afternoons. Also, more laying and incubating hens left clutches and returned to waiting sites after the noon hour. The return of hens on recess to ponds invariably led to increased pair contacts,

chases, and mobility. For these reasons counts might better be restricted to the 0800- to 1200-hour interval when pairs and drakes are least mobile and most likely to be found on ponds.

Pond numbers and breeding pair populations

Discussions of the correlation between spring mallard breeding populations and May or July pond numbers have been presented by a number of authors (Evans and Black, 1956; Bellrose, Scott, Hawkins, and Low, 1961; Salyer, 1962; Lynch, Evans, and Conover, 1963; Crissey, 1963a, 1963b, 1969; Drewien, 1967). Evans and Black (1956), Drewien (1967), and Bellrose *et al.* (1961) show strong positive correlations between May pond numbers and breeding populations of blue-winged teal and mallards, while Crissey (1968) has shown a significant correlation between July pond numbers and number of young mallards produced, and also the subsequent spring breeding population. I have pointed out that supplementary data on pond quality, size, and densities should also be considered in any such correlation attempts (Dzubin, 1969). Little is yet known of the effects of social interactions of duck pairs in limiting breeding population levels or whether "saturation points" of waterfowl occupancy are yearly reached or exceeded on habitat units in which water levels and pond numbers are constantly changing. Over-harvests of local populations (Moyle, 1964) and shifts in populations from one waterfowl stratum to another because of droughts (Lynch, 1949; Crissey, 1957) tend to make inferences from yearly pond-pair correlations difficult. Also, much of the fluctuation in pond numbers revolves about filling and drying of small transient potholes, with the larger, deeper ponds generally holding some water through each summer or until major droughts occur (Dzubin, unpublished). For example, Smith (1949) recorded a 77 per cent decrease in pond numbers in the Alberta parklands in 1949 but a 59 per cent increase in duck populations, indicating that ponds, perhaps the larger, deeper potholes, had not yet reached critical levels of occupancy. A number of smaller ponds may in fact be superfluous to some basic number of large, deep ponds required by pairs in any breeding home range.

Direct counts of indicated breeding pairs utilizing the 10.5-square-mile Kindersley Study Area from 1956 through 1967 show a trend downward from 1957 to 1963 and a partial

recovery thereafter (Table 15). Comparable counts were made only once during each season at the optimum census period for mallards and pintails and therefore the data presented do not lend themselves to particular consideration of fluctuations of other species. From brood surveys I calculated that production of young mallards in any of the four summers, 1956 through 1959, was not sufficient to balance annual mortality.

In a study of mortality of flightless young mallards, banded throughout the Kindersley district from 1954 to 1959, Gollop (1965) showed a loss of 32 per cent of young from 3 to 7 weeks of age. For flying young an average mortality of 61 per cent was calculated for the year following September 1. Mean annual adult mortality was 47 per cent. Assuming that the 1956 adult and immature segments were subject to these mortality rates, there should have been a marked reduction in the returning population in the spring of 1957. Yet breeding populations in 1957 rose markedly over those in 1956. I concluded that in 1957 mallard and pintail pairs moved onto the study area from the surrounding drought-stricken regions. Thereafter all pair populations continued to decrease to a low about 1963. These decreases probably reflected low production rates and their subsequent effects on spring adult populations homing to the area. Also poor May pond quality, i.e. low water levels and extensive mud flats, may have deterred settling of pairs and led to their emigration northward. If production of young was low and if hunting and natural mortality yearly reduced the adult component, the population traditionally homing to the area would be quickly reduced. The study area was completely dry on July 25, 1963, except for a one-quarter-acre, spring-fed pond, and few young of any species were successfully fledged that year. Since 1964 there has been a yearly recovery of the breeding populations of all species, associated with higher May pond numbers, a greater pond acreage, a longer, total shore-line distance, and higher July pond numbers for broods. The population may have also experienced higher survival, or pond quality so improved that it attracted pioneering pairs (cf. Hochbaum, 1946). A lack of adequate supporting data on habitat requirements of each species, young produced yearly, homing rates, extent of nonbreeding, and spatial relationships of pairs precludes any knowledge-

TABLE 15. Yearly trends of indicated breeding populations of dabblers and ponds from mid-May ground counts, Kindersley Study Area, 1956 to 1967

	1956	1957	1958	1959	1960	1961	1962	1963	1964	1965	1966	1967
May date	14	13	10	15	11	10	17	15	10	14	14	20
Mallard	274	401	191	151	69	63	54	37	40	39	97	129
Pintail	193	315	161	47	37	40	40	19	19	60	132	139
Widgeon	75	80	35	37	34	33	19	6	12	23	39	57
Shoveler	31	59	35	27	20	5	12	20	16	32	50	51
Gadwall	63	38	25	16	17	8	13	8	14	16	26	50
Blue-winged teal	29	91	31	23	13	7	8	3	8	18	18	13
Green-winged teal	16	8	29	5	4	24	11	3	5	11	11	7
Total indicated pairs	681	992	507	306	194	180	157	96	114	199	373	446
Number of ponds on census date	81	43	29	22	30	33	35	11	17	59	51	49
Total pond acreage	609	479	227	155	162	158	174	82	115	618	550	571
Total pond shore line feet $\times 10^3$	115,	87,	58,	39,	45,	44,	51,	15,	22,	110,	99,	94,
Number of ponds, June 1	64	14	20	13	15	21*	26	8	9	49	42	43
Number of ponds, July 1	49	7	8	4	8	10*	15	4	3	38	30	24

* After 1961, estimated from May water depths, expected loss to July and general observations August 1-15.
 Note: Estimates accurate for mallards and pintails only, but show general trends for other species.

able discussion of correlations between pond and breeding pair numbers.

A comparison of the number of May and July ponds with mallard and pintail populations from 1956 through 1967 again showed yearly decreases after 1957 to 1963 and 1964, and an immediate recovery after 1964 (Fig. 5). The yearly decreases from 1957 to 1959 were associated with decreasing May and July pond numbers. Thereafter, the recovery was associated with increases in both May and July pond numbers. Increasing numbers of pioneering pairs and higher production rates possibly led to increased numbers of pairs breeding in 1965 through 1967. Pintail populations dropped faster than mallard populations from 1957 to 1960 but recovered faster from 1964 to 1967. Neither species showed an increase in breeding populations from 1959 to 1962 in spite of a slight increase in May and July pond numbers in these years.

From 1964 through 1967, I observed that pintails and shovelers showed a marked propensity

toward using newly flooded depressions. This attribute may be a characteristic of species with strong pioneering tendencies and weaker homing tendencies (Sowls, 1955). Smith (1949) has also commented on the population shifts of these two species. In Alberta, where there was a grassland drought in 1949, he noted that pintails and shovelers showed the greatest individual population losses after 1948, indicating a movement elsewhere. Lynch (1949) reported a major shift of pintails from drought-stricken Saskatchewan grasslands to areas beyond the parklands, even though mallards, widgeon, and blue-winged teal moved into the better watered parkland. Pintails and shovelers may have evolved in habitats containing ephemeral ponds. Any predisposition to quickly shift breeding grounds to better watered areas may hold some adaptive significance, especially where it fosters brood survival. If these two species have evolved in relatively unstable environments, emigration may be a major density regulatory mechanism whereas in mallards and

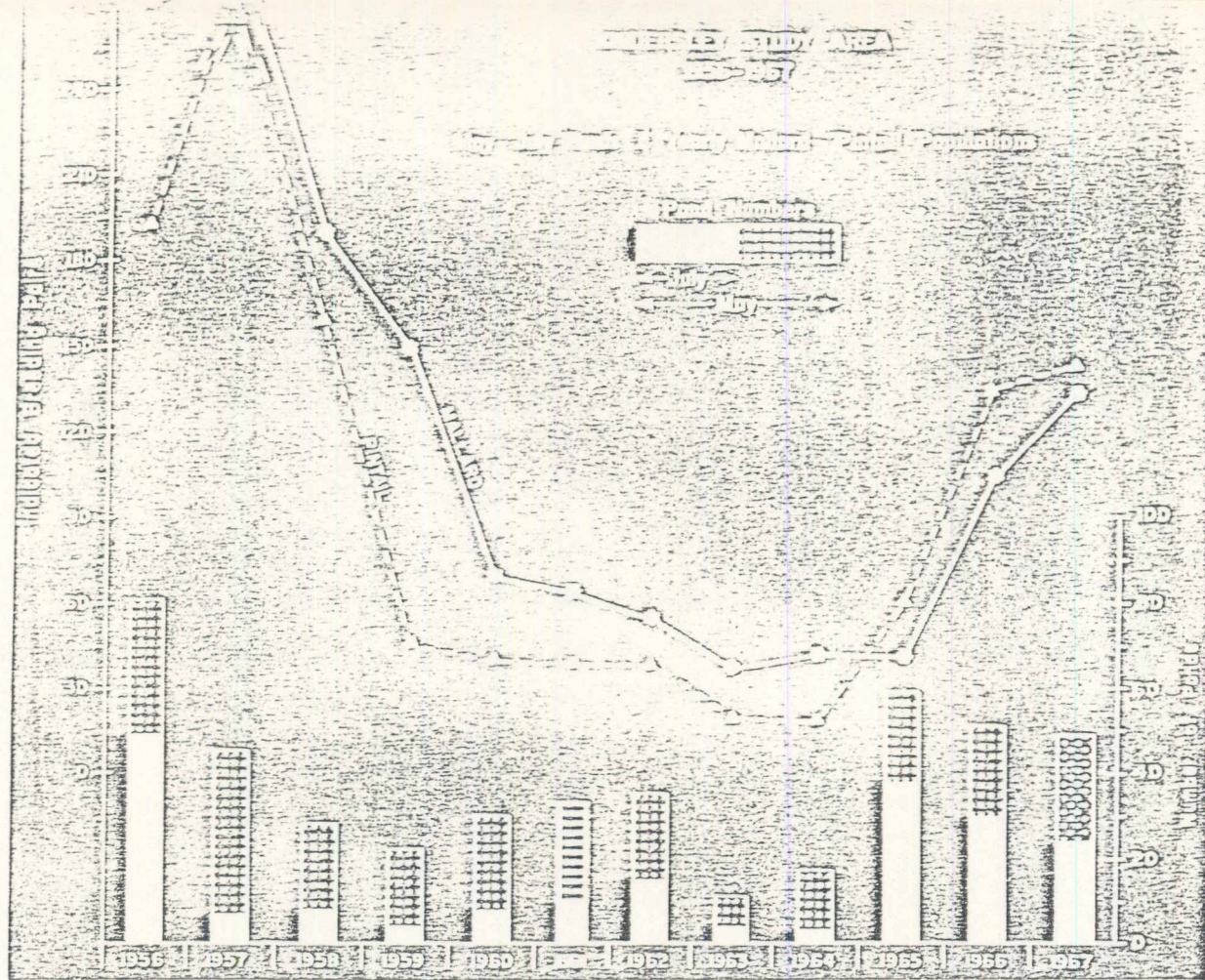


Figure 5 May-July pond numbers and yearly mallard and pintail pair populations, 1956 to 1967. (Note that pintail numbers decreased more sharply than mallard numbers from 1957 to 1959 but increased more rapidly from 1964 to 1967.)

perhaps blue-winged teal, self-regulatory mechanisms concerned with density effects on reproductive rates or behavioural spacing mechanisms controlling density may be more prominent (Dzubin, 1969).

Duck census techniques

Spring and summer duck population estimates, whether based on direct air or ground counts, remain relatively inexact. Even more inexact is the accurate assessment of absolute seasonal populations of pairs attempting to breed in a stratum, along a transect, or on a sample block. It is generally conceded that counts of absolute numbers of birds breeding in a particular habitat are not feasible, and therefore workers are forced to estimate populations on the basis of various sampling procedures. The early works of Nicholson (1931), Leopold (1933), Lack (1937), and Kendeigh (1944) reviewed many of the problems inherent in conducting censuses, while more recent reviews by Fisher (1954) and Davis (1963) discussed sampling problems of various population estimate methods and the assumptions on which census techniques are based. The fol-

lowing discussion covers some of the difficulties inherent in any dabbling duck population determinations.

Moore (1955) described many of the problems involved in using strip-transect methods for estimating upland game birds. A number of these were discussed by Stewart *et al.* (1958) and Diem and Lu (1960) for transect counts of waterfowl. Yapp (1956) discussed the theory of line transect counts and suggested that the number of animals a census taker would see, walking at a constant speed over a straight-line course, depended on (1) the density and speed of the animal, (2) the walking speed of the census taker, and (3) the effective distance of recognition or visibility. Skellam (1958) questioned the method because of inexact derivation of the average speed of the animal and its relationship to the speed of the observer. Many of the problems involved in obtaining increasingly accurate and reliable passerine bird estimates have been examined by Taylor (1965) and Snow (1965) and apply equally well to census of many other bird groups. Seasonal replication of counts and intimate knowledge of species ecology and behaviour tend to make

census techniques more valuable in construction of valid population indices.

Many of the techniques used for ground and aerial census of waterfowl in spring and fall have been summarized for Europe by Isakov (1961, 1963), Formosov and Isakov (1963), Matthews (1960), Tamisier (1965), and Grenquist (1965) and for North America by Smith (1956), Crissey (1957), Stewart, Geis and Evans (1958), Diem and Lu (1960), Smith (1964), and Hammond (1966). Population estimates have been calculated by using marked to unmarked ratios for ducks by Lincoln (1930), for geese by MacInnis (1964, 1966) and Fisher (1954), and for immature ducks by Cowardin and Higgins (1967). Photographic methods of estimating number and density of birds were presented by Chatten (1952), Cowardin and Ashe (1965), and Van Tets (1966).

Recent fluctuations in absolute numbers of the continental mallard population, their yearly production of young, and correlations of production ratios and number of July ponds were discussed by Crissey (1969). Continental trends of all duck species from 1955 to 1966, based on breeding population indices from aerial counts, were given in Martinson and Henry (1966: USBSFW unpublished Administrative Report 119, 10 p.).

Components counted as indicated pairs: a review
Estimates of abundance of waterfowl breeding pairs in various North American habitats have been based on a variety of population components. There has been a remarkable lack of standardization as to categories of each species censused. Differences of census technique have reflected objectives of the census—whether yearly trends, indices, estimates, or absolute numbers were desired. Comparing results of studies based on different components with variable errors of estimation is, at best, difficult.

Counts of lone drakes on waiting sites as reliable indicators of breeding pairs of blue-winged teal was first proposed by Bennett (1938). Hochbaum (1944) expanded the concept of lone drake census to include all dabbling species but pointed out that there were variations in length of localization of the drakes' activity on "territory". Low (1947) concluded that numbers of nesting pairs on an area could be ascertained more accurately by a count of pairs or drakes on their territories than by a nest count. General-

ly, censuses of breeding pairs of waterfowl were based on the premises of drake and pair isolation, activity localization, and conspicuousness during the prelaying, laying, and early incubation periods. Smith and Hawkins (1948) noted that "unique in the spring inventory are the definiteness of the territory, tendency of the drake to display, tameness of ducks in the spring, sparseness of cover and scattered arrangement of birds". They describe a breeding pair census as the tallying of all water areas and breeding birds (as evidenced by pairs or single drakes) falling within a designated strip. For a number of years after 1948 waterfowl pair censuses were based on "the number of breeding birds by species as evidenced by pairs and single drakes and the total number of ducks by species" (Williams, 1948). Reeves, Lundy, and Kreller (1955), Ellig (1955), and Ordal (in Moyle, 1964)* utilized only lone drakes plus pairs to equal breeding pairs. Smith (1953) did not include lone drakes on his counts of territorial pairs on artificial reservoirs in eastern Montana, as counts were conducted only once a month. No workers included grouped males as indicative of breeding pairs.

On 12 Manitoba transects, a single hen component was added to the lone drake and pair categories by Kiel (1949) to arrive at an estimate of indicated diver and dabbling pairs. Groups of males or females or mixed parties of both were recorded as ratios and not considered breeding pairs. Evans and Black (1956) also included lone hens on their Waubay Study Area censuses as did Leitch (1952) for the Caron Study Area. In Alberta, Smith (1957) included lone females, especially as an index of pairs in late season counts. Stoudt (1952, 1964) also included this component in southeastern Saskatchewan. Brood hens were tallied as indicated pairs in late season counts on a Manitoba study area by Evans (1949) and Evans *et al.* (1952).

In Maine, Mendall (1949) used brood counts and a nesting study to estimate pair populations. He noted that because of the spread of the nesting season, accurate waterfowl census by the "territorial count" method had to be supplemented by counts of broods. "When this is done the number of breeding pairs is calculated by using the total number of broods and maternal or "broody" females and adding to this

a proportional number of pairs (to represent the unsuccessful breeders) as based on the annual nesting success study." Later, Mendall (1958) determined population trends through a combination of three techniques: (1) counts of pairs and territorial males, (2) sample nesting studies, and (3) brood counts. In 1957, Rogers (1964) used brood counts divided by successful nests to estimate resident lesser scaup pairs. Jessen, Lindmeier, and Farnes (1964) also used nest counts, nesting success, and brood counts to estimate populations of ducks breeding on a Minnesota study area. They discuss at some length (p. 83-85) the problems involved in estimating numbers of breeding pairs using three components—pairs, lone drakes, and males in groups up to five, especially during protracted breeding seasons.

Lynch (1951), recognizing the behavioural significance of drake groupings, suggested that lone mallard and pintail drakes and all grouped drakes of three or four be enumerated as indicated pairs by aerial crews. Calculated ducks-per-square-mile figures should then be adjusted for the laying or incubating but unseen hens, associated with drakes. He stressed that hens of pairs were more difficult to observe from the air while most drakes were clearly visible. In essence, he recommended enumeration of all apparently resident drakes as pairs. Yearly variations in percentages of lone drakes to all ducks seen were to be utilized as an index to successful first nesting attempts.

Bue (1952) has conducted the most intensive analysis of breeding population dynamics based on weekly censuses of 50 stock ponds in western South Dakota. Counts were made from April to August of 1950 and 1951 and included pairs, lone drakes, lone hens, grouped pairs, drakes and hens, and postbreeding groups. He used four methods to arrive at seasonal breeding pair populations of mallards, pintails, shoveler, gadwall, and blue-winged teal: (1) the weekly indicated breeding pair population represented by lone drakes and pairs; (2) the weekly potential breeding pair population by enumerating all females seen in (1) above plus all hens observed as lone hens, in grouped courting parties, or as brood hens; (3) the indicated breeding pair populations by "accumulative calculated desertion of males" by weeks. This method accounted for a shift of

lone and paired males to grouped drakes and courting parties but the population could not be tallied until the last drake deserted the home range; (4) a weekly breeding pair population by adding the population from (3) to all hens observed as pairs and in courting parties. Females seen as lone hens and with broods were not used. Each method gave fairly comparable results but for different weeks of the breeding season. Bue (1952: 13) noted that the then current single-count census techniques which enumerated only pairs and lone drakes did not account for pairs in which drakes had deserted territories, pairs which arrive late, or pairs which leave the area without attempting to nest.

In South Dakota, Murdy (1953) counted pairs, lone drakes, unpaired males, and unpaired females of five species of ducks during an entire breeding season. Using ratios of pairs to lone drakes plus a knowledge of nesting phenology and migration chronology, he was able to establish optimum census periods for each species for the state. He concluded that (1) various percentages of each species were paired on arrival, with pintails the least paired, (2) lone drake indices may have been affected by presence of unpaired males, (3) lone drake indices fluctuated throughout the season.

In England, Boyd and King (1959) estimated potential breeding pairs of mallards on four reservoirs from frequent direct counts and sex ratio counts made from February to August. They point out that "a nest count is in theory the best measure of the breeding population" but recognized the problems involved in finding all nests and the effects of finding nests on increased predator loss. In Alberta, Keith (1961) used an average of seasonal counts of adult ducks to estimate the number of breeding pairs of 11 species on his study area impoundments. Gates (1965) used Keith's (1961: 66) data on average seasonal nests per pair to calculate breeding pair populations of mallard and blue-winged teal on Wisconsin farmlands. He assumed that reneesting rates were similar in the two areas.

In their intensive evaluation of ground transect census methods in Alberta, Diem and Lu (1960) separated species into four groups based on observed mobility, viz. (1) sedentary puddlers, (2) mobile puddlers, (3) sedentary divers, and (4) mobile divers. They tested the influence of

time of day on three components (the indicated population, single drakes and single hens) of three species—mallard, blue-winged teal, and lesser scaup—but made no mention of enumerating grouped drakes. On the basis of an intensive study of black duck breeding biology and behaviour by Stotts and Davis (1960), Chamberlain and Kaczynski (1965) utilized four components—pairs, single drakes, groups of three drakes, and large groups of five or more drakes—to determine stage of nesting season. The data were used to better predict optimum aerial census periods for black ducks in eastern Canada. In Wisconsin, Jahn and Hunt (1964) enumerated lone males, lone females, pairs, flocked males, and flocked females, but used lone males and pairs only to compute pair densities on ponds. Hammond's (1959) recommendations of censusing only pair and lone drake dabblers but pairs plus extra female divers were used by Burgess, Price, and Trauger (1965) for censuses in Iowa. Martz (1967) also used Hammond's recommendations for censusing waterfowl, mostly gadwall and blue-winged teal, at the Lower Souris National Wildlife Refuge. He excluded flocks of three or more males or three or more pairs from the counts as representing nonbreeding or postbreeding birds. To obtain estimates of breeding populations of blue-winged teal, Glover (1956) recommended counts during spring migration and while males were on waiting stations, with associated nest counts on sample study areas. He utilized a series of seasonal censuses, chiefly of pairs, lone males on waiting stations, and nests per unit of habitat.

Stewart, Geis, and Evans (1958) described how pairs, lone drakes, groups of mixed sexes, and unidentified birds were recorded by aerial survey crews. Each drake on a breeding area, except drakes in groups of mixed sexes, was assumed to be mated to a hen for calculations of the index of ducks per square mile for each provincial stratum. Unidentified birds were allocated to species and sexes on the basis of the proportions in the identified segment. Aerial surveys were designed so that the sampling error of the total duck index, for each province, would be less than 20 per cent at the 0.05 probability level. Smith (1964) in his recommendations for waterfowl breeding ground aerial surveys noted that pairs, lone drakes, and flocked drakes should be enumerated for mallard, pintail, and canvasback

in the May pair surveys, but that groups of two or more drakes or groups of three or more birds of mixed sexes should not be recorded in the July production surveys. In July, late nesting indices should be arrived at by enumerating pairs or single drakes only. Hammond (1966) suggested enumeration of drakes in groups of up to five on large study blocks but only those of two or less on small study areas, i.e., less than 640 acres. Widgeon and shoveler grouped males were not to be tabulated. Lone males were to be enumerated but not lone females, except for lone diver females and hens on artificially constructed ponds, where the waiting drake may be located on a large nearby marsh.

For divers, with heavily distorted sex ratios, counts of all males would naturally lead to overestimation of breeding populations. Murdy (1964) enumerated only observed pairs of lesser scaup and ring-necked ducks on the Yellowknife Study Area, Northwest Territories. In Manitoba, Rogers (1964) considered pairs and lone females as indicated pairs of lesser scaup. In western Montana, Lokemoen (1966) considered only pairs of redheads in estimating breeding populations and discounted lone drakes and lone hens.

European census methods

In Finland, Koskimies (1949), Hilden (1964), and Grenquist (1965, 1966) utilized counts of males, pairs, and the number of nests found in relation to pair numbers to estimate yearly changes in waterfowl population numbers. Most of the counts were conducted around islands of various archipelagos and included velvet scoters (*Melanitta fusca*), mergansers (*Mergus serrator*, *M. merganser*), tufted duck (*Aythya fuligula*), mallard, pintail, goldeneye, shoveler, and teal (*Anas crecca*, *A. querquedula*). Koskimies (1949) discussed the methodological aspects of hourly, daily, and seasonal estimates of island-nesting velvet scoter and red-breasted merganser (*M. serrator*) populations. He concluded that time of day, stage of summer, weather conditions, personnel experience, and other environmental factors all affected the validity of estimates obtained. With velvet scoters, morning and afternoon counts gave comparable results during the early spring. Summer counts showed greater variability, as males left the breeding area and fewer pairs were enumerated. Nonbreeding year-

lings were separable by plumage. Difficulty was experienced in separating nonbreeding and breeding components of merganser populations.

In Iceland, Bengtson (1967) used a composite of methods to arrive at breeding populations of 15 duck species on Lake Myvatn. The lake covered 14 square miles, had an irregular rocky shore line of over 20 miles and contained 30 islands. Direct counts were used in the latter half of May and continued until egg laying was well advanced. Preliminary counts were adjusted when results of nest studies, moulting area counts, and brood studies were available. He felt there was an error of only 15 per cent in his estimates on a population that lay between 13,500 and 18,500 pairs.

For grassland areas I recommend, in a following section, the periodic enumeration of all dabbling pairs, lone drakes, and grouped drakes as indicated breeding pairs before specific dates, based on nest phenology, and the correction of the data with a prelaying season sex ratio to account for unmated males. Lone hens are not enumerated unless they are from an uncommon breeding species. Because of highly distorted sex ratios and aggregation of pairs on certain preferred ponds, diver population estimates are better taken from nesting studies supplemented with periodic counts of pairs and lone drakes on waiting sites.

In all, a number of different population components have been utilized to estimate breeding pair abundance or to arrive at some population index. Although most authors recognize that their estimates are crude, few have attempted to show the magnitude of errors of estimate or describe biases encountered in the use or rejection of a population component. The need for an evaluation of what components to count for each species, what time of year they should be counted, and the standardization of censused components between workers and areas is obvious.

Appraisal of factors influencing inventories

On the basis of field programs on the two study areas, a number of corrections to potential sampling errors and biases and solutions to problems of duck population estimation present themselves. Unmated males and the census

Although the proportion of unmated males that remain through the breeding season on the pot-

hole breeding habitat is unknown, there are observations that May sex ratios may be more distorted in large marshes where unpaired mallard and pintail males congregate (Hochbaum, 1944; Ellig, 1955). For parkland pond habitat, Diem and Lu (1960) discussed the errors involved in censuses because of distorted sex ratios and enumeration of unmated males as indicated pairs. For the present study, I assumed that the greater proportion of unmated males remained on the study areas until immediately prior to the brood season. Firstly, the assumption was based on some incomplete data on marked, unpaired drakes. Of 23 mallard, pintail, gadwall, widgeon, and blue-winged teal unpaired males marked in 8 years, 11 were subsequently seen on or around the study areas where they were marked, for periods up to 42 days. Furthermore, observation of marked pairs showed that as many as one in four may disassociate themselves from the home range because of the disturbance due to marking and capture. Utilizing a similar ratio for unmated drakes, I concluded that from 48 to 65 per cent of the unpaired drakes may also remain on or near a study area, at least during the laying and early incubation periods and be available for censusing. Secondly, in 1964 and 1965, at Wau-bay, South Dakota, Drewien (*in litt.*) established that unmated blue-winged teal drakes composed 15 to 20 per cent of the resident population of drakes of a study block and remained there throughout the breeding season. Unmated males showed varying degrees of site tenacity and localization of activity through the month of May to early June, as did the mated males and breeding pairs. Thirdly, Bossenmaier (1951: 61), who intensively censused a major moulting marsh, Whitewater Lake in southern Manitoba, did not record the first flocks of 10 or more mallard drakes until May 28, 1950, and May 21, 1951. While these may have been either previously paired, postbreeding or unpaired drakes, he gives no records of earlier congregations of drakes. I suggest that the greater proportion of both mated and unmated drakes of most dabbling species do not leave the breeding ponds for the moulting lakes until the nesting season is well under way. They are thus located on the breeding grounds and can be erroneously assessed as potential breeding pairs.

On both study areas, marked, unmated males were seen to aggregate with mated males whose

hens were incubating and to take part in GFAC and ARF. They may also associate with pairs as novice drakes (Hochbaum, 1944) or form groups of two, three or more. In early April, associations of two or more unmated pintail drakes were common but fewer small groupings of unmated drake mallards were observed. During the prenesting period, groupings of two unmated males of other dabbling species were also uncommon except for blue-winged teal.

As all males are counted as potential breeding pairs, the use of a correction factor to disregard unpaired drakes should be valid, in order to assess only true pairs.

With all species the number of unmated drakes observed in the prebreeding period varies slightly from year to year (Table 3). If sufficient counts are made to show a significant difference, then the yearly sex ratio correction factor should be applied to the indicated population based on all drake and pair counts. If no counts are available the average prebreeding male to hen ratios found in Bellrose *et al.* (1961) and in Table 3 might be used.

Sex ratio correction factors

The problem of overestimation by enumerating unmated lone males as indicated mated pairs becomes acute in those dabbling and diving duck species which are regularly known to have distorted sex ratios on the breeding grounds (Bellrose *et al.*, 1961). Since it is almost impossible to separate lone mated from lone unmated drakes on the basis of plumage or obvious behavioural characteristics, I propose that all drakes should be enumerated as breeding pairs 1 to 2 weeks before the first appearance of broods, and that a prelaying sex ratio correction factor should be applied. For yearly trend information, in those species whose sex ratio may not fluctuate widely, enumeration of all drakes should not distort measures of relative abundance. For more sophisticated and accurate measures of populations and the factors limiting recruitment on special study blocks some correction for the unmated male component must be made (cf. Table 9).

The errors involved in assuming that all unmated drakes are indicated pairs have been recognized by many workers (Hochbaum, 1944; Murdy, 1953; SOWLS, 1955; Diem and Lu, 1960; Bellrose *et al.*, 1961; and Hammond, *in litt.*, 1966). Hawkins, Gollop, and Wellein (1951)

concluded that obtaining prebreeding sex ratio data offered a logical method of correcting aerial counts for hens not seen associated with drakes. However, Kiel (1951) cautioned against the use of sex ratio correction factors because egress of pre-moulting males might equal disappearance of nesting females from the transects, the result "being a constant sex ratio but a decreasing countable population". On the Yellowknife Study Area, Northwest Territories, Murdy (1962) enumerated all drake lesser scaup and ring-necked ducks and applied a sex ratio correction factor for the imbalance of males. The method assumes that sufficient prebreeding sex ratio data are available. Murdy (1964) later utilized counts of pairs and drakes on waiting sites to estimate breeding populations.

Late influxes of pairs

In May, the separation of late migrant pairs or drought-displaced birds from residents is nearly impossible to make. The criterion I used revolved around whether pairs were grouped or spaced and general behaviour, such as whether hens gave the persistent quacking call or drakes showed hostility toward hens of pairs. However, during the transitory, postmigration period pairs may be spaced from other pairs but do not yet show activity localization. Such pairs could be included as residents.

Late May and June influxes of breeding pairs nesting for the first time or influxes of re-nesting pairs are apparently common on some marsh and pond study areas (Jessen, Lindmeier, and Farnes, 1964; Hammond, 1959; Kirsch, *in litt.*). Such influxes give rise to a multitude of sampling problems in the accurate assessment of the seasonal or total number of pairs which attempt to nest on a specific area. Hammond (1959; letter June 11, 1967) noted influxes of birds into the marsh habitat of Lower Souris National Wildlife Refuge, when: (1) sheet water disappeared from fields surrounding the marsh, (2) mass destruction of nests occurred through farming practices, (3) drakes and hens made pre-moult movements away from their breeding grounds, possibly after only one nesting attempt. Yearly, I recorded early June influxes of mallard pairs on the Rose-neath Study Area, where ponds were intensively surveyed, but could not differentiate late migrants from resident pairs on the Kindersley Study Area because of much larger populations of all species. At present, the sampling problems in-

involved with adequate census of seasonal populations and the differentiation of residents from new arrivals appear insurmountable. Where influxes occur indirect methods, concerned with nest counts and brood numbers, may have to be used to estimate breeding populations.

GFAC, ARF, TBF and the census

Both mated and unmated drakes join spring and summer aerial flights, i.e., group flights associated with courtship and attempted rape flights, and all drakes in such flights temporarily on ponds have been enumerated on the Kindersley Study Area. As such flights may extend for 1 to 4 miles and gather drakes from a number of ponds they would tend to distort population estimates from narrow one-quarter-mile roadside strip counts and therefore might be deleted. Observations of behaviour of drakes in aerial flights temporarily on ponds should be noted so that late season, postbreeding groups of males and pairs are not classed in error as breeding birds in flights. The number of flights observed is small in relation to over-all population numbers, except for ARF of pintails and GFAC of lesser scaup, where groupings of males with one hen are common through May. Attempted rape flights may be more frequent in all species during late afternoons, at a period when incubating hens are taking their recesses and are more prone to attract drakes. If censuses are conducted in the 0800- to 1200-hour interval the number of three bird flights seen is much reduced over the early morning (0530-hour) and late evening (1800-hour) periods. Therefore, sampling errors due to mobility should be minor. Most mallard ARF were observed in the early mornings and late afternoons, after hens started to incubate. Few were enumerated in the 0800- to 1200-hour census interval. Mallard and pintail GFAC are usually seen in early and mid-April and are commonly associated with migrating flocks. The number observed per day on pond breeding habitat, during any optimum census period in May, will be negligible, especially if transects or study blocks are located at some distance from habitat where migrants congregate. For other dabbling species few GFAC were recorded after May 15 or during the optimum census period.

Pair bond duration and the census

Much variation of pair bond duration exists between and within species of Anatidae. The duration of the pair bond, size of home ranges, and

period of localized activity on a waiting site all affect accuracy of spring pair censuses. Hochbaum (1944) recorded the early abandonment of hens by drake mallards and pintails, usually after laying of the clutch. Sowlis (1955: 101) noted that blue-winged teal and shoveler drakes did not abandon their hens until late incubation, while mallard, pintail, and gadwall did not associate with the hen after clutches were complete. Similar observations were made by Smith (in Bellrose *et al.*, 1960: 427). Leitch (1952) noted that mallard and pintail drakes remained on territories the shortest time, while blue-winged teal, widgeon, and shoveler drakes remained on their territories much longer and population figures for these species, taken from ground counts, should be quite accurate. Bue (1952) pointed out wide variations in the times that species and individual drakes abandon home ranges. Similar variations in stage of incubation at which drakes desert hens were also reported by Oring (1964). McKinney (1965) summarized the available literature on pair bond duration in North American Anatidae. He showed that many diver and dabbling drakes did not associate with their hens after the first week of incubation. However, blue-winged teal, shoveler, gadwall, and lesser scaup generally abandoned their hens only after the second or third week of incubation. Gates (1962) reported that drakes of reneesting pairs of gadwall abandoned their hens sooner than drakes of initial nestings, a conclusion I have substantiated in following reneesting mallards, pintails, and blue-winged teal. In Maine, Stotts and Davis (1960) noted that seven drake black ducks attended hens from 7 to 22 days, averaging a minimum of 14.3 days, during early, first nesting attempts. For eight examples of late reneesting, drake attendance varied from 4 to 16 days and averaged only 9.1 days. I noted that the pair bond may also be retained through a reneesting attempt. Nine hens, of dabbling pairs which reneested, were trapped and marked over an 8-year period. Five of the nine reneesting hens were subsequently seen with their original drake while four had reformed pair bonds with another unmarked drake. Kirsch (*in litt.*) suggested that some mallard and pintail pairs retain the bond for periods of up to 2 months and reneest several times.

I also noted wide yearly variations in time of breaking of the pair bond. In 1958, an exceptionally early breeding season with hatching start-

ing on May 15, 22 mallard hens and broods were observed with associated drakes, whereas in years when hatching peaked after May 25, fewer than five were recorded annually. In 1955, 1956, and 1958, I have recorded newly hatched broods associated with pairs of blue-winged teal and shoveler in late June, 2 weeks after the first broods of this species were recorded. Kirsch (letter, June 27, 1967) noted "many" blue-winged teal broods with associated drakes on the Woodward Study Area, North Dakota. Most drakes were seen with early season broods but seldom remained with the brood beyond the first few days. At Roseneath, I regularly saw drake ruddy ducks associated with hens and broods up to 10 days old. In all cases of drakes with broods the hen did not take the "repulsion posture" and it was therefore assumed to be a mated pair. Thus, some drakes have stronger hen attachments and are associated with their waiting areas for longer periods than other drakes. Therefore, they are more readily seen and available to be censused as indicated pairs.

Pair bond duration is related to strength of site tenacity by the drake and the daily re-use of the activity centre by the hen and drake. Pair bonds are periodically re-enforced through the early and mid-incubation period as long as the drakes return to the waiting sites while hens are on recess. Tight pair bonds are maintained by frequent and joint activity through the migration, postmigration, and laying period but progressively weaken as the pair is associated less and less during incubation. Strong pair bond attachment in males is associated with strong attachment for the waiting site of the home range. Site tenacity to the breeding home range leads to faster pair bond re-establishment whenever the hen returns to the home range to feed, bathe and preen during her infrequent recesses. Pintail drakes appear least attached to the waiting site; other dabbling drakes return regularly to it or to favoured feeding areas in early morning and late afternoon to rejoin the hen on her recesses during these periods. Other dabbling drakes, especially mallards, whose hens are in the same period of incubation do not disassociate themselves from drake aggregations and are therefore found less frequently on the waiting sites. Such differences appear due to individual behaviour.

In short, the period of drake desertion of the home range varies with the species, the individual

pair, the nesting phenology of a season and perhaps density of pairs. There is no sharp break but only a general waning of the pair bond and attachment to home range. Therefore, no accurate and predictable period of drake desertion can be given for a species or for any breeding season. In general, mallard and pintail drakes should be censused before their hens are in their second week of incubation, whereas widgeon, shoveler, gadwall, and blue-winged teal can be accurately censused by counting drakes through the second or third week of incubation. The correlation of census periods with breeding phenology is imperative.

Grouped drakes and the census

In spring the period of strongest pair bond attachments is associated with periods of maximum pair spacing and maximum drake intolerance. These periods extend from the time of dissolution of the migrating flock to the beginning of incubation. Paired mallard drakes rarely associated with each other in the prenesting and early laying periods. Unmated drakes of all species remain gregarious while even some mated pintail drakes may associate with each other during the laying period (Smith, 1963). At Kindersley, there was a strong tendency for groups of four to seven drake pintails to associate, although this may have been a reflection of the higher percentage of unmated males found in this species (Table 3). At Kindersley, more groups of two to eight drakes with a single hen, in GFAC or ARF, were seen of pintail than of mallards (Tables 8a, 8b). In mallards the period of drake intolerance is followed by a period of drake sociability. Mated drakes form small aggregations, usually two or three but up to ten. Such morning and mid-day drake associations are characteristic of mallards and pintails toward the end of the egg laying period and through incubation (Tables 8a and 8b). However, mated drake associations were rarely observed in widgeon, shoveler, gadwall, and blue-winged teal until mid- and late incubation periods (Tables 8c, 8d, 8e, 8f). Bue (1952) and Evans and Black (1956) noted that grouped mallard and pintail drakes were conspicuous before broods appeared. These authors noted that with blue-winged teal, whose drakes stayed with hens until nearly hatching time, grouping of drakes coincided with the appearance of broods. Thus, as the drake-hen bond wanes, drake intolerance for other drakes also wanes and males form

aggregations for varying periods of the day. A number of inter-related phenomena occur with drakes after the hen begins incubation: (1) the hostility of drakes toward hens and other drakes decreases, (2) the tendency to behave sexually toward all hens except his own mate increases, (3) drakes disperse widely from their waiting area sites, (4) they begin to associate with other drakes in larger and larger groups. Most drakes make a final break with the breeding ground from 2 to 5 weeks after the hen has started to incubate when they form large pre-moulting flocks and migrate to moulting lakes. Few drakes of any species, except small groups of blue-winged teal, were recorded moulting in the parkland or grassland study area ponds.

Most mallard drakes with incubating hens tend to form associations with other drakes during the mid-day hours, 0800 to 1600. Before and after this interval drakes either avoid association with other drakes or remain isolated on their waiting areas. Morning counts, i.e., 0800 to 1200 hours, showing a breeding population of predominantly pairs and lone drakes would indicate that the greater portion of the pairs are in the pre-laying and laying interval. Censuses which show a preponderance of lone males and grouped males would indicate that most pairs are laying or incubating.

I made observations in parkland, grassland, and large marsh habitats which suggested that males associated more readily under dense than under sparse population situations. The opportunity for drake association is increased or drakes may be forced to group by lack of surface waters or common loafing spots. Also, if large marsh areas serve as congregating areas for unmated males, they may be seen associated throughout the breeding season (Hochbaum, 1944; Ellig, 1955).

In summary, on block-type study areas, enumeration of groups of males of five or less, especially mallards and pintails, before the appearance of first broods in mid-May, is a valid measure of indicated breeding pairs. They should be enumerated on large sample plots (4 square miles or over) but further investigation of their distribution and activity patterns should be made before all such groups are tallied on narrow transects. For other dabbling species in which groupings of drakes are generally less than five, i.e., two's and three's, all such drakes should also be enumerated

as indicated pairs on block areas prior to recommended cut-off dates.

Optimum census periods

I have recommended that optimum census periods be established yearly for each species. These should be based on migration chronology and nesting phenology. Counts should be conducted when the greatest proportion of any species is in the pre-nesting (including re-nesting), laying, or early incubation stages. For 1956 through 1959 at Kindersley, Saskatchewan, the interval from May 8 to 20 was considered optimum for censusing mallards and pintails, from May 20 to June 5 for widgeon and shovelers, and from May 25 to June 10 for gadwall and blue-winged teal. In years with no April cold snaps, counts for mallards and pintails could be initiated 2 to 3 weeks after the first few hens start to lay or are seen dropping into nesting cover. Egg laying may start from 10 days to 3 weeks after the first pairs migrate into an area. For other dabbling species, counts should start 1 to 2 weeks after the first eggs are noted. All censuses should terminate before the first few broods appear or better still when the first nesting hens are in their third week of incubation. Censuses taken in the above intervals will assess populations of pairs in their first nesting attempt at a relatively stable level. Exceptionally late migrants or drought-displaced birds moving into an area in mid-June would still not be adequately enumerated without later periodic counts.

Murdy (1953) concluded that optimum census periods occurred after the migrants had left and before emergent vegetation and pair behaviour changed. For 1951, he pointed out that the optimum time for the annual duck survey in South Dakota was during the week of May 13 to 23 when mallard, pintail, shoveler, blue-winged teal, and gadwall pairs were all in residence and populations were relatively constant. The optimum survey period for mallard and pintail pairs extended from April 28 to May 28 while for the remaining three species it extended from May 15 to 28. Hammond (1966) noted that optimum census periods vary annually by 7 to 10 days. He recommended a May 7 to 17 census period in North Dakota for mallards, pintails, canvasbacks, and wood ducks and a May 25 to June 7 census period for gadwalls, blue-winged teal, redheads, lesser scaup, and other species. For a study block in the forested habitat of the Northwest Territories, Murdy (1964) recommended two censuses,

one immediately after ice break-up between May 20 and 25 for all puddle ducks except shovelers (but including canvasback) and the second between June 6 and 12 for late nesting divers. Where possible, single censuses should be avoided, although Salyer (1962) felt a single valid census could be conducted in early June at the period of nest initiation of blue-winged teal.

Number of seasonal counts required

Intensive studies of waterfowl breeding chronology and optimum census periods show that all duck species do not migrate into a region or initiate nesting at the same time (Kiel, 1949; Lynch, 1951; Murdy, 1953; Bue, 1952; Stoult, 1952; Smith, 1956; Evans and Black, 1956; and others). All dabbling species show peak indicated populations at different times, usually associated with the period of strongest site attachment, i.e., prenesting, laying, and early incubation periods. Mallards, pintails, and canvasback are generally early breeders; widgeon, shoveler, redhead, and ring-necked duck intermediate; while gadwall, blue-winged teal, lesser scaup, and ruddy ducks are late breeders. Regional differences in start of nesting may occur as Kirsch (*in litt.*) noted that blue-winged teal on the Woodward Study Area, North Dakota, could be considered intermediate breeders. Generally, one census cannot accurately assess peak populations of all species. I concluded that a minimum of two, and possibly three, counts may be necessary to assess pair numbers of a multi-species breeding population with asynchronous nesting periods.

Very early, Mendall (1948) had noted that more than one count might be necessary to enumerate early hatching black ducks and goldeneyes and late hatching ring-necked ducks and teal (*A. carolinensis*; *A. discors*). Kiel (1949) conducted as many as four breeding pair censuses on 12 Manitoba transects. The highest mallard and pintail populations were recorded in the April 21 to 25 count while the highest indicated populations of widgeon, shoveler, gadwall, and blue-winged teal were noted from May 14 to June 6. Lynch (1951) recognized that late breeding blue-winged teal and lesser scaup could not be adequately surveyed in mid-May at the time of the mallard and pintail aerial census. For over 10 years in the parklands of Saskatchewan, Stoult (1964) used two censuses to assess breeding populations, one in May for early breeders and the second in June for all other species. Similar

double censuses were conducted on various Alberta study areas by Smith (1957). Evans and Black (1956) made periodic censuses, April through August, on the Waubay Study Area, South Dakota. All authors utilized the peak number of indicated pairs for any one period as the estimated breeding population for the respective study or transect area. However, as discussed later, I suggest four or five replicate counts and a mean population estimate would better describe species pair numbers than a maximum count taken from one census. To establish trends, and where time and manpower is limited, a single count can be successfully used to estimate total populations, as has been proposed by Hammond (1959; *in litt.*).

Time of day for counts

I have recommended that in grassland areas where emergent vegetation does not affect visibility of ducks, ground counts be conducted between 0800 and 1200 hours. Between these times, pairs and drakes localize their activity and are least mobile; most laying and incubating hens are on their nests, winds are low, and light is favourable. Diem and Lu (1960) recommended that for censusing mallards on transects in parkland habitat, counts be conducted in morning hours after 0530 but before 0930 hours as both pairs and lone drakes are more visible in early morning and leave transect ponds in the forenoon. They showed no statistically significant differences in indicated numbers of blue-winged teal and lesser scaup for counts conducted at 0530, 0930, and 1330 hours. They further concluded that aerial counts made at mid-day may be from 30 to 50 per cent lower than early morning counts and recommended all censuses be made from 0600 to 1200 hours. Smith (1956) concluded that for parkland areas of Alberta mid-day aerial counts, when pairs were most inactive, did not give accurate coverage. Numbers of paired ducks observed in mid-day decreased from early morning counts while numbers of single males increased. In Manitoba, Rogers (1964) began lesser scaup counts between 0800 and 0900 hours, completing them in 2 to 3½ hours. For marshes, pond-habitat blocks, and transects, Hammond (1966) recommended all-day counts starting after 0900 hours, as some duck pairs were in nesting cover prior to this time. Late afternoon counts in large marshes were to be avoided. Kirsch (*in litt.*) censused ducks

For a single species or those with similar phenology.

from 0800 to 1500 hours on the Woodward Study Area. For aerial surveys of ducks of prairie small pond habitat, J.D. Smith (1964) points out that transect counts should be completed by noon of each day. Optimum daily and seasonal times for aerial pair surveys are also discussed by Stewart *et al.* (1958) who point out that winds generally rise toward mid-day, while light is poor in the early morning and evening.

Daily patterns of use of marsh areas or ponds may affect optimum census times. In North Dakota, Lacy (1959) noted that peak use of ditches by nesting pairs occurred 2 hours after sunrise with decreasing evidence of pair use thereafter, as birds retired to an adjacent large marsh. By 1300 hours fewer than half the pairs enumerated in the morning were assessed. In 1967 counts, on part of Lacy's study area, Hammond (letter, June 11, 1967) found substantially more pairs present in the morning than afternoon. Many pairs retired to a nearby marsh after egg laying and drakes of incubating hens also tended to fly to the marsh in afternoons. Hammond pointed out that late afternoons were a good time to find redhead drakes on open bays, especially during the laying period. Sowls (1955: 54) recorded maximum populations of pairs in a roadside ditch from 0400 to 0800 hours, decreasing pair numbers through mid-day, and minimum numbers from 1600 to 2000 hours. He also stressed that sharing of a single loafing spot by several pairs of blue-winged teal and gadwall may occur at different times of the day. A pair located in one spot during one census period need not be the same pair in the spot at a later period. For any one species, a turn-over of pairs occurred with the early, intermediate, and late nesting hens and their drakes using the same spot for varying portions of the morning. Heavy vehicular traffic on transect routes may also tend to flush birds, forcing them away from well-travelled roads after the mid-morning hours.

Generally, high post-noon temperatures and winds tend to affect mobility, visibility, and therefore, countability of ducks. On the Kindersley Study Area many pairs, lone, and grouped drakes rested on shore lines whenever temperatures exceeded 60°F and winds were low, a situation also reported by Diem and Lu (1960). This behaviour and their general inactivity made them difficult to locate visually during the afternoon, from 1200 to 1600 hours. Activity in-

creased after 1700 hours. For parkland and marsh habitats estimates made from early morning counts, 0400 to 0800 hours, when all ducks are most active and visible, may more closely approximate absolute breeding populations. Although visibility is increased, estimate biases will occur because of mobility of pairs and absence of some pairs in nesting cover or distant feeding grounds. Standardization of census times between habitats need not be important if statistical testing of counts shows little hourly variation in countableness or if correction factors can be used. Most studies suggest that more consistent and accurate counts are obtainable in the early and mid-morning than in the afternoon and evening.

Duck and pond distribution

Ducks and ponds are not regularly or randomly distributed over the parkland and grassland pond habitat. Potholes do not occur "in neat patterns or regular numbers" (Smith, Stoudt, Gollop, 1964). Pond distribution and numbers change seasonally as some small, temporary potholes dry through April and May. Ducks themselves tend to be found in aggregations on favourable potholes or portions of any habitat block, i.e., a contagious distribution (Grieg-Smith, 1964; Southwood, 1966). Pairs of some species, e.g., divers and blue-winged teal, appear more social and are found more closely associated on "primary waiting areas" (Dzubin, 1955), than other species. In grasslands, pair and drake pintails are more closely aggregated than mallards. Other dabbler species tend to be more dispersed because of inherent behavioural spacing mechanisms. Since the degree of spacing and intensity of coactions varies with the breeding phase of each pair and the density of pairs (Dzubin, pers. obs.), the spatial distribution of pairs, lone drakes, grouped drakes, and grouped prebreeding and postbreeding birds, throughout the breeding season, is a constantly changing phenomenon. In spring, newly arrived pairs are aggregated. With the advent of nesting, pairs space themselves from other pairs. Spacing mechanisms promote regularity of distribution while sociability leads to contagious arrangement of indicated pairs over the habitat. As early as 1951, Lynch (1951) had recognized seasonal spatial distribution as a major sampling problem for aerial transect counts. He noted that when drakes and pairs start to group in late May the

optimum period for census has passed, especially since enumeration of "ganged" drakes on transects biases the resultant density figures.

Any inferences or predictions of population densities based on single, seasonal counts during an extremely complex period of spatial distribution are subject to wide error, unless sampling conditions are intimately known. The accurate measurement of density of a multi-species population in any habitat is extremely difficult (Odum, Cantlon, and Kornicker, 1960; Preston, 1948, 1962; Williams, 1953) and requires further investigation in pond-type waterfowl habitat.

The statistical concepts underlying strip intersect methods as measures of bird density have been discussed by Moore (1955) and Davis (1963). With waterfowl, transect censuses over one-quarter- or one-eighth-mile-wide strips dissect a large number of home ranges. Ponds on which ducks are enumerated may be resting, feeding, loafing, nesting, waiting, or social congregation areas. The hourly, daily, and seasonal use of ponds varies but replication of counts can be used to pool data and determine average densities of breeding pairs. Density of pairs affects the distribution pattern of pairs or lone drakes, as do favoured feeding or loafing spots. All these factors should be weighed to better plan transect surveys and predict the accuracy and precision obtainable from any strip census.

Recommendations for block study area census

Grassland

On the basis of the behaviour of marked birds, studies of the chronology of nesting and frequent direct counts of pairs, I propose that the following procedures be utilized for ground census on large, square-shaped study areas, e.g., 10 or more square miles, in grassland habitats, where emergent vegetation has little effect on visibility of ducks. Their use should allow estimates which more closely approximate absolute breeding numbers per unit of pond-type breeding habitat. The extrapolation of these recommendations to marsh, parkland, and wooded habitats or to transect counts might require further sampling and modification, as visibility and mobility factors vary among habitats. I assume that all field workers are able to differentiate between waterfowl species and are able to recognize

various component groups: lone drakes, grouped drakes, aerial flights, migrating groups, etc.

1. Censuses should be conducted during an optimum interval of the breeding season, i.e., when most pairs and drakes show maximum site attachment, an indication that the greatest percentage of the population is in the prenesting (including renesting), laying, and early incubation stages. Complementary nest phenology data are required to determine optimum census periods. Breeding chronology can also be crudely deduced from ratios of pairs to lone drakes to grouped drakes taken during mid-morning censuses. For counts made between 0800 and 1200 hours I suggest a simple rule of thumb for optimum census time of mallards and pintails. Ratios of pairs to lone drakes to grouped drakes should be approximately 1:1:1 (i.e., one-third or less of the total indicated population should be enumerated as pairs, with the remaining two-thirds or more as lone or grouped drakes). Phenologically optimum census periods for other dabblers, whose pair bonds and site tenacity are stronger, and whose drakes do not aggregate until after the mid-incubation period, are those in which the pair to lone drake ratio is approximately 1:1 (i.e., one-half or less of the population is counted as pairs). To ensure that pairs or drakes are truly resident and show site attachment, counts for each species must be correlated with time of arrival on the breeding grounds and nesting chronology.

2. Ground census should be conducted between 0800 and 1200 hours, local standard time, when all species are least mobile and pairs and lone drakes are most likely to be on their waiting sites. As few birds as possible should be flushed. Any birds taking flight should be visually followed to locate their points of landing. These birds are then subtracted from counts if they land on ponds yet to be censused or added if they alight on already enumerated potholes. Birds flushing at some distance from the observer should be recorded as unidentified ducks.

3. Census should be conducted on sunny or bright, but not heavily overcast days, with temperatures above 40°F and with winds not in excess of 15 mph, because rain, heavy cloud cover, low temperatures and high winds all affect mobility, dispersion, and visibility of ducks (see Diem and Lu, 1960). Winds increase in velocity

in the Canadian prairies in afternoons. Mornings present more optimum counting and light conditions. Counts should be conducted from the south or east edge of ponds to avoid difficulties in identification caused by backlighting and water reflecting sunlight. Replicate counts should be made at the same time of day during the optimum census period, over the same route and under approximately similar weather conditions.

4. To obtain adequate estimates more than one census should be taken at the optimum period for each species and an average of four to six counts be used rather than maximum or minimum counts of each species. Accuracy and precision are both increased with multiple counts. Average population figures taken from multiple counts give some indication of the magnitude of the error of estimates due to mobility of drakes and the temporary absence of drakes from their waiting sites.

5. Because a single census can not adequately measure populations of early nesters (mallard and pintail), intermediate nesters (widgeon and shoveler), or late nesters (gadwall and blue-winged teal), a minimum of two different censuses must be conducted in the grasslands to sample a multiple-species breeding population. Under the conditions studied from 1956 through 1959, censuses of mallards and pintails made between May 8 and 20 and censuses of widgeon, shoveler, gadwall, and blue-winged teal made between May 25 and June 5 adequately sampled breeding populations for determination of yearly trends. Counts made after these dates tended to underestimate breeding pairs when drakes abandon home ranges or to overestimate populations when small, postbreeding flocks of drakes moved into the region. Drakes whose hens are incubating congregate and may wander away from their home ranges, beyond the boundaries of the study area.

Where only a single census can be conducted, the optimum period in an "average" year (i.e., one with no bimodal peaks in nesting effort) could be described as approximately a week before the first mallard or pintail broods are observed and while most of the intermediate and late nesters are in the prenesting, laying, or incubation stages. At Kindersley May 15 to 25 seemed most suitable to estimate early breeders and late breeders. Single censuses conducted after May 20 will tend to underestimate the mallard and pintail segment

as some drakes have left the breeding home ranges. For the intermediate and late nesters, single counts taken as early as May 15 may not assess late migrants. Censuses of mallard and pintails taken after May 31 tend to overestimate the population if small groups of five or less postbreeding drakes congregate on favoured loafing sites and are counted as indicated pairs and not as postbreeding males. Censuses may be biased in years of extended nesting. When breeding seasons are staggered, with the first broods appearing when the late breeding pairs are initiating their first nests, some drakes have already abandoned home ranges. Two separate censuses may have to be undertaken in years when cold spells protract the breeding season.

6. All censuses should be conducted from a vehicle which is driven to a point overlooking each pond, but not close enough to flush birds. To assure that all birds are visible and not sleeping on shore some minor commotion, slamming of car door or sounding of horn, should be used to alert them. Counts should be conducted in vegetated ponds before new growth becomes dense. In late June, birds may have to be flushed by walking through ponds choked with emergents.

7. All lone pairs and lone drakes should be considered resident, indicated pairs if they are spaced 15 or more feet from other pairs. Before the start of nesting in April and again in June, all aggregated pairs are to be considered migrants, displaced birds, or postbreeding groups. Lone females are not to be considered pairs. Practically all dabbling hens are paired and disassociation of drake and hen is invariably temporary. Late June and July counts of lone hens, after drakes have left the breeding grounds, may be used as evidence of incubation and continued breeding but because of variable daily recess periods among hens, no estimate of total number of hens incubating can be made from single censuses taken during one time interval of the day. The enumeration of lone hens as indicated breeding pairs should be restricted to uncommon or rare breeding species, e.g., at Kindersley, green-winged teal made up less than 1 per cent of the breeding population. Lone hens found over one-half mile from the next nearest drake of an uncommon breeding species could be assessed as a pair.

8. All groupings of males from 2 to 10 should be considered indicated pairs except for the following stipulations:

(a) Mallard and pintail grouped drakes of up to 10 should be considered resident pairs until approximately 1 week before the first two to three broods are observed, i.e., about May 20 at Kindersley. Thereafter, to the first week of July, only groups of five or less should be considered resident pairs. Stage of body moult and behaviour may aid in separation of apparent breeding drakes and those in postbreeding flocks. Prior to mid-incubation, groups of two to five, inclusive, mated mallard drakes can be considered the same as lone males on waiting sites, as periodic shifts toward aggregation and then dispersion occur during the day.

(b) Widgeon and shoveler grouped drakes of five or less in number should be considered resident pairs until the first appearance of two or three broods, i.e., approximately June 5 at Kindersley. Rarely do mated drakes of these species associate before their hens are in mid-incubation. If grouped drakes are observed before May 10 they are invariably unmated but corrections for these individuals can be made using the prebreeding sex ratio.

(c) Gadwall and blue-winged teal grouped drakes of five or less should be considered resident pairs until the first appearance of broods, i.e., about June 15 at Kindersley. Again, rarely do drakes of these species associate before their hens are in mid-incubation. Grouped drakes observed before May 15 are usually unmated, although an unmated blue-winged teal drake may occasionally associate with a pair or with a mated drake.

The validity of those dates depends on time of spring migration and time of nesting of each species. They can be either 1 or 2 weeks earlier or later depending on nest chronology. For mallards and pintails, counts might be initiated 2 to 3 weeks after the first hens begin to lay in mid-April. For intermediate and late breeding dabblers, counts should be started 1 to 2 weeks after the first clutches are noted. An attempt should be made to complete counts before the first nesting hens of any species are in their third week of incubation.

9. Drakes in groupings of 2 to 30 males and one hen, in group flights associated with courtship (GFAC) or attempted rape flights (i.e., aerial flights temporarily on ponds) should be considered resident pairs as both mated and unmated drakes join such flights. Groupings of several pairs or aggregations of five or more males and

two females in apparent postbreeding groups (usually after June 1) should not be enumerated as resident pairs. A drake initiating a three-bird flight ("territorial chase") from a pond should be considered a resident pair even though he may land elsewhere (see Dzubin, 1957; Leuret, 1961; and McKinney, 1965, for descriptions of all aerial flights). Drakes or pairs flying over an area are not to be counted as resident pairs.

10. Because an unknown, but apparently large, proportion of unmated males remain on the breeding grounds and because sex ratios of all dabbler species are unbalanced toward males, a correction factor should be used to reduce the error arising when all drakes are considered potential pairs. Provided all lone and grouped drakes are counted as pairs (under 8 and 9, above) a correction factor to account for unmated males should be applied. Such factors based on prelaying sex ratios for each species as given in this paper (Table 3) and by Bellrose *et al.* (1961) should be utilized to obtain a "sex ratio corrected population". Sex ratios may fluctuate yearly and may also be different in pond and large marsh habitats. Hammond (*in litt.*) has shown that sex ratios of mallards and pintails can vary yearly, especially following a poor production year, e.g., 1961. An attempt should be made to gather these ratios yearly in each census region. Sex ratio corrected populations are important in determining accurate productivity rates of pairs. If sex ratios do not appear to vary yearly in one habitat type, uncorrected indicated pair figures can be used for determining trends on transects. In summary, all dabbler drakes should be enumerated as indicated pairs but a sex ratio correction factor should then be applied to account for the unmated segment of the breeding population.

11. Enumeration of populations of divers (i.e., *Aythya* sp.) is complicated by unbalanced sex ratios and the congregation of breeding pairs on deep ponds used as preferred waiting sites. Although dispersal, through periodic movements of diver breeding pairs to nearby ponds to nest, does occur, divers show contagious and non-random distribution patterns. For portions of any day through the breeding season, diver pairs and drakes are found loosely associated. Canvasback and redhead (and to a minor extent, lesser scaup) are also highly mobile during the breeding season, the maximum extent of the home range being some 2 to 4 miles. Unless counts

of all preferred waiting sites are made on a study block and consideration given to home range sizes, census of divers will be inconsistent. Also, as Weller (1959) has pointed out, a varying proportion of redhead hens are completely parasitic and do not lay in their own nests. They might, therefore, not be considered true breeding pairs. With divers, only visible pairs or lone drakes known by their behaviour to be on waiting sites should be enumerated as indicated pairs. Nest cover searches should encompass all pond-edge and upland habitats for lesser scaup and all pond-emergents plus nearby shrub uplands for canvasback, redhead, and ruddy duck. For block-type study areas I concluded that a better estimate of diver populations could be made during the mid- to late incubation period of the early nesting pairs, through enumeration of nests, including all those which are viable, hatched, or destroyed.

As with divers, ruddy ducks are best enumerated by nest counts as their secretive habits do not lend themselves to accurate ground census. Also, some pairs appear to be nonbreeding, summering birds. It is acknowledged that nesting studies can also tend to distort estimated population sizes per unit area as localization of prime nesting cover may attract hens from 1 to 2 miles away. Also, all nests may not be located and some late nesting pairs may be considered renesters. Enumeration of observed pairs and lone drakes on waiting sites should be used to complement nest counts and aid in estimating pair numbers. I suggest that census errors are smaller using nest estimates than those obtained from a ground count of indicated pairs which includes all drakes. Where nesting studies are not feasible the enumeration of all diver pairs and drakes and subsequent correction of these estimates with prebreeding sex ratios may give crude population estimates useful in measuring trends (Murdy, 1962). On block areas, lone diver hens need not be assessed as indicated pairs as they are invariably mated with a nearby drake, which may be enumerated as a lone male on a waiting site.

Censuses can be further complicated by bimodal nesting peaks which reflect April or early May cold snaps, by differential and late migrations due to inclement weather factors south of the breeding grounds, and by major shifts of transient pairs in mid-breeding season from

drought-stricken areas. Although measures of an influx of late migrants can be made, their breeding status while on a study area is still unclear. At present, little measure can be made of percentage of such pairs which have already attempted to nest and are nonbreeders. On the basis of species behaviour and examination of gonads, few nonbreeding pairs were found in the parkland habitat but more were noted in the grasslands in drought years. Also, no adequate estimates have yet been made of the seasonal turn-over of breeding pairs on an area (Smith and Hawkins, 1947; Ellig, 1955). Presently utilized counts aid in estimating maximum populations during one time period only, whereas in a dynamic breeding population the actual number attempting to breed on one area may be much higher if the total seasonal population is considered. Mortality of hens and drakes on the breeding ground is largely unknown. Keith (1961: 44) estimated a summer mortality of less than two per cent for males and eight per cent for females of all species. If these are representative figures, pair estimates should be further corrected to account for summer mortality of adults. In all, waterfowl censuses which attempt to measure absolute numbers of breeding pairs utilizing a unit of habitat through the spring and summer remain inexact, but closer approximations can be made of resident pair numbers by studying species behaviour, noting nesting phenology, and utilizing the above recommendations.

Parkland

As previously noted, two different methods were used to arrive at dabbling population estimates on the grassland and parkland study areas. In the grassland, periodic counts were averaged and a sex-ratio correction factor applied to account for unmated males. In the parkland, fewer direct counts were made but many ponds were visited daily, which led to a more intimate knowledge of pairs and species using a particular portion of the block. Pair numbers were assigned to the block if pairs were observed on or near a particular pond during three out of four censuses.

The minimum block size, its configuration, pair numbers, species make-up, pond numbers, vegetation, etc., required to obtain statistically adequate estimates for accurately measuring yearly changes in population size are still largely unknown. Small blocks of 1 to 2 square miles have the advantage of being quickly censused and are most

amenable to replication of counts but the assessment of pairs is subject to wide sampling error and various biases because of bird mobility, overlapping home ranges, and small sample sizes of each species. On larger blocks of 10 square miles or over, sample sizes are increased, but mobility on the edges still persists and no differentiation between late migrants and residents can be made.

Many of the above grassland recommendations can be modified for use on small sample plots of parkland habitat, i.e., 600 to 900 acres containing 50 to 100 pairs of 10 species per square mile. A weekly census of dabbling ducks on all ponds of the area, throughout the breeding season, can be used to determine peak indicated numbers of each species. Optimum census periods can then be calculated for the early, intermediate, and late breeders. For each of these three groups, counts might be conducted daily, from 0800 to 1200 hours, for 4 or 5 successive days and all pairs, lone drakes, grouped drakes, aerial flights on ponds, lone hens, and aggregated pairs or mixed-sex groups be plotted on a base map. Such data can be used to determine any localization of activity of indicated pairs. As noted under grassland recommendations, migration and nesting chronology vary with species. Counts of mallards and pintails should be conducted 2 weeks before those of other dabblers, usually in early or mid-May, i.e., about 2 to 3 weeks after the first hens start to lay. All counts can then be used to aid in estimating breeding pair abundance of dabblers, if the assumption is made that the average indicated population taken from four or five counts during the optimum census period is in fact an accurate representation of the seasonal breeding population. If late migrant pairs are noted moving into the area through the summer, periodic counts from April through July may be necessary.

It should be recognized that any counts conducted over a 5- to 7-day period will not adequately assess the seasonal turn-over of pairs on a block and will not measure late season migrants or breeders. Peak indicated populations may occur in June, after late season influxes of pairs (Jessen, Lindmeier, and Farnes, 1964; Evans and Black, 1956; Kirsch, *in litt.*). More accurate estimates of breeding pairs on small study areas can be made by use of the above census recommendations supplemented by an intimate seasonal knowledge of the behaviour, biology, and nesting success of each pair using

the block. By observing pair behaviour and mobility and by locating nests, a better estimate of resident pairs can be made. Such intense field work requires that a worker confine his summer activities to only one block area. Objectives of any study will determine the degree of accuracy or precision required of any population estimate.

As in the grasslands, counts of diver breeding pair populations are complicated by irregular congregations of drakes and pairs on favoured areas. Seasonal counts of viable, hatched, or destroyed diver nests obtained through periodic nest searches, supplemented by periodic counts of pairs and lone drakes on waiting stations, can be used to assess diver populations on a small block. Census of ruddy ducks is difficult because of their secretive habitat and use of congregating ponds by mated and unmated drakes. A number of hens arrive on the breeding ground unpaired. Early morning (0400 to 0600 hours) and late evening (1900 to 2100 hours) counts on preferred congregating and nesting ponds, in which the observer quietly watches one pond for one-half to 1 hour, can be used to assess breeding pair numbers. Again, a nesting study should complement any census.

Behaviour and census

Waterfowl census, although requiring an appreciation of statistical methods and an adequate knowledge of species biology, also requires an intimate knowledge of species behaviour under a variety of population densities and environmental conditions. The decision whether to include a group of drakes and a single hen of an aerial flight temporarily on a pond or a group of pairs, in the potential breeding pair column of a census sheet, will depend on how well the census-taker knows the seasonal behaviour of each species. Waterfowl census then becomes, in part, an art for those knowledgeable workers who can appreciate key attack, sexual, and escape patterns in drakes and hens and apply such observations to decisions as to whether to include a bird, an aerial flight, or group of birds in a count. Similar sentiments have been echoed by Stokes and Balph (1965) who stress the need for an appreciation of species behaviour for a better understanding of all population ecology phenomena and by Diem and Lu (1960) who point out that "accurate interpretation of census data requires more basic knowledge of the behaviour and physiology of the individual bird".

Today, waterfowl censusing remains highly subjective. Counts made by two workers are not strictly comparable for the same or different areas: Census-takers, themselves, can help infuse more objectivity into counts. Recognition of ducks must be instantaneous. They should also be able to determine by sample counts of pair, lone drake, and grouped bird ratios, the optimum census periods. They should readily recognize any biases and potential sampling errors involved. Accuracy and precision of estimates can, in large part, be a reflection of the knowledge and mental alertness of the individual conducting the census.

Seasonal counts and periodic replication of censuses tend to increase accuracy of estimates. A high degree of accuracy and precision is justifiable on special study areas from which pair population estimates are used to calculate the true number of pairs successful in producing broods. Also, increased precision leads to the better detection of the effects of various limiting factors, however minor, on final production. Valid comparison of results of work in various habitat types is facilitated by data with known sampling errors and variability. Statistically describable estimates of seasonal breeding populations based on proven census techniques still remain a basic need of most waterfowl research and management programs.

Supplementary data required

Waterfowl breeding pair census will become more meaningful as data become available on the following topics:

1. The proportion of any pair population which is nonbreeding and the climatic, density, or habitat factors which lead to nonbreeding: do all yearling lesser scaup and late-hatched mallards of the previous year nest? If they do breed, are they late nesters?

2. Duration of the pair bond in seasons of varying phenology: how long does the "average" drake of each species remain on his activity centre and when do drakes abandon home ranges, i.e., how long are drakes available for counting as indicated pairs? Does site attachment strength change with increasing density?

3. Mobility radii and home range sizes of lone drakes, pairs, and grouped drakes: how does pond density and availability of breeding requisites in each habitat affect home range and activity centre size? What are the daily and

seasonal patterns of activity for each species and each population component? How do daily activity patterns of lone or grouped drakes affect spatial distribution and census?

4. Yearly prelaying sex ratios of all species on the breeding grounds: what is a statistically adequate sample to describe prelaying sex ratios of a species? How long is the period of residence of unmated drakes on nesting grounds and when do they leave for moulting marshes? Do unmated drakes migrate earlier or later than mated ones?

5. Turn-over rates of local populations and the adequate census of total seasonal populations: should indicated pair population estimates obtained in early May be added to mid-June estimates to account for delayed nesting by late migrants, yearlings, and shifting populations? Does the maximum or mean pair population counted during one 3-week period of a 2½-month-long breeding season adequately assess breeding populations actually breeding on a block or transect?

6. The effect of nonrandom and contagious distribution patterns of ponds, pairs, lone drakes and aggregated drakes, on sampling procedures: how do periods of intense spacing activity followed by increased sociability of drakes affect pair and drake distribution and their countability on strips or blocks of habitat?

7. Length of breeding home range residence of pairs which have lost clutches: preliminary observations indicate that some mallard pairs may remain on or near their home range for periods up to 3 weeks after their clutch is destroyed. These pairs make no attempt to re-nest in this interval, and may never re-nest, but they are enumerated as indicated breeding pairs.

As early as 1951, Murdy (1953) stressed that a number of variations of waterfowl activity patterns affected census results: (1) some pairs made only one nesting attempt, while others made several, (2) some pairs of a species completed clutches before others had settled, (3) nesting was asynchronous among species, with pintail drakes deserting hens before blue-winged teal had dispersed for nesting, (4) paired birds were more conspicuous and behaved differently than lone drakes which had deserted hens, (5) shifting of ducks from drought areas during the census interval influenced counts. These same problems are still with us today.

Thirty years after the publication of Bennett's (1938) census recommendations, waterfowl biologists are still using methods which are not being constantly challenged, improved, and tested. Field workers have commendably adapted recommended census methods to varying habitat conditions but too few of them have published or tested their counting techniques. Meaningful comparisons of results of studies by two workers using different methods, with varying error estimates, are almost impossible to make. Apparent differences of yearly estimates may be due more to variations in census methods than to actual population status (Diem and Lu, 1960). Although trend data obtained from population indices are sufficiently accurate for yearly management purposes (Crissey, 1957), trends are not adequate for precise measures and descriptions of species population dynamics.

Summary

From 1952 to 1959, various seasonal counts and census techniques were utilized to obtain estimates of breeding populations of ducks on an 895-acre study block in the parklands of Manitoba and a 6,720-acre area in the grasslands of Saskatchewan. It was determined that:

1. Pintails and mallards arrived first on both areas during the last week of March or first week of April. Later arrivals through mid-April included widgeon, green-winged teal, shoveler, gadwall, and blue-winged teal. Redheads, canvasback, and lesser scaup generally migrated during mid-April. Ruddy ducks were the last to arrive in late April.

2. Spring sex ratio counts showed various degrees of imbalance toward males. Of dabblers, widgeon showed the least disproportionate prelaying sex ratio, 108:100, while blue-winged teal showed the greatest, 120:100. All divers showed marked ratios in favour of males, from a low of 134:100 for redheads to 172:100 for ruddy ducks. No marked yearly variations in sex ratios were noted, although samples were small.

3. The parkland block contained a 4-year average, i.e., 1952 to 1955, population of 75 pairs of dabblers and 20 pairs of divers. It enclosed 129 basins per square mile. The grassland area breeding population averaged 50 pairs of dabblers and 2 pairs of divers on 11 basins per square mile for the 1956 to 1959 period. Basins averaged 0.7 acre on the parkland block and 5.7 acres

on the grassland area. Mallards were the most common breeders on both areas. Nonbreeding lesser scaup were recorded on the grassland block during drought years, 1957 to 1959.

4. Each year, for every species, there is an optimum census period in which the greatest proportion of potential breeding pairs show ties with specific pond sites, i.e., activity localization. These periods vary yearly with time of migration, spring weather, and nesting phenology. However, numbers of early and late nesting pairs may either have abandoned or not yet settled on breeding areas at the time of the optimum census interval. Therefore, counts during this interval may not adequately measure the over-all seasonal population breeding in a unit of habitat. A single spring count cannot adequately assess all pairs of a multiple breeding population with asynchronous nesting periods. Two and occasionally three counts may be necessary to enumerate early, intermediate and late breeding species.

From 1956 to 1959, the optimum census period for mallards and pintails in grassland habitat was May 8 to 20; for widgeon and shoveler May 20 to June 5; and for gadwall and blue-winged teal May 25 to June 10. During these intervals indicated pair populations showed the least fluctuation. Estimates of diver populations should be based on a nesting study, supplemented by counts of observed pairs and lone drakes on waiting stations. A number of recommendations are given elsewhere in the paper for conducting census on grassland and parkland study plots. In grasslands, breeding waterfowl counts should be made from 0800 to 1200 hours, when winds are less than 15 mph and temperatures above 40°F.

5. The most important potential source of error in presently used waterfowl census techniques is the nonenumeration of groups of mallard and pintail drakes of five or less as indicated breeding pairs. Since drakes of other dabbler species do not congregate until the mid-incubation period of their hens, this error becomes minor. Another major source of error is the enumeration of unmated males as potential breeding pairs. Pair, lone drake, and grouped drake components should be enumerated as indicated pairs for all dabbler species. The resultant pair figure should be corrected for the unmated male segment by applying a prelaying sex-ratio correction factor. Grouped drake components were common in mallard and pintail populations and reflect weak pair bond and

site attachments of drakes during the early incubation period of hens. For widgeon, shoveler, gadwall, and blue-winged teal, rarely were grouped drakes seen until mid- and late incubation as these species have stronger site attachment and pair bonds. Replicate counts on the grassland area, whether taken by walking or from a vehicle, showed marked consistency of estimates for mallards but large coefficients of variability for other species.

6. Pair, lone drake, and grouped drake components of a censused population change seasonally and throughout the day. In a mallard population, in which most pairs were laying or in the early incubation stages, counts made periodically throughout a day showed differences in components enumerated with each census. Few pairs were recorded on censuses started at 0530 hours but increasing numbers were seen at 0800, 1300, and 1530 hours with a maximum after 1800 hours. During the same censuses, there were decreasing numbers of both lone drake and grouped drake components seen through the day, after morning peaks at 0530 hours. As more pairs reached the early and mid-incubation stages, fewer lone males and more grouped drakes up to five in number were recorded.

7. There are no published, standardized methods recognized to enumerate indicated duck pairs in all habitats, nor to estimate pair numbers accurately from direct count data. Presently used aerial census methods, through which yearly trend data are gathered, are not sufficiently refined for use in intensive studies of population dynamics. Comparison of results of studies that use different population components and have no sex ratio correction on estimates is nearly impossible to make. An urgent need exists for more testing of estimate variances and evaluating the magnitude of sampling errors and biases in pair population estimates.

8. Waterfowl pair estimation techniques remain inexact. Presently used methods crudely assess populations during a very narrow time period but do not measure weekly turn-over rates or seasonal populations. An apparently insurmountable problem exists in attempts to count all pairs of one species breeding on a habitat unit from April through June. With an extended breeding season in which first arriving pairs have nested and drakes have abandoned home ranges before late arrivals localize their activity and commence

nesting, assessment of populations may ultimately be based on two separate counts that are added. The presence of reneesting pairs further complicates results obtained from adding May and June counts. Late migrants or drought-displaced pairs moving into an area in June are still not adequately assessed. A further need exists for more intensive studies of the behaviour, biology, and physiology of pairs and how these factors relate to activity, mobility, and visibility of birds. What is ultimately required is a field method to separate and assess nonbreeding, reneesting, early breeding, and late breeding pairs.

9. Where (1) spring weather affects or protracts nesting phenology, (2) late arrivals do not initiate nesting until mid-June, and (3) vegetation makes observation of pairs difficult, assessment of populations may better be accomplished indirectly. Intensive nesting studies and accurate measures of brood production can be used to estimate original pair numbers. A composite of methods to arrive at population indices may be required in some habitats. In all, the precision obtained in population estimates will depend on the intensity of coverage and the degree of accuracy required to fulfill the objectives.

Acknowledgements

A number of state, federal, and provincial biologists have aided in gathering field data or suggesting new approaches. I am much indebted to all of them. Help with counts on the Roseneath Study Area was received from Barry Iliffe, Murray Evans, Stanley Kost, Helen Hays, B.M. Cram, Gerald Pospichal, Glen Parsons, Wesley Newcomb, W.H. Kiel, C.D. Evans, A.S. Hawkins, Peter Ward, and H.A. Hochbaum. On the Kindersley Study Area, Ernie Kuyt, W.J.D. Stephen, R.A. Lamont, J.B. Gollop, and various Saskatchewan Department of Natural Resources' biologists helped with censuses. My wife, Delores, provided assistance on both study areas. I am grateful to the many friendly landowners who allowed me access and turned a blind eye to periodic trampling of cropland by census crews. I also owe a special debt of gratitude to the A. Macdonald family of Minnedosa, Manitoba.

I have benefited from consultations and discussion of waterfowl census techniques with J.J. Lynch, A.G. Smith, J.H. Stoudt, H.M. Murdy, M.C. Hammond, D.F. McKinney, R.T. Sterling, J.B. Millar, A.S. Goodman, L.M. Kirsch, and

J.B. Gollop. Early in the study E.G. Wellein and R.W. Balham gave me much valuable advice. J.J. Lynch, H.M. Murdy, J.H. Stoudt, and A.G. Smith granted permission to use unpublished material. To all these individuals my sincere thanks.

Financial aid was received from the Wildlife Management Institute through the Delta Waterfowl Research Station and from the Department of Wildlife Management, University of Wisconsin, for the Manitoba project. All Saskatchewan work was done under auspices of the Canadian Wildlife Service. A grant covering various meteorological instruments was received from the National Research Council of Canada in 1953, 1954, and 1955. In 1953, a financial grant was also received from the National Research Council to attend the University of Wisconsin.

In 1952 and 1953 the Manitoba study was conducted under direction of Dr. I.McT. Cowan of the University of British Columbia and for all subsequent years under supervision of Dr. R.A. McCabe of the University of Wisconsin. Dr. H.A. Hochbaum directed part of the field program in Manitoba as did Dr. J.B. Gollop in Saskatchewan.

I sincerely acknowledge the comments and suggestions received from J.B. Gollop, M.C. Hammond, and L.M. Kirsch on early drafts of this paper. I am also indebted to Drs. J.J. Hickey, R.A. McCabe, and L.B. Keith for helpful criticisms and editorial assistance.

Literature cited

- American Ornithologists' Union. 1957. Checklist of North American Birds. Fifth ed. (published by the Union, Baltimore, Md.). 691 p.
- Beer, J.R. 1945. Sex ratios of ducks in southwestern Washington. *Auk* 62:117-124.
- Bellrose, F.C., Jr., T.G. Scott, A.S. Hawkins, and J.B. Low. 1961. Sex ratios and age ratios in North American ducks. *Illinois Natur. Hist. Surv. Bull.* 27(6):391-474.
- Bengtson, Sven-Axel. 1967. Waterfowl research in Lake Myvatn area, N.E. Iceland in 1966. *In The Wildfowlers' Assoc. of Great Britain and Ireland Ann. Rep.* 1966-1967. Liverpool. p. 40-45.
- Bennett, L.J. 1938. *The Blue-winged Teal*. Collegiate Press, Inc., Ames, Iowa. 144 p.
- Bird, R.D. 1961. Ecology of the Aspen Parkland of Western Canada in relation to land use. Canada Dep. Agriculture Contrib. No. 27, Ottawa. 155 p.
- Boughner, C.C., R.W. Longley, and M.K. Thomas. 1956. Climatic summaries for selected meteorological stations in Canada. Vol. III. Canada Dep. Trans., Meteor. Div., Toronto. 94 p.
- Boyd, H., and B. King. 1959. A breeding population of the mallard. *The Wildfowl Trust Ann. Rep.* 11:137-143.
- Bue, I.G. 1952. The dynamics of a waterfowl breeding population. Unpublished Master's thesis. Univ. Minnesota, Minneapolis. 90 p.
- Burgess, H.H., H.H. Prince, and D.L. Trauger. 1965. Blue-winged Teal nesting success as related to land use. *J. Wildl. Mgmt.* 29: 89-95.
- Chamberlain, E.B., and C.F. Kaczynski. 1965. Problems in aerial surveys of waterfowl in Eastern Canada. U.S. Fish and Wildl. Serv. Spec. Sci. Rep. No. 93. Washington, D.C. 21 p.
- Chaffin, J.E. 1952. Appraisal of California waterfowl concentrations by aerial photography. *Trans. N. Amer. Wildl. Conf.* 17: 421-426.
- Coupland, R.T. 1950. Ecology of mixed prairie in Canada. *Ecol. Monogr.* 20:271-315.
- Coupland, R.T. 1961. A reconsideration of grassland classification in the northern great plains of North America. *J. Ecol.* 49:135-167.
- Cowardin, L.M., and J.E. Ashe. 1965. An automatic camera device for measuring waterfowl use. *J. Wildl. Mgmt.* 29:636-639.
- Cowardin, L.M., and K.F. Higgins. 1967. Visibility, movement and behavior of waterfowl on a river habitat in Minnesota. *Trans. N. Amer. Wildl. and Nat. Res. Conf.* 32:301-315.
- Crissey, W.F. 1957. Forecasting waterfowl harvest by flyways. *Trans. N. Amer. Wildl. Conf.* 22:256-268.
- Crissey, W.F. 1963a. Wildlife population management. *In Hearings before Subcommittee on Fisheries and Wildlife Conservation. 88th Congress, First Session, July 18, 19, August 5, 1963, Serial 88-9. U.S. Govt. Printing Office, Washington, D.C.* p. 136-166.

- Crissey, W.F. 1963b. Exploitation of migratory waterfowl populations in North America. Proc. First European Meeting on Wildfowl Conserv. St. Andrews, The Nature Conservancy, London. p. 105-120.
- Crissey, W.F. 1969. Prairie potholes from a continental viewpoint. This publication.
- Davis, D.E. 1963. Estimating the number of game populations. In Wildlife investigational techniques. The Wildlife Society, Blacksburg, Va. p. 89-118.
- Diem, K.L., and K.H. Lu. 1960. Factors influencing waterfowl censuses in the parklands, Alberta, Canada. J. Wildl. Mgmt. 24:113-133.
- Drewien, R.C. 1967. Ecological relationships of breeding waterfowl to prairie potholes. South Dakota Dep. Game, Fish and Parks. PR Proj. W-75-R-8. Feb. 10, 1967. 10 p.
- Dzubin, A. 1954. An intensive study of waterfowl populations on a small block of agricultural land, Minnedosa, Manitoba. Unpubl. M.A. thesis. Univ. British Columbia, Vancouver. 95 p.
- Dzubin, A. 1955. Some evidence of home range in waterfowl. Trans. N. Amer. Wildl. Conf. 20:278-298.
- Dzubin, A. 1957. Pairing display and spring and summer flights of the mallard. Blue Jay 15: 10-13.
- Dzubin, A. 1969. Comments on carrying capacity of small ponds for ducks and possible density effects on mallard production. This publication.
- Ellig, L.J. 1955. Waterfowl relationships to Greenfields Lake, Teton County, Montana. Montana Fish and Game Dep. Tech. Bull. No. 1. 35 p.
- Erickson, A.B. 1943. Sex ratios of ducks in Minnesota, 1938-1940. Auk 60: 20-34.
- Evans, C.D. 1949. Roseneath area brood study, Manitoba, 1949. In Waterfowl populations and breeding conditions—summer 1949. U.S. Fish and Wildl. Serv. Spec. Sci. Rep. Wildl. No. 2. Washington, D.C. p. 71-75.
- Evans, C.D., and K.E. Black. 1956. Duck production studies on the prairie potholes of South Dakota. U.S. Fish and Wildl. Serv. Spec. Sci. Rep. Wildl. No. 32, 59 p. Washington, D.C.
- Evans, C.D., A.S. Hawkins, and W.H. Marshall. 1952. Movement of waterfowl broods in Manitoba. U.S. Fish and Wildl. Serv. Spec. Sci. Rep. Wildl. No. 16, 47 p. Washington, D.C.
- Eygenraam, J.A. 1957. The sex-ratio and the production of the mallard, *Anas platyrhynchos* L. Ardea 45:117-143.
- Fisher, J. 1954. A history of birds. Hutchinson House, London. 205 p.
- Formosov, A.N., and Y.A. Isakov. 1963. Organization and methods of counting birds and harmful rodents [in Russian]. Akad. Nauk, Moscow. 256 p.
- Furniss, O.C. 1938. The 1937 waterfowl season in the Prince Albert district, central Saskatchewan. Wilson Bull. 50:17-27.
- Gates, J.M. 1962. Breeding biology of the gadwall in northern Utah. Wilson Bull. 74: 43-67.
- Gates, J.M. 1965. Duck nesting and production on Wisconsin farmlands. J. Wildl. Mgmt. 29:515-523.
- Glover, F.A. 1956. Nesting and production of the Blue-winged Teal (*Anas discors* Linnaeus) in Northwest Iowa. J. Wildl. Mgmt. 20:28-46.
- Gollop, J.B. 1954. Waterfowl breeding ground survey—Saskatchewan, 1954. Special Study Area—Kindersley-Eston. In Waterfowl populations and breeding conditions, summer 1954. U.S. Fish and Wildl. Serv. Spec. Sci. Rep. Wildl. No. 27, Washington, D.C. p. 66-70.
- Gollop, J.B. 1965. Dispersal and annual survival of the mallard. Unpubl. Rep. Can. Wildl. Serv., Saskatoon. 104 p.
- Gollop, J.B., and J.J. Lynch. 1954. Waterfowl breeding ground survey, Saskatchewan—1954. In Waterfowl populations and breeding conditions, summer 1954. U.S. Fish and Wildl. Serv. Spec. Sci. Rep. Wildl. No. 27, Washington, D.C. p. 45-55.
- Greig-Smith, P. 1964. Quantitative plant ecology. Second ed. Butterworths, London. 256 p.
- Grenquist, P. 1965. Changes in abundance of some duck and sea bird populations off the coast of Finland 1949-1963. Finnish Game Res. No. 27. Helsinki. 114 p.
- Grenquist, P. 1966. A summary of changes in abundance of Finnish duck and sea bird populations in four southern archipelago areas 1950-1962 and some causes influencing them. Finnish Game Res. No. 28. 8 p.

- Hammond, M.C. 1959. Waterfowl breeding population census techniques. U.S. Bur. Sport Fisheries and Wildl., Minneapolis. Mimeo report. 18 p.
- Hammond, M.C. 1966. Waterfowl breeding population surveys. U.S. Fish and Wildl. Serv. Mimeo report. Upham, N.D. 25 p.
- Hawkins, A.S., J.B. Gollop, and E.G. Wellein. 1951. Waterfowl breeding ground survey in Manitoba, 1951. *In* Waterfowl populations and breeding conditions, summer 1951. U.S. Fish and Wildl. Serv. Spec. Sci. Rep. Wildl. No. 13, Washington, D.C. p. 41-49.
- Hilden, O. 1964. Ecology of duck populations in the island group of Valassaaret, Gulf of Bothnia. *Ann. Zool. Fenn.* 1:153-277.
- Hochbaum, H.A. 1944. The canvasback on a prairie marsh. *Amer. Wildl. Inst.*, Washington, D.C. 201 p.
- Hochbaum, H.A. 1946. Recovery potentials of North American waterfowl. *Trans. N. Amer. Wildl. Conf.* 11:403-418.
- Isakov, Y.A. (ed.) 1961. Organization and methods of censusing terrestrial vertebrate faunal resources. Moscow Naturalist Soc. Symposium, March 4-8, 1961. *Transl. Nat. Science Found.*, Washington, D.C. 1963. 104 p.
- Isakov, Y.A. 1963. Census and forecasting numbers of waterfowl [in Russian]. *Akademiya Nauk, Moscow.* p. 36-82. (Reprint from W.G. Leitch).
- Jahn, L.R., and R.A. Hunt. 1964. Duck and coot ecology and management in Wisconsin. *Wisconsin Conserv. Dep. Tech. Bull. No. 33.* 212 p.
- Jessen, R.L., J.P. Lindmeier, and R.E. Farnes. 1964. A study of duck nesting and production as related to land use in Mahanomen County, Minnesota. *In* Ducks and land use in Minnesota. (Ed.) J.B. Moyle. *Minnesota Dep. Conserv. Tech. Bull. No. 8.* p. 26-85.
- Johnsgard, P.A. 1965. Handbook of waterfowl behavior. Cornell Univ. Press, Ithaca. 378 p.
- Johnsgard, P.A., and I.O. Buss. 1956. Waterfowl sex ratios during spring in Washington State and their interpretation. *J. Wildl. Mgmt.* 20:384-388.
- Keith, L.B. 1961. A study of waterfowl ecology on small impoundments in southeastern Alberta. *Wildl. Monogr. No. 6.* 88 p.
- Kendeigh, S.C. 1944. Measurement of bird populations. *Ecol. Monogr.* 14:67-106.
- Kiel, W.H. 1949. Waterfowl productivity in the Newdale-Erickson District of Manitoba. *In* Waterfowl populations and breeding conditions—summer 1949. U.S. Fish and Wildl. Serv. Spec. Sci. Rep. Wildl. No. 2. Washington, D.C. p. 76-81.
- Kiel, W.H. 1951. Waterfowl breeding populations and production in the Newdale-Erickson District of Manitoba, 1951. *In* Waterfowl populations and breeding conditions, summer 1951. U.S. Fish and Wildl. Serv. Spec. Sci. Rep. Wildl. No. 13. Washington, D.C. p. 50-59.
- Koskimies, J. 1949. Some methodological notes concerning the waterfowl census in the archipelago. *Pap. on Game Res.* 3. Helsinki. 18 p.
- Lack, D. 1937. A review of bird census work and bird population problems. *Ibis* 14:369-395.
- Lacy, C.M. 1959. Artificial potholes and level ditch development as a means of increasing waterfowl production. Unpublished M.Sc. thesis. Utah State University, Logan. 103 p.
- Lebret, T. 1961. The pair formation in the annual cycle of the Mallard, *Anas platyrhynchos* L. *Ardea* 49:97-158.
- Leitch, W.G. 1952. Ecology of nesting waterfowl in the Missouri Coteau of Southern Saskatchewan. Unpublished M.Sc. thesis. Univ. Manitoba, Winnipeg. 133 p.
- Leopold, A. 1933. Game management. Scribner's, New York. 481 p.
- Lincoln, F.C. 1930. Calculating waterfowl abundance on the basis of banding returns. U.S. Dep. Agriculture. Circ. No. 118. 4 p.
- Lokemoen, J.T. 1966. Breeding ecology of the Redhead duck in western Montana. *J. Wildl. Mgmt.* 30:668-681.
- Low, J.B. 1947. Review of new techniques—waterfowl. *Trans. N. Amer. Wildl. Conf.* 12:339-346.
- Lynch, J. 1949. Waterfowl breeding ground survey in Saskatchewan, 1949. *In* Waterfowl populations and breeding conditions, summer 1949. U.S. Fish and Wildl. Serv. Spec. Sci. Rep. Wildl. No. 2, Washington, D.C. p. 48-82.
- Lynch, J.J. 1951. This lone drake business. U.S. Fish and Wildl. Serv. Unpublished typed report. 13 p. Abbeville, La., June 6, 1951.

- Matthews, G.V.T. 1960. An examination of basic data from wildfowl counts. *Int. Ornith. Cong.* 12:483-491. Helsinki.
- MacInnis, C.D. 1964. The status of the Ross' Goose in 1962-63. *The Wildfowl Trust Ann. Rep.* 15:137-139.
- MacInnis, C.D. 1966. Population behavior of eastern Arctic Canada geese. *J. Wildl. Mgmt.* 30:536-553.
- Martz, G.F. 1967. Effects of nesting cover removal on breeding puddle ducks. *J. Wildl. Mgmt.* 31:236-247.
- McKinney, F. 1965. Spacing and chasing in breeding ducks. *Wildfowl Trust Ann. Rep.* 16:92-106.
- McKnight, D.E., and I.O. Buss. 1962. Evidence of breeding in yearling female lesser scaup. *J. Wildl. Mgmt.* 26:328-329.
- Mendall, H.L. 1949. Waterfowl breeding ground survey in Maine, 1949. *In Waterfowl populations and breeding conditions—summer 1949.* U.S. Fish and Wildl. Serv. Spec. Sci. Rep. Wildl. No. 2, Washington, D.C. p. 214-217.
- Mendall, H.L. 1958. The ring-necked duck in the northeast. *Univ. Maine Studies, Sec. Series No. 73.* 317 p.
- Mitchell, J., H.C. Moss, and J.S. Clayton. 1944. Soil survey of southern Saskatchewan. *Univ. Saskatchewan, Soil Survey Rep. No. 12,* Saskatoon. 259 p.
- Moore, P. 1955. The strip intersect method. *Trans. N. Amer. Wildl. Conf.* 20:390-405.
- Moyle, J.B. (ed.). 1964. *Waterfowl in Minnesota.* Minn. Dep. Conserv. Tech. Bull. 7. 210 p.
- Munro, J.A. 1941. Studies of waterfowl in British Columbia. Greater Scaup, Lesser Scaup. *Can. J. Res., Series D.* 19:113-138.
- Murdy, H.W. 1953. Chronology of the 1951 waterfowl breeding season. *South Dakota Dep. Game, Fish and Parks. Job Completion Rep. Project W-17-R-7.* 43 p.
- Murdy, H.W. 1962. Progress report on the Yellowknife Waterfowl Study Area, Northwest Territories. *Ann. Progress Rep., Denver Wildl. Res. Center.* 46 p.
- Murdy, H.W. 1964. Population dynamics and breeding biology of waterfowl on the Yellowknife study area, Northwest Territories. *U.S. Fish and Wildl. Serv. Unpubl. Progress Rep. 1964.* Jamestown, N.D. 61 p.
- Nicholson, E.M. 1931. *The art of bird watching.* Scribner's, London. 217 p.
- Odum, H.T., J.E. Cantlon, and L.S. Kornicker. 1960. An organizational hierarchy postulate for the interpretation of species-individual distributions, species entropy, ecosystem evolution and the meaning of a species-variety index. *Ecology* 41:395-399.
- Oring, L.W. 1964. Behavior and ecology of certain ducks during the postbreeding period. *J. Wildl. Mgmt.* 28:223-233.
- Pospichal, G., B.M. Cram, and G. Parsons. 1954. Waterfowl breeding populations and production studies, Newdale-Erickson Study Area, Manitoba, 1954. *In Waterfowl populations and breeding conditions, summer 1954.* U.S. Fish and Wildl. Serv. Spec. Sci. Rep. Wildl. No. 27. Washington, D.C. p. 82-91.
- Preston, F.W. 1948. The commonness and rarity of species. *Ecology* 29:254-283.
- Preston, F.W. 1962. The canonical distribution of commonness and rarity. *Ecology* 39:185-215, and 39:410-432.
- Raitasuo, K. 1964. Social behavior of the mallard, *Anas platyrhynchos*, in the course of the annual cycle. *Papers on Game Res.* 24. Helsinki. 72 p.
- Reeves, H., M. Lundy, and F. Kreller. 1956. Waterfowl breeding ground survey—Success Study Area, Saskatchewan, 1955. *In Waterfowl populations and breeding conditions—summer 1955.* U.S. Fish and Wildl. Serv. Spec. Sci. Rep. Wildl. No. 30. Washington, D.C. p. 54-62.
- Rogers, J.P. 1963. The ecological effects of drought on reproduction of the Lesser Scaup. Unpubl. Ph.D. thesis. Univ. Missouri, Columbia.
- Rogers, J.P. 1964. Effect of drought on reproduction of the Lesser Scaup. *J. Wildl. Mgmt.* 28:213-220.
- Salyer, J.W. 1962. Effects of drought and land use on prairie nesting ducks. *Trans. N. Amer. Wildl. Conf.* 27:69-79.
- Skellam, J.G. 1958. The mathematical foundations underlying the use of line transects in animal ecology. *Biometrics* 14:385-400.
- Smith, A.G. 1949. Waterfowl breeding ground survey in Alberta, 1949. *In Waterfowl populations and breeding conditions—sum-*

- mer 1949. U.S. Fish and Wildl. Serv. Spec. Sci. Rep. Wildl. No. 2. Washington, D.C. p. 40-47.
- Smith, A.G. 1956. A progress report on the Lousana Waterfowl Study Area, 1953-1955. Lousana, Alberta, Canada. Unpublished report. U.S. Fish and Wildl. Serv., Brigham City, Utah. 89 p.
- Smith, A.G. 1957. The 1956 aerial and ground waterfowl surveys in Alberta, Canada. U.S. Fish and Wildl. Serv., Brigham City, Utah. 34 p. (mimeo.).
- Smith, A.G. 1961. Waterfowl survey of the Lousana Study Area, Alberta, Canada. U.S. Fish and Wildl. Serv., Wildl. Res. Lab., Denver, Colorado. Unpublished report. 33 p. mimeo.
- Smith, A.G., J.H. Stoudt, and J.B. Gollop. 1964. Prairie potholes and marshes. In *Waterfowl tomorrow*. (Ed.) J.J. Linduska. U.S. Dep. Interior, Washington. p. 39-50.
- Smith, J.D. 1964. Revision of standard operating procedures. Waterfowl air survey instruction for the Prairie operation. U.S. Fish and Wildl. Serv. Div. Mgmt. and Enforcement. Washington, D.C. 8 p. + attach.
- Smith, R.H. 1953. A study of waterfowl production on artificial reservoirs in eastern Montana. *J. Wildl. Mgmt.* 17:276-291.
- Smith, R.H., and A.S. Hawkins. 1948. Appraising waterfowl breeding populations. *Trans. N. Amer. Wildl. Conf.* 13:57-69.
- Smith, R.I. 1963. The social aspects of reproductive behavior in the Pintail (*Anas acuta acuta*, L.). Ph.D. thesis. Utah State Univ., Logan. 78 p.
- Snow, D.W. 1965. The relationship between census results and the breeding population of birds on farmland. *Bird Study* 12(4):287-304.
- Southwood, T.R.E. 1966. *Ecological methods*. Methuen and Co. Ltd., London. 391 p.
- Sowls, L.K. 1947. New techniques for breeding ground surveys. *Trans. N. Amer. Wildl. Conf.* 12:448-454.
- Sowls, L.K. 1955. *Prairie ducks*. The Stackpole Co., Harrisburg, Pennsylvania. 193 p.
- Steel, R.G.D., and J.H. Torrie. 1960. *Principles and procedures of statistics*. McGraw-Hill, Toronto. 481 p.
- Stewart, R.E., A.D. Geis, and C.D. Evans. 1958. Distribution of populations and hunting kill of the Canvasback. *J. Wildl. Mgmt.* 22:333-370.
- Stokes, A.W., and D.F. Balph. 1965. The relation of animal behavior to wildlife management. *Trans. N. Amer. Wildl. Conf.* 30:401-410.
- Stotts, V.D., and D.E. Davis. 1960. The black duck in the Chesapeake Bay of Maryland: breeding behavior and biology. *Chesapeake Science* 1(3/4):127-154.
- Stoudt, J.H. 1952. Waterfowl breeding ground survey of Redvers Area, Saskatchewan. In *Waterfowl populations and breeding conditions, summer 1952*. U.S. Fish and Wildl. Serv. Sci. Rep. No. 21. Washington, D.C. p. 52-60.
- Stoudt, J.H. 1964. Factors affecting waterfowl breeding populations and the production of young in the parklands of Canada. *Ann. Progress Rep. Wildl. Res. Work Unit A-8.2*. U.S. Fish and Wildl. Serv., Jamestown, N.D. Unpublished mimeo report. 55 p.
- Tamisier, A. 1965. Dénombrements d'Anatides hivernant en Carmargue. Saison 1964-65. *Alauda* 33:265-293.
- Taylor, S.M. 1965. The common bird census—some statistical aspects. *Bird Study* 12:268-286.
- Van Tets, G.F. 1966. A photographic method of estimating densities of bird flocks in flight. *C.S.I.R.O. Wildl. Res.* 11:103-110.
- Weller, M.W. 1959. Parasitic egg laying in the Redhead (*Aythya americana*) and other North American Anatidae. *Ecol. Monogr.* 29:333-365.
- Williams, C.S. 1948. Introduction. In *Waterfowl populations and breeding conditions—summer 1948*. U.S. Fish and Wildl. Serv. Spec. Sci. Rep. 60. Washington, D.C. p. 1-4.
- Williams, C.B. 1953. The relative abundance of different species in a wild animal population. *J. Anim. Ecol.* 22:14-31.
- Yapp, W.B. 1956. The theory of line transects. *Bird Study* 3:93-104.