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Abstract

Habitat use and production by Canvasbacks (*Aythya valisineria*) were studied during 1971–75 on a 31.1-km² block (15.54 km² in 1971 and 1972) of Saskatchewan parkland to determine the extent that habitat might be limiting production of young. Mean annual pond densities ranged from 18 to 26 per km². Mean annual pair (pairs and lone drakes) densities ranged from about 1.16/km² to 3.05/km². Changes in pair densities did not correspond to habitat changes. Within the block, pair densities on 259-ha sections were correlated with areas of the more permanent type 4 and 5 ponds. Pond use increased with size and permanency. Tree growth and land use around ponds did not affect pair distribution.

Hens tended to nest solitarily on ponds and emergent cover was the main factor influencing pond use by nesting females. Generally, medium-sized, permanent ponds received the highest use. Nesting Canvasbacks showed considerable ability to adapt to changing habitat conditions. Of 200 nests found during the 5 years, 87 (43.5%) were successful. Predation by crows (*Corvus brachyrhynchos*) was the main cause of nest loss. Redheads (*Aythya americana*) parasitized 65% of the incubated nests. Average size of incubated clutches was 6.8, and parasitized clutches averaged 2.6 eggs less than unparasitized clutches.

Canvasback broods favoured large, permanent ponds with substantial areas of open water, a habitat feature related to their feeding and escape behaviour. Mean size of broods close to fledging was about 3.8. Significant loss of entire broods was evident in one year, 1974, and was attributed to local hail storms. Estimated young fledged averaged 1.04 per pair during 1971–74 and ranged from 0.81 to 1.56.

Annually, nesting effort (expressed as total nests per pair) ranged from 0.65 to 1.42 and was directly related to habitat (area of type 4 and 5 ponds) available per pair. It is postulated that when pair densities are high relative to habitat a mechanism suppresses nest initiation through increased intraspecific pair contacts. Thus, although the number of pairs attracted to each area may fluctuate annually, mean densities would be stable over the long term.

Historically, Canvasback pair densities have seldom exceeded 5 pairs/km², even in the best prairie pothole habitat. Such relatively low densities reflect the species' intrinsic need for a large home range.

Because Canvasbacks favour the more permanent ponds on their breeding grounds and nest in emergent cover, they will suffer less from the impact of agriculture than upland nesting species which make extensive use of temporary wetlands that are vulnerable to drainage and filling.

Résumé

De 1971 à 1975, nous avons étudié le schème d'utilisation des habitats et la reproduction chez le morillon à dos blanc (*Aythya valisineria*). Les études, qui ont porté sur 31.1 km carrés (15.54 km² en 1971 et autant en 1972) dans les savanes de la Saskatchewan, visaient à déterminer dans quelle mesure l'habitat peut limiter la production de jeunes. Le nombre moyen d'étangs par kilomètre carré en une année donnée a varié de 18 à 26, tandis que la densité annuelle moyenne des couples (couples et mâles solitaires) oscillait entre 1.16 et 3.05 km². Les fluctuations dans la densité des couples ne correspondaient pas aux modifications des habitats. Nous avons comparé les densités de couples par secteurs de 259 ha à celles des régions renfermant des étangs plus stables, des types 4 et 5. Nous avons remarqué que l'utilisation des étangs était fonction de leur dimension et de leur stabilité. Par ailleurs, ni les arbres ni l'utilisation des terres avoisinantes n'ont perturbé la répartition des couples nicheurs.

Les canes nichaient le plus souvent seules sur des étangs, où leur présence tenait surtout à la végétation émergente. En règle générale, les étangs permanents de dimensions moyennes étaient les plus recherchés. Les morillons à dos blanc nicheurs nous ont semblé s'adapter avec facilité aux modifications de leurs habitats. Des 200 nids dénombrés durant les cinq années de l'étude, 87 (43.5 p.cent) ont donné des petits. C'est la destruction des nids par les corneilles d'Amérique (*Corvus brachyrhynchos*) qui a le plus entravé les activités de nidification. Les morillons à tête rouge (*Aythya americana*) ont parasité 65 p.cent des nids actifs. Les couvées comptaient 6.8 œufs en moyenne alors que les nids envahis par les morillons à tête rouge comptaient en moyenne 2.6 œufs de moins que les autres.

Les jeunes morillons à dos blanc choisissaient de préférence de grands étangs permanents avec une certaine étendue d'eau libre, un habitat qui convient bien à leurs habitudes alimentaires et à leur comportement de fuite. A l'époque où les jeunes avaient presque acquis le plumage nécessaire pour voler, chaque nid en comptait en moyenne 3.8. En 1974, nous avons observé une destruction massive de couvées entières; des tempêtes de grêle à divers endroits en étaient la cause. On a calculé que chaque couple a élevé 1.04 oisillon en moyenne entre 1971 et 1974 (0.81 à 1.56).

Chaque couple a construit en moyenne entre 0.65 et 1.42 nid par année (chiffre obtenu en divisant le nombre total des nids par celui des couples nicheurs). Cette activité était directement fonction de la superficie de l'habitat accessible à chaque couple (région renfermant des étangs des types 4 et 5). Nous croyons que lorsque la densité des couples dans un habitat donné est forte, un mécanisme se déclenche: les contacts entre les couples de la même espèce restreignent la construction de nids. Ainsi, bien que le nombre de couples fréquentant un étang donné fluctue d'année en année, la densité moyenne se stabilise à la longue.

La densité des couples a rarement été supérieure à cinq par kilomètre carré, même dans les cuvettes des prairies qui réunissent les meilleures conditions. Ces faibles densités reflètent le besoin primordial que constitue pour l'espèce un domaine vital étendu.

La préférence des morillons pour les étangs les plus stables compris dans leur aire de reproduction et l'habitude qu'ils ont de construire leur nid dans la végétation émergente les mettent à l'abri des répercussions néfastes de l'exploitation agricole; ce n'est pas le cas pour les espèces qui nichent surtout dans les hautes terres et qui font grand usage des terres humides temporaires, plus exposées au drainage et au remplissage.

Introduction

Management of migratory birds in Canada by the Canadian Wildlife Service (CWS) is guided by a basic philosophy which dictates that the resource must be managed "for the maximum benefit of existing and future generations of Canadians and other people having access to the resource" (Loughrey 1975:26). Specific objectives deal with the identification and preservation of potentially endangered species and the production of migratory game birds for consumptive recreational use.

The Canvasback (*Aythya valisineria*) is not considered an endangered or threatened species in Canada (Godfrey 1970). In the United States, Peterson (1974) suggested the species was threatened but not endangered because means were available to undertake positive management programs. The National Audubon Society (U.S.) included the Canvasback on its 1976 "Blue List" (Arbib 1975). This lists species whose status is believed to be endangered on all or a significant part of their ranges. Official American concern for the status of the Canvasback has led to the comprehensive Canvasback research programs undertaken by the U.S. Bureau of Sport Fisheries and Wildlife (Trauger 1974).

Because of their low numbers, Canvasbacks do not contribute significantly (about 1%) to continental duck harvests (Geis and Cooch 1972). However, they are considered a quality trophy and, in areas with a tradition of good populations, have been the primary quarry sought by hunters (Hochbaum 1944).

Restrictive hunting regulations since the late 1950s have helped Canvasback survival rates according to Geis and Crissey (1969), but populations have not increased as was anticipated under the assumption that hunting mortality was solely responsible for the low numbers. This suggested that the underlying reason might involve factors that depressed annual production of young, operating after the adults reached the breeding grounds. My study, from 1971 through 1975, was undertaken to quantitatively describe habitat used by breeding Canvasbacks, and to determine to what extent, if any, habitat was limiting production on a study block in Saskatchewan parkland.

Study area

The study area (52°N, 106°W), 48 km east of Saskatoon and near the town of Meacham, was a block of six sections (15.54 km²) in 1971 and 1972. For the remaining 3 years, the area was doubled to 31.1 km² by adding three sections to either side of the original block. The block comprised Sections 14-17, 20-23, and 26-29 of Tp36, R28, W2. The sections, each 2.59 km², were separated by roads or fencelines and were used as sampling units.

The area is in the aspen parkland (Bird 1961) and annual precipitation averages about 36 cm. Topography is rolling to gently rolling. Soils are Dark Brown and predominantly of loam texture (Mitchell *et al.* 1944). Areas of about 390 ha and 260 ha in the southeast corner lie on soils of sandy loam and silty clay, respectively. Most of the area occupies Class 1 (highest) waterfowl breeding habitat according to the categories of the Canada Land Inventory system (R.E.G. Murray, pers. comm.).

Land use was illustrated by 1975 percentages: grain (barley and wheat), 41.5; summer fallow, 29.4; rapeseed, 5.9; pasture, 6.1, about one-half of which was grazed; farmyards and roads, 1.2; wasteland (mainly uncultivated areas around ponds), 6.3; and ponds, 9.6. Pond densities averaged from about 18 to 26 per km². Size of ponds ranged from less than 0.04 ha to 8.1 ha. Most ponds were wholly or partly bordered by trees, mainly willows (*Salix* spp.) and aspen (*Populus tremuloides*).

Wetland vegetation on the area followed closely the lists given by Millar (1976) for species found in various freshwater vegetation zones of prairie wetlands. One exception was the scarcity of *Scirpus* spp. on my area. The most common emergent species occurring in ponds used by Canvasbacks were whitetop (*Scolochloa festucacea*), cattail (*Typha latifolia*), and sedge (*Carex atherodes*).

From 1971 through 1973, some supplementary data were collected on a 6.8 x 10.1 km rectangular system of roadside transects (Smith 1971) 3.2 km south of the block. The transects, 402 m wide (excluding road) and 70.8 km in length, provided a sample of 26.7 km². Most of this area has soils of silty clay textures (Mitchell *et al.* 1944), and topography is less rolling than on the block. Also, pond densities averaged about one-half those of the block. Waterfowl habitat was rated Class 3 by Canada Land Inventory — a somewhat lower capability than on the block.

Methods

Maximum depth of ponds was measured in early May and again in July. Ponds were assigned to permanency categories similar to those described by Martin *et al.* (1953) and Evans and Black (1956). Type 1 ponds are shallow depressions, seldom having over 25 cm of water and, except in wet years, dry up before July. Type 3 ponds are shallow marshes usually not more than 60 cm deep. These ponds tend to dry up during summer except in wet years. Type 1 and 3 ponds that contain water through the growing season usually become overgrown with emergent vegetation. Type 4 ponds have up to 120 cm of water in the spring and seldom become dry. Growth of emergent vegetation leaves little or no open water by July. Type 5 ponds are over 120 cm deep in spring and contain water even in dry years. Emergent vegetation usually occurs only around the pond margin and a majority of the area remains open. This is the main distinction between type 4 and type 5 ponds. Pond areas were measured from maps prepared from aerial photographs (Appendix 1). For data analysis, ponds were assigned to five area classes (Appendix 2). Similarly, the percentage of shoreline bordered by trees (mainly willows) was estimated and each pond was assigned to one of three categories of woody shore growth (WSG); (1) open, 0–33%; (2) half-open, 34–66%; and (3) closed, 67–100% (Smith 1971). Land use around ponds was recorded in late May as summer fallow, seeded to grain, seeded to oil-seed, or pasture.

When ponds were checked in May, the kinds of emergent plants suitable for supporting Canvasback nests were noted and the proportion of the pond area occupied by these was estimated to the nearest 5%. After 1972, a four-point scale (Appendix 3) was used to rate ponds on their potential for accommodating Canvasback nests. This was done to compensate for weaknesses in the emergent cover data. To illustrate, a single

dense stand of cattail is more attractive to nesting Canvasbacks than many isolated clumps. Flooded willows are enhanced when mixed with whitetop or sedge, the latter used as nest material. For the most part, this was a subjective rating and was based on our own observations as well as descriptions in the literature (Hochbaum 1944, Dzubin 1955). Ratings pertained to conditions in May and, except for flooded willows and shrubs, were based on dead emergent cover persisting from the previous year.

In July, the proportion of the pond area occupied by all emergent vegetation was again estimated. Land use around ponds in July was recorded as fallow, cropped with grain, cropped with oil-seed, or pasture.

Two breeding pair counts were made in May of 1971, ten in 1972 and 1973, and nine in 1974 and 1975. A census was completed in one day between 08:30 and 15:30. During counts, every pond was visited and Canvasbacks present were recorded as pairs, lone males, lone females, or flocked birds. Pairs and singles were designated as such when spaced approximately 5 or more metres from other birds (Dzubin 1969b). We tried not to disturb ducks to minimize risk of duplicate counts and, when they occasionally did flush, we attempted to determine their destination for the same reason. Annual estimates of breeding pair densities were based on the average of at least six counts made during the period of greatest population stability as recommended by Dzubin (1969b). (An exception was 1971 when only two counts were used.) Pairs and lone drakes were used to indicate breeding pairs.

Two nest searches were made, the first starting in late May and the second ending in late July. All emergent cover and much of the shore cover of each pond was searched systematically. Active nests were revisited after the predicted hatching date (Westerskov 1950). Special effort was made

to keep nest visits at a minimum and to otherwise disturb nesting hens as little as possible.

Nest initiation dates were estimated on the basis of a laying rate of one egg per day, a 2-day period of nest building, and an incubation period of 24 days (Hochbaum 1944). A few nests were found long after termination. Initiation dates of these were estimated on the basis of the few clues available, but were subject to large error. Usually, however, they could be assigned to a specific month with confidence. Likewise, the fate of some unsuccessful nests was uncertain. Some, apparently destroyed by predators, may have been deserted first.

One brood count was made in 1971, two in 1972, six in 1973, three in 1974, and none in 1975. The counts required 2 to 3 days to complete. Broods believed to represent duplicate counts were not included in the final estimates. Broods were aged using the method of Gollop and Marshall (1954).

Results and discussion

1. Pond characteristics

In terms of pond numbers and wetland area, 1971 and 1972 might be considered about average, 1973 below average and 1974 and 1975 above average (Appendices 1 and 2). Water levels in the more permanent ponds changed correspondingly. Each year, most type 1 and some type 3 ponds were dry by mid July. Generally, the proportion of ponds drying up reflected overall water conditions on the area. No pond designated as type 4 or 5 dried up. The increased water area in 1974 and 1975 comprised mainly additional ponds of each type and, to some extent, larger ponds within type categories. Much of the tree growth around ponds was inundated during these years.

The proportion of ponds bordered with trees did not change significantly throughout the study and averaged 49% open, 13% half-open, and 38% closed. These ratios are similar to those reported for Redvers, Saskatchewan by Stoudt (1971) and Lousana, Alberta by Smith (1971). Openness tended to be associated with temporary ponds that were, on the average, relatively small, and large type 4 or 5 ponds.

Ponds in cultivated fields did not always have the same land use around them in early May due to changes in cropping. However, overall proportions did not change significantly among years and averaged 50% fallow or seeded, 37% stubble, and 13% pasture. Likewise, land use around ponds in July averaged 36% fallow, 45% grain, 13% pasture, and 6% oil-seed.

2. Habitat use by Canvasback pairs

Each spring, Canvasbacks arrived on the study area during the latter half of April, rapidly increased in numbers in late April and early May, and reached a peak during the first or second week of May. For the 5-year period, 1971–75, average densities of indicated pairs on the original

Figure 1

Figure 1

land area (21% decrease in pond numbers), Canvasback pairs declined from 40 in 1972 (mean of seven counts) to 26 in 1973 (mean of five counts). It appeared that the comparatively good habitat conditions on the block in 1973 attracted birds from surrounding areas that had undergone greater deterioration.

The number of pairs in 1974 was much lower, suggesting that the immigrants of 1973 had returned to their traditional breeding grounds, by then much improved over 1973. (Only one count in 1974 could be made on the transect and, though late and, therefore, not comparable, it indicated a higher pair density than in 1973.) The modest increase in 1975 over 1974 could have resulted from normal recruitment of young in 1974 on the block and a high tendency to home to their natal range.

Within the large study block, pair densities tended to be directly related to the total available area of favoured wetlands (Fig. 2). The correlation was strongest and the regression slope steepest in 1973 with a high pair population on reduced habitat. In 1974, habitat was plentiful, Canvasback numbers were low, and pairs tended to disperse throughout the block in a more or less uniform density. An increased pair density relative to habitat in 1975 resulted in less random dispersion and pairs again tended to distribute themselves according to available habitat. Wetland areas were similar in 1974 and 1975.

In all years, pond use by Canvasback pairs increased with both pond permanency type and size class. Type 1 ponds provided less than 1% on the average; type 3, 5%; type 4, 36%; and type 5 ponds provided 59% of the use. Similarly, the smallest size class (<.21 ha) contributed 6%; .21–.40 ha, 13%; .41–.81 ha, 23%; .82–1.62 ha, 26%; and ponds over 1.62 ha, 32%. Generally, occupancy rate tended to be directly correlated with pond size. In terms of hectares per pair,
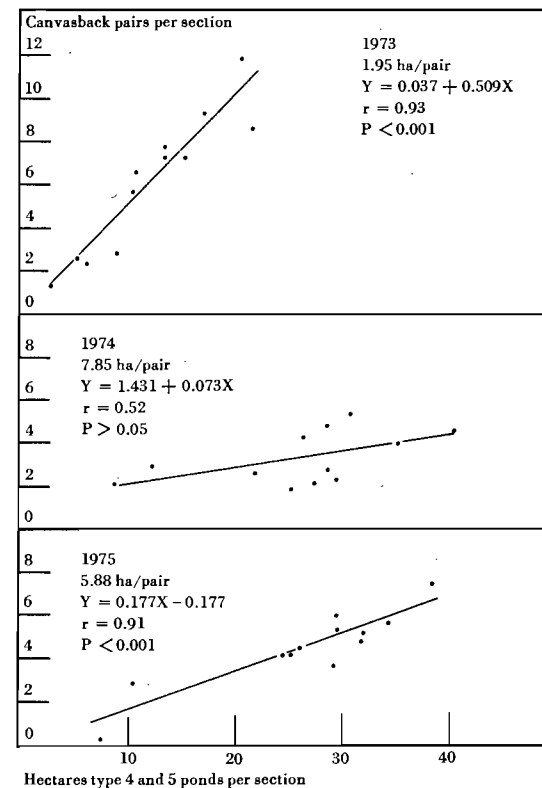
15.54 km² area were, respectively, 1.16/km², 1.74/km², 3.05/km², 1.41/km², and 2.15/km².

Changes in pair numbers did not correspond to habitat changes, the latter measured as changes in total area of type 4 and 5 ponds — the ponds most frequently used by indicated pairs (Fig. 1). There was a marked increase in pairs in 1973 from 1972 despite reduced habitat (11 % decrease in area of type 4 and 5 ponds and 12% decrease in pond numbers). Since production in 1972 could not account for all (or any?) of this increase, I concluded that Canvasbacks, displaced from deteriorated habitat elsewhere, contributed to the population on the study block. This was supported by data from the transect area south of the block (see description of the study area) where, with a 27% decrease in type 4 and 5 wet-

Figure 2

Hectares type 4 and 5 ponds per section

Table 1
Average number of indicated Canvasback pairs (pairs and lone drakes) seen per pond per count and per hectare per count during 5 years, by pond permanency type and size class

Pond type		<.21	.21–.40	.41–.81	.82–1.62	>1.62	Total
				Pond size class, ha			
1	pairs/pond	t*	t	0	0	—	t
	pairs/ha	.01	.01	0	0	—	.01
3	pairs/pond	.01	.01	.04	.07	.08	.01
	pairs/ha	.05	.05	.07	.07	.03	.06
4	pairs/pond	.02	.07	.10	.21	.52	.09
	pairs/ha	.14	.22	.17	.19	.21	.19
5	pairs/pond	.03	.09	.19	.23	.60	.23
	pairs/ha	.18	.28	.31	.20	.19	.22
All	pairs/pond	.01	.05	.12	.20	.54	.08
	pairs/ha	.07	.16	.20	.18	.18	.17

*t < .01

there was little difference in use among the various pond size classes. The relationship between Canvasback pair use and pond type and size class is illustrated by average occupancy rates (Table 1). A similar preference by Canvasback pairs for large permanent ponds was reported for Redvers, Saskatchewan by Stoudt (1971).

Canvasback pair use of ponds was related to the degree of woody shore growth (WSG) only in 1973. In that year open ponds received significantly more use than closed ponds. This differential use was not due to WSG *per se*. Rather, Canvasbacks used large ponds extensively that year, and these tended to be open.

The effect of the three habitat factors on pair use was analysed for the last 4 years with one-way and three-way analyses of variance. Duncan multiple range tests were performed to illustrate differences between factor means (Table 2). In the table, "yes" and "no" indicate significance and nonsignificance, respectively. For the one-way analysis of variance, the means of factors whose numerical designations are underscored by the same line were not significantly different. Conversely, those not underscored by the same line were significantly different.

The levels of significance are indicated in the "main effects" columns of the three-way analysis of variance. The two-factor and three-factor interactions indicate whether the described interactions are significant in explaining the variance of the sample.

Canvasback pair use did not differ significantly between ponds in tilled fields and ponds in stubble fields. Both types of field represent cropped land so they would have the same effect on wetland ecosystems. There was some indication that ponds surrounded by pasture received relatively more use, but there were not enough ponds in this type of habitat to make valid tests.

Table 2
Results of analysis of variance and Duncan multiple range tests on three variables affecting Canvasback pair use of ponds. Those means of factor categories (designated numerically) underscored by the same line were not significantly different

Year Pairs Ponds	One-way analysis of variance			Three-way analysis of variance						
				Main effects			Two-factor interaction			Three-factor interaction
	Type	Size	WSG*	Type	Size	WSG	Type Size	Type WSG	Size WSG	Type Size WSG
1972 249 318	Yes† 1 3 4 5	Yes 1 2 3 4 5	No	Yes .001	Yes .001	No .999	Yes .001	Yes .004	No .272	Yes .001
1973 688 548	Yes 1 3 4 5	Yes 1 2 3 4 5	Yes 1 2 3	Yes .001	Yes .001	Yes .01	Yes .001	No .999	Yes .001	Yes .001
1974 361 734	Yes 1 3 4 5	Yes 1 2 3 4 5	No	Yes .001	Yes .001	No .999	Yes .009	No .264	Yes .021	No .354
1975 448 813	Yes 1 3 4 5	Yes 1 2 3 4 5	No	Yes .001	Yes .001	No .999	Yes .027	Yes .04	No .098	No .999

*WSG, woody shore growth.
†Yes and no indicate significance and nonsignificance, respectively.

Table 3
Results of analysis of variance and Duncan multiple range tests on three variables affecting Canvasback flocked male use of ponds. Those means of factor categories (designated numerically) underscored by the same line were not significantly different

Year Males Ponds	One-way analysis of variance			Three-way analysis of variance						
				Main effects			Two-factor interaction			Three-factor interaction
	Type	Size	WSG*	Type	Size	WSG	Type Size	Type WSG	Size WSG	Type Size WSG
1972 234 318	Yes† 1 3 4 5	Yes 1 2 3 4 5	No	No .148	Yes .001	No .999	Yes .002	No .101	Yes .031	No .176
1973 70 548	No	Yes 1 2 3 4 5	No	No .999	Yes .001	No .999	Yes .001	No .132	Yes .001	No .428
1974 144 734	No	Yes 1 2 3 4 5	No	No .999	Yes .001	No .999	Yes .001	No .284	Yes .001	Yes .006
1975 96 813	Yes 1 3 4 5	Yes 1 2 3 4 5	No	No .999	Yes .001	No .273	No .277	No .999	No .116	No .999

*WSG, woody shore growth.
†Yes and no indicate significance and nonsignificance, respectively.

Table 4
Canvasback nest densities for 5 years

Year	Nests per section			Total nests
	Low	High	Mean	
1971*	1	5	2.8	17
1972*	1	7	3.5	21
1973	0	10	3.7	45
1974	1	8	4.3	51
1975	1	12	5.5	66

*Six sections or 15.54 km² block.

3. Habitat use by flocked birds

We observed 234 flocked males during counts in 1972, 70 in 1973, 144 in 1974, and 96 in 1975. The relatively large number in 1972 was attributed to the influx of males during the latter half of May that apparently were attracted to the Canvasback females released on the area that spring (Sugden 1976). On the average, 1% of flocked males were seen on type 1 ponds, 7% on type 3 ponds, 44% on type 4 ponds, and 48% on type 5 ponds. Significant differences are indicated in Table 3.

In each year there were significant differences in use among pond size classes. In particular, flocked drakes showed a preference for ponds over 1.62 ha. Amount of WSG or land use around ponds had no effect on their distribution.

Factors affecting the distribution of flocked females were not analysed. The numbers seen the four successive years, 1972 through 1975, were 19, 31, 33, and 8. Because they were always associated with flocked males, they would have similar habitat use.

4. Habitat use by nesting hens

Earliest Canvasback nests were initiated in the first week of May each year (Fig. 3) and latest nests during mid-to-late June. An average of 77% of the nests were started during the 30-day period 11 May to 9 June, with 30% being started during 21 May to 1 June. There was no definite second peak in nest initiation dates, so it was impossible to make any inferences regarding renesting rates, though the temporal distribution suggests that the rate did not vary much among years.

Total nests found each year and mean densities are given in Table 4. At any given time, densities of active nests were lower. Maximum numbers of active nests were present in early June before hatching started and averaged about 58% of total nests found.

Most hens nested solitarily on ponds. Of 177 ponds with nests, there were 160 with one, 13 with two, 3 with three, and 1 with five nests. The data suggested that the tendency to nest alone was weakest in 1973 which may have been a response to the reduction in ponds that year and greater use of large ponds for nesting. Also, all nests on such ponds were not always active simultaneously. Some likely represented more than one nesting attempt by the same hen.

Variability in nest densities among sections was higher than that for pair densities. The relationship between nest and pair densities on the different sections was neither clear nor consistent. In 1971, 1974 and 1975 there was no correlation between the two (P > 0.2). In 1972 there was an inverse relationship between pairs and nests on the 6 sections (r = −.86, P < 0.05). I can offer no biological explanation for this isolated relationship. In 1973, there was a positive correlation between pair and nest numbers on the 12 sections (r = .80, P < 0.01). I believe this resulted from the relatively high use of large ponds by nesting hens in 1973 (discussed later); these were the same kind of ponds that attracted indicated pairs (pairs and lone drakes). For the most part, indicated pair data reflected the distribution of feeding ponds and drake waiting areas which may be some distance from nest ponds (Dzubin 1955). Thus, a correlation between pairs and nests should not be expected on areas as small as one section (259 ha) except in years like 1973 when nesting hens tended to use the same ponds as the drakes and feeding pairs.

Generally, nesting Canvasbacks confirmed our ability to rate nesting habitat. In 1973–75, no May nests were found on ponds rated "nil" (see Appendix 3 for description). In 1973 and 1975, fewer than expected were found on "poor" ponds, about the expected number were on "fair" ponds, and more than expected were found on

Figure 3
Temporal distribution of Canvasback nests.
Each square indicates one nest start

Figure 3
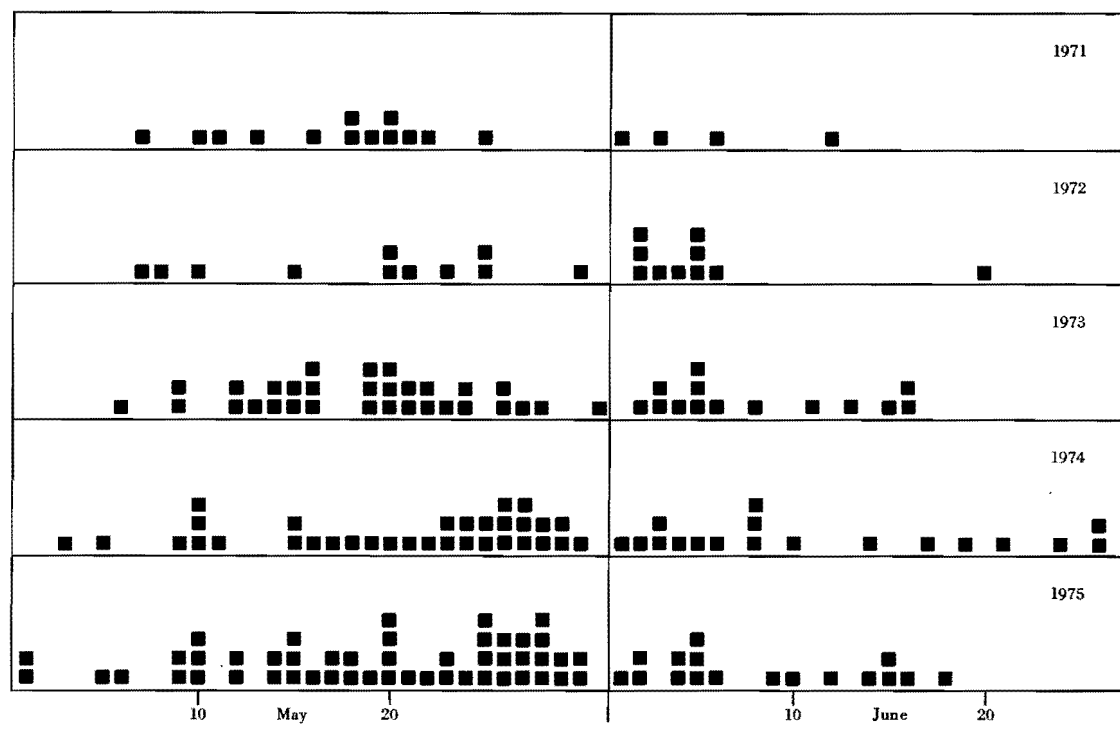
Table 5
Average nests per pond and nests per hectare for 5 years, by pond permanency type and size class

Pond type		<.21	.21–.40	.41–.81	.82–1.62	>1.62	Total
3	nests/pond	.04	.10	.05	.19	.36	.06
	nests/ha	.40	.32	.09	.20	.15	.25
	total nests	21	15	4	6	4	50
4	nests/pond	.07	.05	.17	.12	.10	.09
	nests/ha	.53	.16	.29	.11	.04	.19
	total nests	23	10	31	13	3	80
5	nests/pond	.02	.07	.11	.16	.28	.13
	nests/ha	.11	.21	.18	.14	.09	.12
	total nests	1	8	15	21	25	70
All	nests/pond	.05	.07	.12	.15	.25	.09
	nests/ha	.43	.22	.21	.13	.08	.17
	total nests	45	33	50	40	32	200

ponds rated "good" (P < 0.001). A similar relationship occurred in 1974 but there were too few nests and ponds in the highest category to make valid tests. The same pattern was evident for nests initiated in June.

Although the data show that some selection of favourable ponds (as rated by us) took place, other factors must have influenced pond selection by a substantial part of the nesting population because many of these ponds remained unused while many Canvasbacks used less favourable ponds. For ponds rated good, 76 to 82% were not used, and for those rated fair, 88 to 94% received no use. At the same time, 31 to 51% of the birds nested on ponds rated poor.

No Canvasback nests were found on type 1 ponds. Generally, the birds tended to select ponds in higher permanency types, but such a relationship was significant only in 1973 and 1975 (P < 0.001). Table 5, which pools data for all years, illustrates the ducks' tendency to select more permanent ponds. However, in terms of nests/hectare, the less permanent ponds averaged higher densities because mean areas were smaller.

In all years, fewer nests than expected were found on ponds under 0.2 ha. During the drier years, 1971, 1972 and particularly 1973, con-

siderably more nests than expected occurred on ponds over 0.8 ha (P < 0.001). Ponds from 0.2 to 0.8 ha had approximately the expected numbers. In 1974 and 1975, the wet years, use of ponds over 0.8 ha was little more than expected, but 0.4- to 0.8-ha ponds had more than expected use (P < 0.001). I attributed the shift in use from large to smaller ponds to two reasons. In the drier years, the large ponds had comparatively good stands of residual nesting cover, particularly cattails. This was not the case in 1974 and 1975. Also, smaller ponds tended to deteriorate faster in the dry years so would not be as attractive to late-nesting birds. Average nest densities usually decreased with increasing pond size (Table 5). An exception was ponds over 1.62 ha in 1973 which averaged 0.35 nests/ha.

In 3 years, 1971 and 1972 (pooled) and 1975, nest distribution with regard to the three categories of WSG around ponds did not deviate significantly from randomness (P > 0.05). In 1973, there was higher than expected use of open ponds with a concomitant low use of closed ponds (P < 0.02). I attributed this to the high use in 1973 of large ponds which tended to be open. Many of the small wooded ponds were dry or drying during the 1973 nesting season.

In contrast, open and half-open ponds in 1974 experienced less than expected use, whereas closed ponds received more than expected use (P < 0.01). The marked shift from open to wooded ponds between 1973 and 1974 was believed due to the general lack of residual cattail and whitetop cover in 1974 resulting from a large rise in water levels. This shift to wooded ponds was reflected in the increased use of willows and associated shrubs for nest support in 1974 over 1973 (80 vs. 11%).

Land use around ponds in May (tilled, stubble or pasture) apparently did not affect pond use by nesting Canvasbacks (P > 0.5).

The main factor influencing pond selection by nesting Canvasbacks was nesting cover, a conclusion also proposed by Dzubin (1955). Generally, cover was better on the more permanent ponds so these received the highest use. Permanency type tended to be directly related to pond size, so use increased with pond size. Likewise, there was no evidence that WSG *per se* influenced nest distribution. Flooded willow cover and hence, wooded ponds, became important as nesting sites when residual cattail and whitetop cover was scarce. Stoudt (1971) also observed greater use of willow cover at Redvers, Saskatchewan when preferred cover was scarce in wet years.

Despite the tendency for Canvasbacks to nest on ponds with preferred nesting cover such as cattail and whitetop, many seemingly chose ponds at random. Often, these were small, heavily wooded ponds with little open water and with sparse nesting material. Others used piles of rubble bulldozed into the middle of small ponds. As will be shown later, success of nests on such ponds, not traditionally considered "good" Canvasback habitat, was equal to, or better than those located in cattails and whitetop. Perhaps, as J. Stoudt (pers. comm.) has suggested, selection of such ponds, particularly small, wooded ponds, is an avoidance response to Redhead (*Aythya americana*) nest parasitism. Bengtson (1970) believed that nesting cover was the main factor in site selection by ducks but selection could be modified by past experience. In this case, Redhead parasitism may be a modifying influence.

Most authors stressed the importance of cattail for Canvasback nesting cover, and Stoudt (1971) stated that the presence or absence of cattail at Redvers, Saskatchewan governed the extent of Canvasback nesting there. However, observed selection of a habitat feature does not

Table 6
Canvasback nests, by nest support category and year

Support	1971	1972	1973	1974	1975	Total	% of grand total
Salix spp.	6	7	4	38	37	92	46.0
Typha latifolia	3	6	16	6	16	47	23.5
Scolochloa festucacea	4	2	13			19	9.5
Pond bottom	4	3	5		5	17	8.5
Rubble island		1	1	4	4	10	5.0
Carex spp.		2	5			7	3.5
Symphoricarpos sp.			1	2	2	5	2.5
Muskrat house					2	2	1.0
Spiraea sp.				1		1	0.5

Table 7
Mean, standard deviation and range of water depth at Canvasback nest sites and distance from dry land. (Island and muskrat house sites are excluded)

Year	Depth, cm	Distance, m
1971	30.3 ± 9.9 (14–50)	9.3 ± 6.3 (3–22)
1972	34.7 ± 19.4 (10–90)	8.2 ± 4.0 (3–15)
1973	45.4 ± 21.3 (5–80)	14.4 ± 15.2 (2–64)
1974	50.5 ± 18.9 (20–107)	7.1 ± 4.1 (1–23)
1975	46.0 ± 21.6 (14–97)	7.8 ± 4.0 (1–18)
All	44.4 ± 20.6 (5–107)	9.3 ± 8.7 (1–64)

necessarily reflect the need or importance of that feature (Zwickel and Bendell 1972). In my study, Canvasbacks made considerable use of cattail when it was present but were not dependent on it. They showed considerable ability to adapt to changing habitat conditions. There was no evidence that lack of cover restricted nesting effort in any year. However, receding water levels during successive years of drought likely would cause a shortage of all emergent nesting cover.

Nest support used by Canvasbacks (Table 6) generally reflected available cover which, in turn, was affected by water levels. During the drier years, 1971, 1972 and particularly 1973, the birds made relatively greater use of cattail, whitetop and sedge, and less use of flooded willows and associated shrubs. In 1974 and 1975 the relationship was reversed (P <0.001). High water in the spring of 1974 eliminated all residual whitetop and sedge cover and much of the cattail cover. At the same time, it inundated willows and shrubs at pond margins; these provided most of the nesting sites. More residual cattail cover

was present in 1975 but virtually no whitetop or sedge. Flooded willows and cattails provided support for most of the nests.

Measurements of nest distance from dry land and particularly water depth at nest site taken when the nest was found did not always reflect conditions prevailing when the nest was initiated. Therefore, some relationships between nest site selection and these features were perhaps already obscured. Water depth at nest sites was variable (Table 7). Average depth at nests built up from the bottom (20 cm) was significantly (P <0.001) less than depths of other sites. Differences among the latter or among years were not significant (P >0.05).

Distance of nests from dry land was also variable (Table 7) and did not differ significantly among support categories. However, the mean distance in 1973 was significantly greater (P <0.05) than those of other years. This was related to the high use of cattail, whitetop, and sedge cover distributed throughout large ponds in 1973. In other years, support cover tended to be confined closer to shore.

Nests supported by cattail, whitetop, or sedge were made from the support material. Willow-supported nests usually were made of whitetop, sedge, or a mixture of the two. Five of 100 nests supported by willows or shrubs were made mainly of willow twigs. Whitetop was the primary material used for bottom-supported nests.

5. Habitat use by broods
Canvasback broods were never seen on type 1 ponds and rarely on type 3 ponds during counts. Generally, they preferred large, permanent ponds with substantial areas of water free of emergent plants. This was also the case at Redvers (Stoudt 1971). In 1973 and 1974 when there were adequate data for analysis, brood use was significantly (P <0.001) correlated with

Table 8
Average number of broods seen per pond during six counts, by pond permanency type and size class, 1973

Pond type	Pond size class, ha					Total
	<.21	.21–.40	.41–.81	.82–1.62	>1.62	
3	.01	0	.15	0	0	.03
4	.02	.11	.35	.50	.60	.21
5	0	.36	.46	1.06	3.33	.86
All	.01	.09	.32	.59	1.83	.24

estimated amount of open water on ponds during July.

Pond use by broods is illustrated by 1973 data (Table 8). In 1974, a wet year, 95% of the broods were seen on ponds over 0.81 ha, and 90% on type 5 ponds. Woody shore growth and land use around ponds had no apparent effect on brood use of ponds. Broods were seen more often on ponds with little tree growth but this was also a feature of the large ponds that they tended to use.

Stoudt (1971) believed that the use of ponds by broods is related to the species' characteristic feeding and escape behaviour. Although newly-hatched Canvasbacks obtain most of their food at the water surface (Hochbaum 1944), older ducklings and adults feed mainly by diving. This is also their chief means of escape. Open water, featured mainly in large, permanent ponds, provides these requirements.

6. Canvasback production
Apart from densities of breeding pairs initially attracted to the area, several factors affected production of fledged young by the study area populations. These included the proportion of pairs nesting (nesting effort), the success of nests, size of incubated clutches, and survival of young to fledging.

6.1. Nesting effort
Nesting effort expressed as total nests per indicated pair on the original six-section block

Figure 4

Nests per Canvasback pair

$Y = 0.339 + 0.118X$
$r = 0.96$
$P < 0.02$

Hectares type 4 and 5 ponds per pair
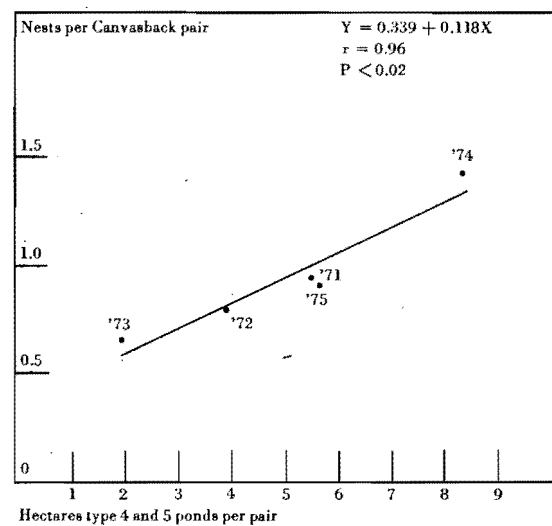
was 0.94 in 1971, 0.78 in 1972, 0.65 in 1973, 1.42 in 1974, and 0.90 in 1975. This measure included renests, the number of which was unknown, though the temporal distribution of all nests (Fig. 3) suggested that some renesting took place each year and that the rate of renesting did not vary much from year to year. Regardless of renesting, part of the population did not nest in 1972 or in 1973. Most, if not all, nested in the other years. Similar annual variations in nesting effort by Canvasbacks at Redvers (Stoudt 1971) and Lousana (Smith 1971) are indicated by figures for censused pairs and broods, and nest success. The long-term average for Redvers was 0.94 nests/pair and for Lousana, 1.73 nests/pair. The difference was related to a comparatively low nest success at Lousana (36%) that must have resulted in a high renesting rate.

Nesting effort was directly related to habitat (area of type 4 and 5 ponds) available per pair

(Fig. 4). When more habitat per pair became available through decreased pair populations and increased habitat, nesting effort increased. This indicates a mechanism operating at high pair densities relative to habitat that suppresses nest initiation through intraspecific behavioural interactions. I postulate that, as pairs per habitat unit increase, the frequency of pair contacts also increases and, in some way, inhibits nest starts.

Like the Ring-necked Duck (*Aythya collaris*), Canvasbacks do not show high levels of overt pair interactions (Mendall 1958). No territory is defended by the drake. Rather, a mated-female distance mechanism is displayed and the drake defends a small area around the female (Erickson 1948, Dzubin 1955). Such behaviour can be interpreted as defense of the female rather than defense of an area (Mendall 1958, McKinney 1965); that is, little site tenacity is evident. Behaviour that tends to space breeding Canvasback pairs appears to be avoidance—termed "mutual respect" by Mendall (1958)—rather than one involving pursuit, characteristic of many dabbling species. But the signals that release such behaviour have been difficult to observe and quantify. Canvasbacks are mobile ducks with large, overlapping home ranges, each encompassing 5 to 10 km² (Dzubin 1955). Thus, there is ample opportunity for pairs to receive signals from others at a frequency related to pair density.

Although the number of pairs attracted to each area may fluctuate from year to year, I believe long-term stability around a mean density is effected by density-related production. On my area, the 5-year mean was 2 pairs/km². At Minnedosa, Manitoba, an area with higher pond (habitat) densities, the 12-year average exceeded 3 pairs/km² and ranged from about 2 to 5/km² (Trauger and Stoudt 1974).

The reproductive response of waterfowl is closely linked to the relationship between pair

densities and available habitat. Some pairs usually secure space and breed despite severe shortages of habitat. Thus, intraspecific behavioural factors as well as habitat factors must affect the number of nesting pairs on an area. The various reproductive strategies and spacing mechanisms of ducks are closely tied to specific social systems (McKinney 1965 and 1973). The response of ducks to small changes in the habitat/pair ratio is not easily measured. Small decreases in this ratio may simply result in proportionately more birds using marginal habitat (Dzubin 1969a, Bengtson 1970). Lower nesting effort is likely manifested first as non-nesting by yearlings or otherwise less experienced birds (Grice and Rogers 1965, Trauger 1971, Trauger and Stoudt 1974).

The notion that Canvasback nesting effort is related to the frequency of intraspecific pair contacts presupposes an inhibitory reproductive effect brought about by some element of social behaviour. The positive effects of social behaviour in bird reproduction are well documented (Immelmann 1971), and the role of behaviour in non-breeding is readily observed in territorial species that exclude other pairs from optimum habitat (e.g., Young 1970). However, in species where potential breeders are not obviously excluded, the role of social behaviour in non-breeding is less evident. Carrick (1972) described how intraspecific aggression caused non-laying in the territorial (group) Australian Magpie (*Gymnorhina tibicen*) through a psychosomatic inhibition of ovarian development, and Phillips and van Tienhoven (1960) concluded that captivity in Pintails (*Anas acuta*) inhibited normal gonadotrophin secretion necessary for ovarian development. Perhaps high levels of pair interactions similarly affect Canvasbacks, but detailed studies of behaviour and physiology during the period of pair dispersal on the breeding grounds would be necessary to verify this.

I have noted that Canvasback nesting effort varied among years and have postulated that, indirectly, available habitat per pair was responsible. Alternative explanations for variations in nesting effort should be examined. In 1973, the year with the lowest nesting effort, an unknown part of the pair population comprised ducks likely displaced by drought from their traditional breeding areas. It could be argued that some of these birds failed to nest simply because they had been displaced. There was no evidence to substantiate this. Pairs were well dispersed and dispersal was not delayed in spring. There were never any flocks of obviously non-breeding birds as described by Smith (1969) for displaced ducks during years with drought. I do not believe that displacement *per se* was a cause of non-nesting on the study block in 1973. In the other years, there was no evidence that habitat conditions elsewhere affected Canvasback populations on the block.

Trauger (1971) noted variations in the nesting rate in a population of Lesser Scaup (*Aythya affinis*) and showed that it was largely age-related, i.e., nesting effort declined with increasing proportions of young females. Although age ratios of female Canvasbacks may have influenced nesting effort in my study, changes in age ratios could hardly have accounted for the wide differences observed. There is little quantitative information on the relative nesting rates of adult and yearling Canvasbacks; however, if yearlings had but half the nesting drive of adults, a rather large change in age ratio would be necessary to markedly affect overall nesting effort.

Because nesting effort is based on all nests including renests, differences in renesting rate could affect overall nesting effort. I have no direct measure of renesting effort. An indirect but crude measure might be the ratio of late

(June) nests to early (May) nests. Percentages of nests started after May did not differ significantly among years and bore no relationship to overall nesting effort. In any case, if increased pair densities did depress nesting effort as suggested, initial nests and at least early second attempts (pair numbers were still relatively high in late May) must have been affected.

Captive-reared Canvasbacks were released on the area in May 1972 in another experiment (Sugden 1976). These birds had no apparent effect on the wild breeding population. Counts made before, during and after the releases revealed no population changes in wild Canvasback pairs that might have been related to the presence of the released ducks. Some of the released hens formed pair bonds with wild males but the bonds were weak, of short duration, and occurred when the wild pair population (pairs and lone drakes) was normally declining. The effects of intraspecific pair interactions are most likely pronounced during pre-nesting, nesting, and early incubation stages (Dzubin 1969a). Whether the released Canvasbacks were capable of, or in fact did inhibit nesting attempts by wild birds in 1972 remains unknown.

Bengtson (1972) believed that food abundance could affect the incidence of non-breeding in diving ducks in Iceland. A marked decrease in chironomid larvae in one year was accompanied by increased non-breeding, particularly by scaups (*Aythya marila*) and scoters (*Melanitta nigra*) that depended largely on the larvae for food. I did not investigate food resources. However, considering the variety of foods eaten by Canvasbacks during the breeding season (Bartonek and Hickey 1969), and the wide variety and large number of ponds available to them, it seems unlikely that lack of food could have been a cause of non-breeding even in 1973 when the habitat/ pair ratio was lowest.

6.2. Nest success

The influence of field studies on duck nesting success should be evaluated (Dzubin and Gollop 1972). Hammond and Forward (1956) believed that nest markers, flushing ducks from nests, and the investigator's presence around nests could increase predation and thereby bias nest success data. Picozzi (1975) showed that artificial upland nests marked with stakes 5 m away received higher predation by Carrion Crows (*Corvus corone*) than unmarked nests. On the other hand, Newton and Campbell (1975) concluded that marking upland duck nests on their area did not affect predation rate by Jackdaws (*C. monedula*) — the main predators — because nest densities were relatively high and searching by Jackdaws with or without the aid of markers would be equally rewarding. However, the investigators' presence did increase predation rates and subsequent nest losses by at least 9 to 14% because nests were left unattended by females more often.

Nest markers were not used in my study, and disturbance was minimal, a female being flushed but once in most cases. Of 200 Canvasback nests found on the block, 56 or 28% had been terminated when found. Five of these were successful. The high loss of nests occurring before those nests had been located suggested that our influence on the success of found active nests was minimal. Of the 144 nests that were active when found, 82 or 57% were successful. Females were flushed from 108 nests and never from 36. Success of these two groups did not differ significantly (adj. $X^2 = 0.15$, 1 d.f., $P = 0.7$), so I conclude that flushing the hen did not bias results through increased predation or desertion.

The influence of visiting nests (whether or not a hen flushed) is difficult to evaluate. However, if flushing the hens did not increase predation by Common Crows (*C. brachyrhynchos*) — the main predators — it is unlikely that simply visiting nests would have any effect. While searching for Canvasback nests we recorded data on many nests of American Coots (*Fulica americana*). Predation on these was insignificant (Sugden, unpubl.). I believe such activity on our part tended to prevent crows from forming an association between our checking a nest and a food reward. Of nine nests that were located by seeing the hen from a distance and that were not visited until they had terminated, four were successful — a success rate similar to that of all nests. Though the sample is small, it supports my belief that nest-hunting activity did not significantly affect nesting success of Canvasbacks.

Forty-three per cent of the Canvasback nests were successful (at least one egg hatching) during the 5 years (Table 9). The low of 31% in 1973 and the high of 57% in 1974 did not depart significantly ($P > 0.1$) from the 5-year mean. The relatively high loss of nests in 1973 was due to a high desertion rate, probably related to deteriorating habitat conditions. Similar conditions at Minnedosa, Manitoba in 1973 also caused high rates of desertion and predation of Canvasback nests (Trauger and Stoudt 1974). There, average success during 1961–72 was 45% and ranged from 21 to 62%. In another Manitoba study, Olson (1964) reported an average success of 21% for 3 years (range, 10 to 37%) and concluded that success was related to the quality and quantity of nesting habitat. Nest success at Redvers, Saskatchewan averaged 68% and ranged from 45 to 84% during 1952–65 (Stoudt 1971). In the

Table 9
Fate of Canvasback nests by year

Fate	1971	1972	1973	1974	1975	Total	% of grand total
Hatched	8	9	14	29	27	87	43.5
Destroyed by predator	8	10	19	8	25	70	35.0
Deserted	0	2	11	4	6	23	11.5
Hail, flood	0	0	0	2	5	7	3.5
Lost, cause unknown	1	0	1	8	3	13	6.5

same period at Lousana, Alberta, nest success averaged 36% (Smith 1971).

The relatively high success (57%) of Canvasback nests on my area in 1974 seemed related to a low predation rate although some of the losses recorded as "unknown" also were likely due to predation (Table 9). I have no data on annual changes in predator populations that might reflect the observed predation rates. Most of the destruction by predators was due to crows. A few nests were lost to Black-billed Magpies (*Pica pica*). Only two nests were definitely lost to mammalian predators, presumably striped skunks (*Mephitis mephitis*). Predation was a major cause of nest loss in other studies also. At Minnedosa, raccoons (*Procyon lotor*) were most important (Trauger and Stoudt 1974); crows and various mammals were equally important at Redvers (Stoudt 1971); crows were the main predators at Lousana (Smith 1971). The Oregon study (Erickson 1948) was an exception and desertion accounted for most losses with predation by ravens (*Corvus corax*) of lesser importance.

There was no evidence that nesting success was influenced by pond type, pond size, woody shore growth, land use around ponds, or kind of nest support. There was some indication that nests initiated after May were more successful than those initiated during May (51 vs. 40%), though the difference was not significant ($P > 0.1$). In 4 out of 5 years post-May nests averaged higher success than May nests. Higher success of late nests might be expected because nesting cover is better then and more buffer food is available for predators.

Nesting success was influenced by quality of nesting pond ($P < 0.05$). Average success of May-initiated nests was 52% on ponds rated poor (Appendix 3), 26% on ponds rated fair, and 33% on ponds rated good. The same relationship held

for total nests. This seeming contradiction (higher success on "poor" ponds) may have been related to the incidence of Redhead nest parasitism which increased significantly (P <0.02) with quality of nest pond. Considering all nests this parasitism was 34% for poor ponds, 53% for fair ponds, and 60% for good ponds. When looking for nests outside the block, we selected ponds with what we considered to be prime nesting cover — usually good stands of cattail. Of 77 incubated nests found by such selective searching, 82% were parasitized, a rate significantly higher than that derived from systematic nest hunts on the block. This also indicated that the incidence of parasitism was related to kind of nesting habitat. The observed relationship strengthens the notion that Canvasbacks respond to parasitism by seeking "poor" ponds for nesting (J. Stoudt, pers. comm.).

Success of incubated nests was not affected significantly by parasitism. Of 45 nests that reached incubation and were not parasitized, hatching success was 69% compared with 61% for 84 parasitized nests. Weller (1959) believed that Canvasback nest success would be significantly reduced when parasitism reached an incidence of 60 to 70% and when the number of parasite eggs reached 4 to 6 per nest. In Joyner's (1976) study, interspecific parasitism did not increase desertion or predation of Cinnamon Teal (*Anas cyanoptera*), Mallard, and Pintail nests. On the other hand, Erickson (1948) believed that Redhead nest parasitism was a major cause of desertion by Canvasbacks in Oregon.

The effect of Redhead intrusions on nests abandoned or destroyed prior to incubation is not easily measured. My criterion of a parasitized nest was one or more Redhead eggs in or by the nest. Of 38 nests that contained at least one Canvasback egg and that were terminated before incubation, 12 or 32% were parasitized, which

suggested that parasitism was an unimportant factor in the loss of nests before incubation, considering the proportion of incubated nests that were parasitized (65%). This is not necessarily so, however, because parasitic Redheads could have been responsible for the loss of a majority of the parasitized nests. It is reasonable to assume that individual Canvasback hens react differently to the intrusion of Redheads. Those with the strongest nesting drive are likely the ones that persevere despite the addition of parasitic eggs. Less persistent hens may desert readily. In fact, it is possible that some nests that lacked evidence of parasitism (Redhead eggs), also may have been abandoned due to Redhead intrusions. These possibilities must be investigated before the real effect of parasitism on nest success can be determined.

6.3. Clutch size

Clutch data pertain only to nests that were completed, i.e., incubation had started. Clutch size refers to the number of Canvasback eggs in the nest during the last visit (often the only one) prior to nest termination. Average size of 129 clutches was 6.8 ± 2.8 and ranged from 0 to 14 eggs. (A nest contained Redhead eggs only, with Canvasback eggs outside it.) Mean clutch size was the same for successful and unsuccessful nests. Eighty-eight clutches initiated in May averaged 7.5 ± 2.7 compared with 5.4 ± 2.3 for 41 initiated later. The mean difference of 2.1 eggs per clutch was significant (P <0.001) and may reflect a higher incidence of renests in the post-May sample, those tending to have smaller clutches (Sowls 1955).

Mean clutch size of 84 nests parasitized with Redhead eggs was 5.9 ± 2.7 compared with 8.5 ± 2.1 for 45 nests not parasitized. The difference of 2.6 eggs per clutch was significant (P <0.001) and represents an average reduction

in Canvasback eggs of 30% in parasitized nests. Because 65% of incubated nests were parasitized, the overall reduction of host eggs due to parasitism was about 20%. Similar reduced clutches due to parasitism have been summarized from the literature by Bellrose (1976). The reduction can be attributed to suppressed ovulation and loss of eggs from the nest (Weller 1959).

Because nests were not studied intensively, I have no precise estimate of the number of eggs hatching. Average clutch size at hatching would be slightly lower than figures given above because at times it was apparent from membrane counts and eggs outside nests that some eggs had been lost during the interval between last visit and hatching. Also, all eggs in a nest did not always hatch, but the number of failures could not always be verified.

The average clutch size (6.8) in my study was lower than most published values. Bellrose (1976) calculated a mean size of 7.9 eggs for 519 nests — including parasitized nests — reported in the literature. Mean sizes ranged from about 7.2 (Townsend 1966) to 10 (Hochbaum 1944). It is not always clear if published averages included eggs outside nests so comparisons are difficult. Had I included them, my average clutch size would have been about 8 eggs.

6.4. Survival of young

Two problems peculiar to Canvasbacks in this region complicate the use of data from brood counts. Some broods contain Redheads and, while these can be distinguished in older broods, the two species are difficult to separate when very small (Hochbaum 1944). This was evident from recorded brood data; most class Ia broods (Gollop and Marshall 1954) were recorded as having none, whereas 43% of the class II and III broods contained Redheads. Therefore, average size recorded from class I Canvasback broods was

Table 10
Canvasback production data for Meacham study block

Year	1971*	1972*	1973	1974	1975	All
Successful nests	8	9	14	29	27	87
Average clutch size	8.2	6.5	6.5	7.4	6.4	6.8
Mean number of broods	5	10	15	14	—	44
Mean size Class II–III	4.5	4.2	4.0	3.0	—	3.8
Estimated production	22	42	60	42	—	166
Censused pairs	18	27	74	40	54	159†
Broods per pair	0.28	0.37	0.20	0.35	—	0.28
Young per pair	1.22	1.56	0.81	1.05	—	1.04

*Six-section block
†Excluding 1975

considered too high. On the other hand, older broods sometimes split up, so averages based on these, particularly class III broods, underestimate size (J. Stoudt, pers. comm.). By the same token, estimates of total broods would be inflated and this would compensate for underestimates of size when calculating production by traditional methods.

Average sizes of class II and III broods were 3.9 and 3.7, respectively, and did not differ significantly. Using the prehatching mean clutch size of 6.8, and 3.9 for class II broods, the loss to that age averaged about 2.9 ducklings per brood or 40%. The estimate may be high because, for reasons previously stated, the number of ducklings hatching was probably less than the recorded clutch size. Stoudt (1971) and Smith (1971) estimated the average loss from class Ia to class III to be 1.2 ducklings or about 20%. At Athabasca–Peace Delta, Nieman (1971) calculated a decrease of 3.4 ducklings per brood or 48% between hatching and class III age. Based on Nieman's (1971) average for class II broods, the loss would have been about 2.5 ducklings or 36%. In view of the various sources of error in these data, no conclusions can be made about the apparent differences in duckling survival. In any case, these calculations do not account for loss of entire broods that may occur (Reed 1975).

Brood counts in the first 3 years agreed reasonably well with the number of successful nests on the same areas (Table 10), but in 1974,

Conclusions

the average number seen during three counts (16, 16 and 10) was but half the number of nests that hatched. Movement of broods off the block without compensatory immigration was ruled out because the block contained some of the best brood habitat in the area. We found downy young near two nests in 1974 that we attributed to hail storms, at least two of which hit parts of the study block during the brood season. None had been found before then. Direct evidence of duckling mortality is seldom witnessed in the field so the two examples may be significant. Smith and Webster (1955) documented extensive duckling mortality from a hail storm in Alberta, albeit much more severe than any encountered on my area. If hail storms did cause the apparent brood loss in 1974, any conclusions concerning production probably would not have widespread application because damage from such storms is usually local in extent (Smith and Webster 1955). Regardless of the reason for poor brood survival, the results reinforce the point made by Reed (1975) concerning production estimates that ignore loss of entire broods.

Estimates of production rate (young per pair) based on censused pairs and broods and mean size of broods (Table 10) are low compared with rates of 2.8, 3.3 and 2.8 young per pair reported by Smith (1971), Stoudt (1971) and Erickson (1948), respectively. Part of the difference was due to the smaller clutches and broods on my area. The main difference, however, seems to be the comparatively low number of broods. This was due to poor survival in 1974 (believed to be a local phenomenon), poor nesting success compared with Redvers (Stoudt 1971), and without a high compensatory renesting rate that must have been the case at Lousana (Smith 1971) and Oregon (Erickson 1948).

The number of Canvasback pairs attracted to the study block varied annually and, in the short term, changes were not correlated with habitat changes. Considering the response of pairs to available habitat (Fig. 2), it is clear that the area could have accommodated more pairs except perhaps in 1973. However, carrying capacity of an area should not be measured in terms of pair densities, but rather, as the maximum density (expressed as pairs per area of type 4 and 5 ponds in this case) attainable without impairment of production rate (fledged young per pair). In extreme cases, brood survival may be affected by density-dependent factors (Dzubin 1969a, Newton and Campbell 1975, Riggert 1977), but there was no reason to believe that such was the case with the low densities of Canvasback broods on the block. Likewise, nest success, affected mainly by crow predation, apparently was unrelated to density, though under exceptional circumstances, factors such as predation and desertion may be subject to density-dependent influences. Nesting effort was the only phase apparently influenced by density as related to available habitat. Thus, using the definition of carrying capacity above, I conclude that the habitat was filled in all years with the probable exception of 1974, because nesting effort was, to some degree, suppressed. Although breeding pair densities will lag in response to rapid changes in habitat (e.g., 1974 from 1973), long-term mean densities will characterize a given area.

A mechanism which effects long-term stability of population densities which, in turn, reflect breeding habitat is also indicated in the relationship between Canvasback pair and pond densities for eight study areas during the period, 1951–55 (Fig. 5). (There were no comparable data for this number of areas during any other period.) The early 1950s represented the termina-

Figure 5

Canvasback pairs per 259-ha section

$Y = 0.87X - 0.564$
$r = 0.99^{***}$

May ponds per 259-ha section
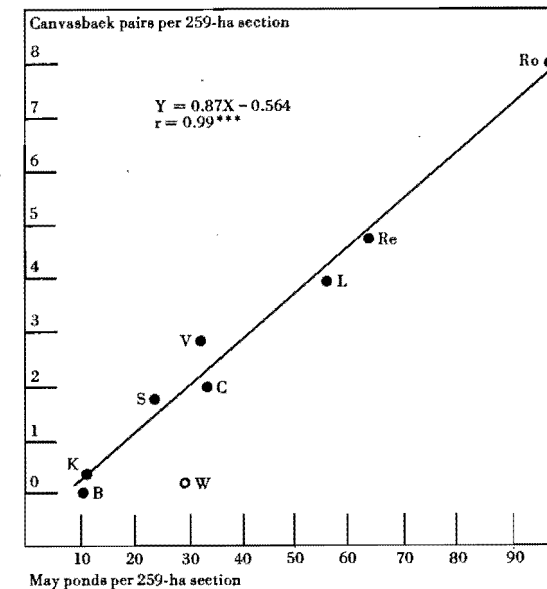
tion of a period of relatively stable and good habitat conditions that followed the drought of the 1930s. I believe such conditions favoured the observed pattern. The nonconformity of Waubay, S.D. data (Fig. 5) suggests that additional factors were affecting Canvasback populations there. The comparatively low density may reflect greater hunting mortality, or simply the southern limits of the species' breeding range.

Historically, Canvasbacks on pothole breeding habitat never have occurred in densities as high as those we know for several other species. The unpublished reports of biologists who observed waterfowl conditions in the prairie provinces during the 1930s tell us that Canvasbacks, like many species, were generally scarce. Systematic ground counts apparently began in 1949 in Manitoba (Kiel et al. 1972) and have since

expanded to include up to 13 areas in the prairie provinces, though not simultaneously. These included the best pothole breeding habitat for Canvasbacks. The highest recorded density was about 5 pairs/km², and densities exceeding 4 pairs/km² were rare except for the Minnedosa-Roseneath area of Manitoba. I suggest that the comparatively low density of breeding Canvasbacks reflects an intrinsic trait and that it is related to the species' need for a large home range. An inverse relationship between density and size of home range in ducks has been reported by Mendall (1958).

During the breeding season, Canvasbacks possess rather specialized habitat requirements. Pairs and broods favour large, permanent ponds. Nesting hens require ponds with emergent vegetation for nest support. Although the ideal nest pond can be described as one that is permanent, not more than 0.8 ha in size, and having a dense stand of residual cattails or *Scirpus* (Dzubin 1955), such ponds are not essential for satisfactory Canvasback reproduction. The birds show considerable adaptability in choice of nest ponds and reproduce successfully under a wide range of habitat conditions. The advantages of high quality nesting habitat may be negated in part by the propensity of Redheads to parasitize nests located in such habitat.

Compared with species that nest in the upland and that depend extensively on the less permanent ponds, breeding Canvasbacks enjoy a relatively secure habitat. Locally, farming activities sometimes destroy Canvasback nesting cover through burning (Trauger and Stoudt 1974), but do not cause widespread damage to cover and nests (Higgins 1977). Permanent ponds, though not immune to drainage, are less likely to be drained than seasonal and temporary ponds (Kiel et al. 1972). On my area, burning de-

stroyed an insignificant amount of emergent cover in any year. A few small, temporary ponds had been eliminated but there was no evidence that any of the more permanent ponds had been altered significantly. (Because of the topography, it would be difficult and costly to drain in this area.) Trees had been cleared from around some ponds; but that has not made them less attractive to Canvasbacks, though it would reduce available nest support in wet years. On the other hand, rubble islands resulting from clearing provided relatively secure nesting sites for several species including the Canvasback. Loss of any waterfowl habitat, including that of the Canvasback must be viewed with concern. However, in the long term, overwater nesters like Canvasbacks that also depend extensively on permanent ponds during the breeding season will likely suffer least from the impact of agricultural land use.

Appendices

Appendix 1
Wetland area (ha) by permanency type on 15.54-km² study area

Year	Permanency type				
	1	3	4	5	Total
1971	13.80	32.50	53.70	45.73	145.73
1972	12.18	31.40	53.46	51.64	148.68
1973	9.26	30.56	44.19	49.29	133.30
1974	5.26	12.38	61.51	121.65	200.80
1975	3.24	13.84	58.56	129.10	204.74

Appendix 2
Numbers of May ponds by permanency type (see text), size class and year.
The study area was 15.54 km² in 1971 and 1972 and 31.1 km² thereafter

Year	Type	Size class, ha					
		<.21	.21–.40	.41–.81	.82–1.62	>1.62	Total
1971	1	73	12	2	1	0	88
	3	41	20	15	6	3	85
	4	27	21	20	15	5	88
	5	4	9	9	11	6	39
	Total	145	62	46	33	14	300
1972	1	80	10	2	0	0	92
	3	46	19	12	7	3	87
	4	29	22	21	16	4	92
	5	6	12	11	10	8	47
	Total	161	63	46	33	15	318
1973	1	111	28	7	1	0	147
	3	97	49	27	10	4	187
	4	49	35	31	20	5	140
	5	9	14	26	16	9	74
	Total	266	126	91	47	18	548
1974	1	87	10	2	0	0	99
	3	124	35	13	7	1	180
	4	110	54	50	28	8	250
	5	28	41	56	50	30	205
	Total	349	140	121	85	39	734
1975	1	109	3	0	0	0	112
	3	202	29	16	1	0	248
	4	117	64	64	27	7	279
	5	13	40	38	46	37	174
	Total	441	136	118	74	44	813

Appendix 3
Description of four categories of May nesting potential

1. *Nil* — no suitable support or nest material.
2. *Poor* — very little support material present (usually flooded willows) and sparse nest material.
3. *Fair* — both support and nest material present in moderate amounts; often flooded willows mixed with whitetop or sedges, or isolated clumps of cattail.
4. *Good* — extensive, dense stands of residual cattails or whitetop (*Scirpus* was scarce).

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