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Productivity of Canada Geese in Northwestern Iowa[1]

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Productivity, gosling habitat use, and survival of giant Canada geese *(Branta canadensis maxima)* in northwestern Iowa were studied in 1977 and 1978. Arrival of geese on the breeding grounds in March coincided with the first open water in smaller wetlands. Initial laying dates (25 March 1977 and 26 March 1978) were probably influenced by photoperiod, timing of arrival at the breeding grounds, and ice conditions. The density of successful nests in 1978 averaged .12 nests/ha of wetland. Nest density was highest in cover class 2 wetlands. The large mean clutch size of 6.0 eggs for 185 nests suggested that most of the breeding population was fairly old. Most nests hatched 10-20 May. Of all the 211 nests found during the study, 166 (79%) hatched. Nesting success was greater ($P < 0.01$) in artificial nest structures than in natural nest sites. Desertion was the main cause of nest failure. Of 1,126 eggs laid in 205 nests, 862 (77%) hatched. Hatching success of 1,002 eggs in 167 clutches incubated full term was 86%. Fewer geese renested in 1977 than in 1978, possibly because reduced water levels in 1977 made nest sites unattractive. The mean initial brood size for 165 nests was 5.3. Mudflats, pasture-like uplands, and artificial islands were used by goslings for foraging, loafing, and roosting. Gosling survival was 73-90+%; inclement weather was the major mortality factor.
INDEX DESCRIPTORS: Northwestern Iowa, *Branta canadensis maxima*, productivity, nesting success, gosling survival.

In recent years, state and federal wildlife agencies have attempted to establish local breeding populations of Canada geese (Nelson 1963, Dill and Lee 1970). The most popular and successful subspecies has been the giant Canada goose. Before settlement, the breeding range of the giant subspecies was the tallgrass prairies of the north-central states and southern Canada (Hanson 1965). Loss of habitat and unrestricted hunting severely reduced the numbers of giants so that this subspecies once was thought to be extinct. In 1962 it was rediscovered (Hanson 1965).

In Iowa, wild giant Canada geese were extirpated by 1906 (R. Howing, pers. comm). The Iowa Conservation Commission began a restoration program in northwestern Iowa in 1964 (Bishop and Howing 1972, Bishop 1978). However, little information on the productivity or habitat requirements of the Iowa Canada goose population was available.

The objectives of this study were to determine the nesting success and other reproductive parameters for giant Canada geese in northwestern Iowa, estimate gosling survival, and describe gosling habitat use. Such information could then be used in managing this population.

STUDY AREA

This study was conducted in 1977 and 1978 on several state-owned wetlands in Clay, Emmet, and Palo Alto counties in northwestern Iowa (Fig. 1). From 1975 through 1977, a severe drought in this region reduced water levels and increased vegetation in many wetlands.

The principal study area was a 21 km^2 complex of permanent and semi-permanent lakes and marshes interspersed with state- and privately-owned uplands and woodlands around Ingham and High lakes (Fig. 1). This area, in Emmet County, contains 11 wetlands totaling 673 ha. Additional information was obtained from 5 other wetlands in the 3-county area (Fig. 1). All wetlands were described using the classification system of Stewart and Kantrud (1971).

Artificial nest structures (ANS) have been placed in most of these wetlands. These structures were of 3 basic types: 1) a basket or barrel elevated by a single pipe, 2) a barrel fastened to a small raft, and 3) artificial islands. Structures were repaired and received fresh nesting material annually.

METHODS

In both years, field work began in late March. In 1977, only 4 wetlands in the principal study area were searched for nests. In 1978, all wetlands listed in Fig. 1 were searched for nests. All ANS in each wetland were inspected several times during the nesting season. The presence of at least 1 egg or small amounts of down indicated an ANS was being used. Wetlands were also searched for natural nest sites (NNS).

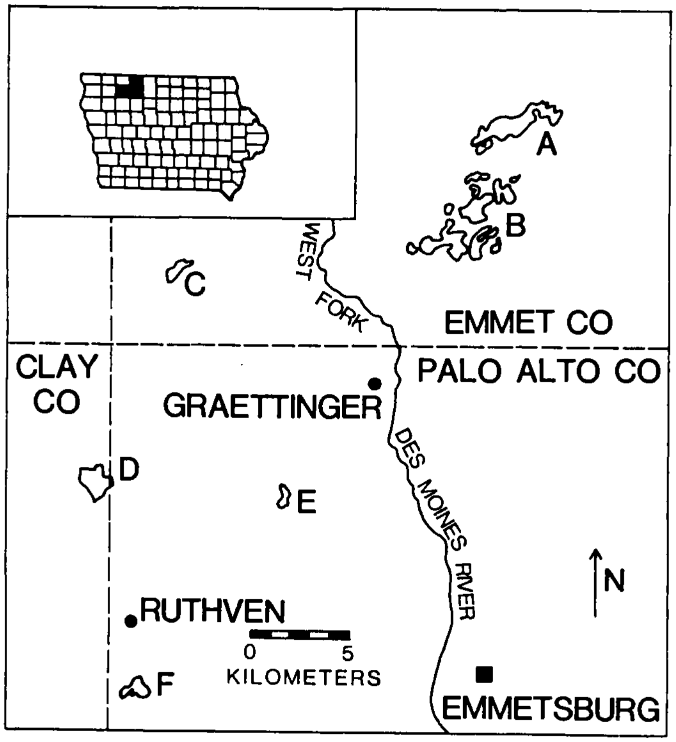

Figure 1. *Map of the general study area in northwestern Iowa (insert shows the location of Clay, Emmet, and Palo Alto counties). A) West Swan Lake, B) Principal Study Area, C) Twelve Mile Lake, D) Dewey's Pasture, E) Fallow Marsh, F) Virgin Lake.*

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Each ANS and NNS was visited 3 times during the nesting season. Initial laying date was estimated by floating incubated eggs in water (Westerkov 1950) and by using a laying rate of 1.5 days/egg (Kossack 1950, Brakhage 1965). The flotation technique was accurate before 10 days of incubation. Hatching date was estimated using an incubation period of 28 days (Kossack 1950, Brakhage 1965). Shortly after the estimated hatching date, nests were revisited and both nesting and hatching success were determined. Time spent at a nest was minimized to reduce desertion and avoid attracting predators. Nests were not visited on extremely windy, cold, or rainy days to avoid chilling the eggs.

Survival of goslings to banding age (5-7 weeks) was estimated by comparing the number of goslings hatched with the number observed just before banding. In 1977 and 1978, survival was estimated for goslings hatched in the principal study area. In 1978, additional data on gosling survival were obtained from 2 isolated wetlands.

RESULTS

Nesting Season

Giant Canada geese returned to the study area during the first week of March 1977 and on 15 March 1978 (L. Kropf, pers. comm.). Snow cover had melted by the time geese arrived in both years, but all wetlands were icebound except those with medium to dense stands of emergent vegetation. Mean daily air temperatures during the first half of March were higher in 1977 (range, − 7 to 10°C) than in 1978 (range, − 16 to 3°C).

Nests were initiated first in shallow wetlands with medium to dense vegetation that were the first to become free of ice. The last nests were initiated in deep-water, permanent lakes. In both years, the permanent lakes were icefree by 3 April.

Initial laying dates were determined for 40 nests in 1977 and 91 nests in 1978. The first egg was laid on 25 March 1977 and 26 March 1978 respectively. The peak of initial egg laying for each season was 1 April 1977 and 2 April 1978 (Fig. 2). These peaks were at least 23 and 18 days following first arrival for 1977 and 1978 respectively. The last initial laying date was 29 April in 1977 and 11 May in 1978.

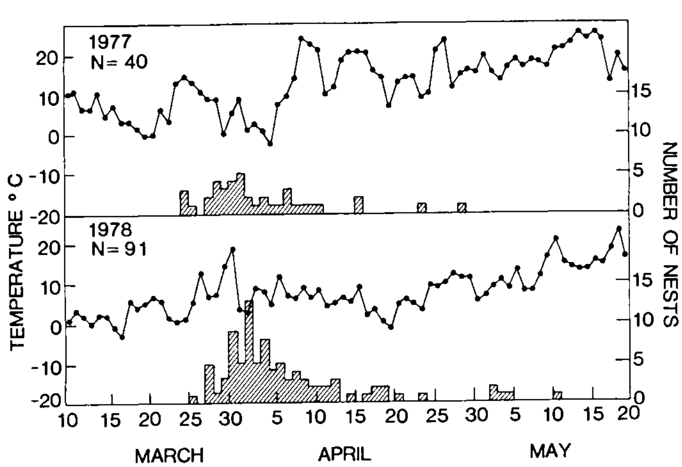

Figure 2. *Mean daily air temperature (circles) and Canada goose initial laying dates (histogram), northwestern Iowa, 1977-1978. Air temperature data from the U.S. Weather Bureau, Spencer, Iowa, 40 km southwest of the principal study area.*

It was impossible to determine the number of pairs competing for nest sites in each wetland. The number of successful nests in each wetland in the principal study area in 1978 gave an estimate of nest density. This estimate avoided the bias of renesting pairs, but it did not account for pairs that failed to renest.

The overall nest density for the principal study area was .12 nests/ha of wetland. Nest density in the 11 wetlands ranged from .01 to .90 nests/ha. The Stewart and Kantrud (1971) wetland cover classes, in order of decreasing nest density, were 2, 1, 3, and 4.

The first eggs hatched on 4 May 1977 and 3 May 1978. Most hatched between 10-20 May. The last eggs hatched on 3 June in 1977 and 11 June in 1978.

The length of the nesting season (date of the first egg laid to the date that the last nest ends) in 1977 was 71 days (25 March-3 June) and ended with the hatching of eggs. In 1978, the season lasted 85 days (26 March-18 June) and ended with the desertion of failed eggs after overtime incubation.

Table 1. *Distribution of clutch sizes for completed clutches found in artificial nest structures (ANS) and natural nest sites (NNS) in 1977 and 1978.*

Clutch Size	ANS	NNS	Total
2	2	—	2
3	4	1	5
4	8	2	10
5	34	5	39
6	58	3	61
7	51	4	55
8	10	—	10
9	2	1	3
Total nests	169	16	185
Mean clutch size	6.0	5.7	6.0
Standard deviation	1.2	1.5	1.2

Productivity

Clutch size in completed clutches averaged 6.0 eggs (range, 2-9 eggs, Table 1) and did not differ between years ($P > 0.25$). The most frequent clutch sizes, in order of decreasing frequency, were 6, 7, and 5 eggs (Table 1).

No difference in mean clutch size could be detected ($P > 0.20$) between ANS and NNS (Table 1). Clutch size decreased with later initial laying dates in 1977 but not in 1978 (Figs. 3 and 4). For both years, the mean clutch size for the first half of all clutches initiated was significantly greater than the mean for the second half (1977, $P < 0.0005$; 1978, $P < 0.0005$).

Seventy-nine percent of all nests found during the study hatched at least 1 egg (Table 2). Nest success was 69% in 1977 and 82% in 1978. There was no difference in the nesting success among 6 wetland types in 1978 ($\chi^2 = 6.65$, $0.10 < P < 0.25$).

Desertion was the main cause of nest failure (Table 2) and was greater in 1977 (17%) than in 1978 (9%). Predation was not an important cause of failure either year, and nest flooding occurred only in 1978. Egg failure (infertile or dead embryo), stolen clutches, and nests destroyed by wind or muskrats *(Ondatra zibethicus)*, when combined, accounted for the failure of 6% of all nests.

To evaluate tolerance between nesting pairs, distances between nearest neighboring nest sites were measured for 147 goose nests in 1978. Successful nests (n = 121) had a mean distance of 129 m from

Table 2. *Fate of giant Canada goose nests grouped according to nest site, 1977-1978.*

Nest fate	Elevated barrel		Floating barrel		Nest basket		Artificial island		Natural island		Hummock or muskrat house		Ground		Total	
Hatched	97	(82)[a]	21	(84)	2	(100)	36	(83)	4	(80)	3	(23)	3	(60)	166	(79)
Deserted	15	(13)	2	(8)	0	(0)	4	(10)	0	(0)	2	(16)	1	(20)	24	(11)
Preyed upon	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)	3	(23)	0	(0)	3	(1)
Flooded	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)	5	(38)	1	(20)	6	(3)
Other[b]	6	(5)	2	(8)	0	(0)	3	(7)	1	(20)	0	(0)	0	(0)	12	(6)
Total 1977	34		10		1		0		0		7		2		54	
1978	84		15		1		43		5		6		3		157	
Combined	118	(100)	25	(100)	2	(100)	43	(100)	5	(100)	13	(100)	5	(100)	211	(100)

[a]Percent.
[b]Includes clutches failed, stolen, blown apart by wind, or disturbed by muskrats.

Table 3. *Fate of giant Canada goose eggs in northwestern Iowa, 1977-1978.*

Egg fate	1977 Number	1977 Percent	1978 Number	1978 Percent	Combined Number	Combined Percent
Hatched	195	68.2	667	79.4	862	76.6
Deserted	25	8.7	43	5.1	68	6.0
Preyed upon	9	3.1	5	0.6	14	1.2
Flooded	—	—	19	2.3	19	1.7
Egg failure[a]	46	16.2	83	9.9	129	11.5
Broken by hen	—	—	3	0.3	3	0.3
Lost from nest	5	1.7	20	2.4	25	2.2
Stolen	6	2.1	—	—	6	0.5
Total eggs	286	100.0	840	100.0	1,126	100.0
Nests	52		153		205	

[a]Includes embryo death and infertile eggs.

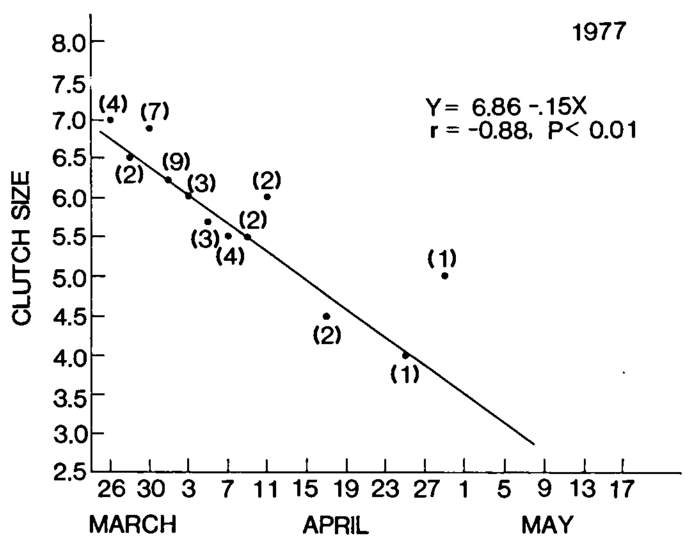

Figure 3. *The effect of initial laying date on clutch size, 1977. Mean clutch sizes are shown for 2-day periods. Number of clutches is in parentheses.*

other nests while failed nests (n = 26) averaged 92 m apart. These distances were not significantly different ($t = 1.68, 0.10 > P > 0.05$).

Nests placed in elevated barrels, floating barrels, artificial islands, and natural islands had similar, high nesting success (Table 2). The poorest nesting success (23%) occurred on vegetation hummocks and muskrat houses (Table 2). Overall, nesting success was significantly greater in ANS than in NNS ($\chi^2 = 19.06$, $P < 0.01$).

Few nests failed once incubation began. Nesting success for the 2 years in all nests in which incubation started was 91%. The major cause of nest failure after incubation started was egg failure of the entire clutch.

Seventy-seven percent of the eggs laid hatched (Table 3). Egg failure and desertion were the 2 major reasons that eggs did not hatch (Table 3). Hatching success (percentage of eggs in clutches incubated full term that hatched) for both years was 86%.

Although geese were not individually marked, indirect evidence of second nesting was seen each year. Second nests were of the 2 types described by Brakhage (1965) and Cooper (1978): 1) a continuation nest in which a goose, after losing the original nest during laying, continued the laying cycle in a new location, and 2) a renest in which a goose, after losing the original nest during incubation, began a new laying cycle in a new nest.

No evidence of continuation nesting was seen in 1977. In 1978, new nests were found in the vicinity of 4 nests that were flooded and deserted during the laying cycle. If these new nests were continuation nests, then the geese involved each laid 8-10 eggs that season.

Renests can usually be identified by the lateness of their establishment (Cooper 1978). Using this criterion, there were probably 4 renests in 1977 and 12 renests in 1978 (Fig. 2). In 1978, 1 known renest was observed. The goose involved lost a 6 egg clutch during the second week of incubation and a renest, located less than 70 m from the original nest, also contained 6 eggs. Both nests were destroyed by high winds.

No dead goslings were found in 1977. In 1978, 4 goslings were found dead in nests; two were trampled, and 2 were trapped between nesting material and the inside wall of elevated barrels.

Mean initial brood size was 5.3 goslings (Table 4). Mean initial brood size was significantly greater from ANS than from NNS ($P < 0.05$, Table 4). No difference in mean initial brood size could be detected ($P > 0.20$) between years.

Gosling Habitat Use and Survival

Drought conditions during the brood-rearing season in 1977 caused many wetlands to shrink in size, leaving a ring of mudflats covered with golden dock *(Rumex maritimus)* and smartweed *(Polygonum lapathifolium)*. Goslings spent most of their time loafing and foraging on these two species along mudflats.

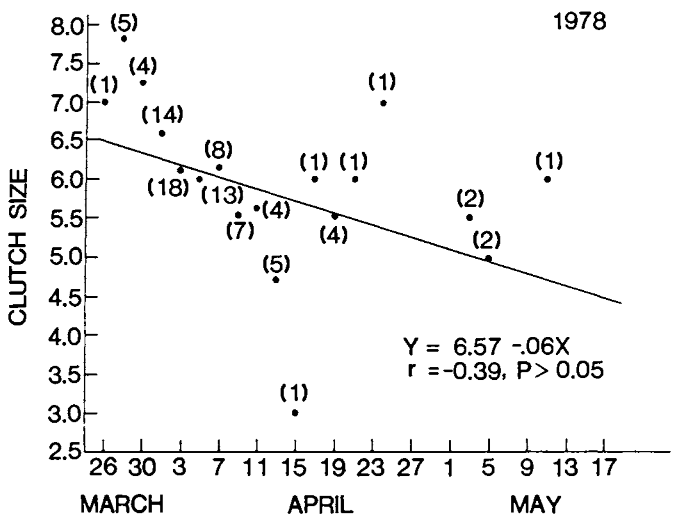

Figure 4. *The effect of initial laying date on clutch size, 1978. Mean clutch sizes are shown for 2-day periods. Number of clutches is in parentheses.*

In 1978, adequate water levels prevailed throughout the brood-rearing season. Perennial plants, mostly hardstem and softstem bulrush *(Scirpus acutus* and *S. validus)*, river bulrush *(S. fluviatilis)*, and cattail *(Typha* sp.), became abundant in wetlands where mudflats existed the previous year. Where mudflats were available, broods used them. In 1978, many more artificial islands were available for use as loafing sites by broods. Artificial islands receiving heavy use by broods lacked vegetation and were surrounded by water as well as dense stands of emergent vegetation. In these situations, goslings foraged on softstem and river bulrush.

Many of the brood-rearing areas that were protected from wind and had nearby upland vegetation for foraging were used both years. These areas were utilized by increasing numbers of goslings as the season progressed. Some broods moved as much as 1.6 km to reach these areas.

Gosling survival was higher in 1977 than in 1978. In 1977, an estimated 288 goslings left their nests in the principal study area. At least 283 goslings (98%) were alive at the time of banding. This estimate was possibly biased by not finding all the nests, seeing all goslings, or unequal numbers of goslings entering and leaving the study area. The warm, dry weather in 1977 was excellent for rearing broods, and gosling survival was estimated to be greater than 90%.

In 1978, 463 goslings left their nests in the principal study area. An estimated 340 goslings (73%) survived to banding age. At 2 outlying, isolated wetlands, 32 of 40 goslings (80%) survived to banding age. Survival of goslings in 1978 was probably 73-80%. During the first 2 weeks of the hatching season, the weather was cold and wet, and several broods lost more than half of their goslings during the first few days after hatching.

Table 4. *Initial brood size of giant Canada geese from successful nests in northwestern Iowa, 1977-1978.*

	ANS	NNS	All nests
Number of nests	155	10	165
Total goslings	835	42	877
Mean brood size	5.4	4.2	5.3
Standard deviation	1.5	2.0	1.6

Table 5. *Comparison of reproductive parameters from selected giant Canada goose flocks.*

Location	Mean clutch (all nests)	Nest success (%)	Egg success (%)	Hatching success (%)	Mean brood size at nest departure	Est. gosling survival to fledging (%)	Source
Dog Lake, Manitoba	5.1	46	51	—	5.1	—	Klopman 1958
Trimble, Missouri	5.6	65	73	77	4.2	68	Brakhage 1965
Seney, Michigan	5.1	65	62	—	4.6	75	Sherwood 1966
Huron River, Michigan	5.4	82	70	86-93	4.4	75	Kaminski et al. 1979
Crex Meadows, Wisconsin	5.9	74	—	97	5.0	—	Zicus 1974
E. Colorado	4.7	74	—	—	3.7	62-84	Szymczak 1975
N.E. South Dakota	5.2	87	78	—	4.7	—	Hilley 1976
Twin Cities, Minnesota	5.6	67	61	96	4.8	68	Sayler 1977
Marshy Point, Manitoba	5.6	75	67	97	5.0	—	Cooper 1978
N.W. Iowa	6.0	79	77	86	5.3	73-90+[a]	This study

[a]Survival estimated to banding age.

Most of the goslings observed seemed to be in excellent condition both years. Weak goslings were rarely seen with broods after nest departure.

Unfavorable weather was the greatest mortality factor during this study. Predation by dogs and great horned owls *(Bubo virginianus)* occurred but was unimportant. No evidence of gosling mortality from disease was observed.

DISCUSSION

Nesting Season and Productivity

Spring arrival dates observed during this study were similar to dates for most flocks in the north-central states (Hanson 1965, Dill and Lee 1970, Hilley 1976). As in similar studies of giant Canada geese, major lakes were icebound when geese arrived (Hanson 1965, Cooper 1978). At Marshy Point, Manitoba, geese arrived when mean daily air temperatures reached 0°C, and shallow, well-vegetated marshes were free of ice (Cooper 1978). These conditions coincided with the peak of spring arrival in Iowa both years. Temperature is considered a major factor controlling arrival for this flock.

Initial egg laying dates were similar to those found in other studies of giant Canada geese in the north-central states (Brakhage 1965, Zicus 1974, Hilley 1976, Sayler 1977, Kaminski et al. 1979). Cooper (1978) stated that temperature indirectly controls initiation of laying by its influence on snow and ice melt. However, the dates that the first eggs were laid were nearly identical both years despite warmer temperatures and earlier ice melt on smaller marshes in 1977. Geese were on the nesting grounds sooner in 1977 than in 1978. This suggests that photoperiod, as well as temperature and ice conditions, determine laying by north-central nesting geese (see Murton and Westwood 1977, Murton and Kear 1978). Yolk development, which commences 10-13 days prior to laying (Grau 1976), is stimulated in northern nesting geese by their arrival at the breeding grounds or by their departure from the final migration staging area (Raveling 1978). Arrival may have stimulated yolk development in 1978, but in 1977 geese were on the Iowa nesting grounds longer than the period necessary for yolk development.

The overall nest density of .12 nests/ha of wetland found in 1978 cannot be compared to densities reported for most Canada goose populations. Usually these densities are reported for island-nesting colonies and are quite high (e.g. 222 nests/ha at Dog Lake, Manitoba, Klopman 1958). At Marshy Point, Manitoba, Canada geese nesting in ANS, muskrat houses, and marsh vegetation, had densities ranging from .04 to .05 nests/ha (Cooper 1978). In Iowa, nest densities ranged from .01 to .90 nests/ha with highest densities occurring in wetland cover class 2 (hemi-marsh, Weller and Spatcher 1965). The hemi-marsh might allow higher densities to exist because of visual isolation. In Alberta, higher densities of Canada goose nests occurred on areas having sufficient vegetation to visually isolate nests (Ewaschuk and Boag 1972).

The mean clutch size (6.0 eggs) for completed clutches was higher than those reported for other populations of Canada geese (Table 5). The mean clutch size for 63 nests from 1966 through 1970 for this Iowa population was 5.0 eggs (Bishop and Howing 1972). Since Canada geese 5 years old and older lay the largest clutches (Brakhage 1965, Cooper 1978), the high mean clutch size in this study could be because most nesting geese were over 5 years old.

Clutch size declined as the nesting season progressed in 1977 but not in 1978 (Figs. 3 and 4). Cooper (1978) has hypothesized this may be due to younger geese initiating nests later in the season and/or to smaller clutches in continuation nests. Atwater (1959), Brakhage (1965), and Cooper (1978) have shown that there are no significant differences between the clutch sizes of original nests and renests. The decline of .15 eggs/day in 1977 was similar to that found at Hudson Bay, Ontario (Raveling and Lumsden 1977) and at Marshy Point, Manitoba (Cooper 1978). The lack of a decline in 1978 was probably due to a greater number of renests that year.

The length of the nesting season (71 days in 1977 and 85 days in 1978) was similar to those reported for other populations in the north-central states (Kossack 1950, Brakhage 1965, Zicus 1974). The nesting season is shorter in Canada (53-61 days at Dog Lake, Manitoba, Klopman 1958, and 50-53 days at Hudson Bay, Ontario, Raveling and Lumsden 1977). At northern latitudes, weather is the most important factor controlling the length of the nesting season because less time is available for renesting. North-central nesting geese have sufficient time for renesting, which directly affects the nesting season length. More renesting occurred in 1978 and accounts for the longer nesting season. Fewer geese renested in 1977 because low water levels apparently made most nest sites unattractive.

The 79% nesting success found in this study is higher than that for most Canada goose populations (Table 5.). Nesting success for 63 nests from 1966 through 1970 for this Iowa population was 76% (Bishop and Howing 1972). Nesting success was high in this study because most geese nested in the safe, secure ANS. Other studies have shown higher nesting success in ANS than in NNS (Craighead and Stockstad 1961, Brakhage 1965, Hilley 1976, Sayler 1977, Cooper 1978).

Desertion, especially during laying, was the major cause of nest failure. Many other studies found desertion to be the major cause of nest failure (Geis 1956, Munro 1960, Hanson and Eberhardt 1971, Ewaschuk and Boag 1972, Hilley 1976, Sayler 1977, Cooper 1978). Most studies attribute desertion to intense competition for nest sites or crowded conditions on islands. Cooper (1978) found a positive linear relationship between nest density and desertion rates. In our study, nearest nesting neighbors were farther (but not significantly) away from successful nests than from unsuccessful nests. On the principal study area, ANS were abundant, but attractive or suitable ANS (due to placement) may have been limited. Desertion was greater there in 1977. That year low water levels may have limited the number of suitable nest sites.

The estimated egg success of 77% is higher than that reported for most Canada goose populations (Table 5). Egg success for 63 nests from 1966 through 1970 for this Iowa population was 81% (Bishop and Howing 1972). Egg failure and desertion were the main reasons that eggs did not hatch in this study.

Hatching success (86%) was lower than found for other Canada goose populations (Table 5). The reasons for this lower hatching success, particularly in 1977, are not known but could be due, in part, to disrupted incubation.

During this study, few original nests failed, and second nests added little to overall productivity. Cooper (1978) made a similar conclusion. In studies by Geis (1956) and Brakhage (1965), nest failure was more common, and second nests added significantly to productivity. Second nests could become very important in years when many original nests fail. In this study, there were more renests in 1978 than in 1977 (Fig. 2). Low water levels and a lack of suitable nest sites in 1977 may have discouraged renesting even though nest success was low.

Mean brood size (5.3 goslings) at nest departure was higher than that found for other populations of Canada geese (Table 5). This can be explained by the larger clutches found in this study. The significant difference in mean brood size between ANS and NNS, despite the lack of difference in clutch size between the two, was a result of increased hatching success in ANS.

Gosling Habitat Use and Survival

Mudflats and artificial islands were an important component of brood-rearing habitat. Broods made extensive use of mudflats in 1977 and used what few were available in 1978. Sandbars and mudflats were preferred areas due to their proximity to succulent, green plants for forage and to water for escape (Dill and Lee 1970). In 1978 many broods used artificial islands for loafing and roosting. Brakhage (1965) reported similar use of small islands by broods in Missouri. Along the Columbia River in Washington, popular brood-rearing areas had gently sloping shorelines, were free from human disturbance, and had a nearby abundance of pasture grasses (Hanson and Eberhardt 1971). Hanson (1965) stressed the importance of bluegrass *(Poa pratensis)* as food for both adults and goslings. In Iowa, several brood-rearing areas were adjacent to uplands containing bluegrass.

Several brood-rearing areas were used both years, indicating that their use may be traditional. Other studies have found that some areas attract large numbers of goslings every year (Williams and Marshall 1938, Geis 1956, Hanson and Eberhardt 1971, Szymczak 1975). These areas contained the previously mentioned characteristics of preferred brood-rearing habitat. Szymczak (1975) also noted that broods moved from small wetlands to traditional locations on large impoundments. In Iowa, broods typically moved from densely vegetated wetlands to less vegetated, more permanent wetlands.

Creches or gang broods were common both years of the study. Creches were especially large at the traditional brood-rearing areas. This has been noted by others (Geis 1956, Brakhage 1965, Warhurst 1974). In Ohio, goslings in the largest creches were extremely wary (Warhurst 1974). Creches also protected goslings that were separated from their own brood from predation, exposure, or accident.

Gosling survival in this study was in the range reported for other studies (Table 5), severe weather being the major mortality factor. More cold, rainy weather occurred in 1978, causing greater mortality than in 1977. Other studies have cited hailstorms and predation as major mortality factors (Geis 1956, Brakhage 1965).

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