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FACTORS AFFECTING HATCHING SUCCESS AND GOSLING SURVIVAL IN GIANT CANADA GEESE

The Ohio State University

Ph.D. 1982

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FACTORs AFFECTING HATCHING SUCCESS AND GOSLING SURVIVAL
IN
GIANT CANADA GEESE

DISSERTATION

Presented in Partial Fulfillment of the Requirements for
the Degree Doctor of Philosophy in the Graduate
School of The Ohio State University

By

Ying T. Yang, B.S., M.S.T.

* * * * *

The Ohio State University
December, 1982

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INTRODUCTION

One goal of a successful goose management program is to optimize gosling production, i.e., to reduce gosling mortality to the extent possible. Otherwise, the cost per fledged gosling increases, and when excessive mortality occurs the cost becomes prohibitive. If gosling production is to be increased through effective management, the logical step is to document the actual egg hatching rate and gosling survival rate, the principal causes of mortality, the temporal distribution of mortality, and the breeding performance of females and their age distribution in the population.

The gosling production estimated by annual summer roundup in the mid-1970s was relatively low at Killdeer Plains State Wildlife Area, one of 4 Ohio Division of Wildlife goose production Areas. The Ohio Cooperative Wildlife Research Unit was asked to study the problems that might be associated with low gosling production at that area. To study gosling production, background information on goose breeding and nesting activities that related to goose fitness in terms of hatching success and gosling survival becomes necessary. Because the Ohio Division of Wildlife calculated gosling production from the number of goslings captured during roundup, the low production could be either due to the high gosling mortality or due to the
inappropriate procedure in estimating gosling production resulting from low roundup efficiency or emigration of goslings to other areas before roundup. Objectives of the study were:

1. to obtain background information on goose breeding and to study nesting activities that related to goose fitness.
2. to study predation on gosling production.
3. to study and evaluate the procedures of estimating gosling production.

The review of literature was divided into 3 parts according to objectives.

LITERATURE REVIEW

NESTING ACTIVITIES RELATED TO GOOSE FITNESS

The fitness of a goose is determined by its nest hatching success and gosling survival. Thus, any factor or nesting activity that relates to or associates with hatching success and gosling survival would affect the fitness of geese. The effects of egg weight, laying sequence, clutch size, laying date, and female age on hatching success and the effect of egg quality, egg weight or gosling hatching weight, hatching sequence, brood size, hatching date, and female age on gosling survival were demonstrated in many studies. I grouped those factors together or considered them singly according to their effects on hatching success.
and gosling survival and presented them in the following order: egg weight and hatching weight, egg weight and quality, laying and hatching sequence, clutch and brood size, laying and hatching date, and female age.

**Egg Weight and Hatching Weight**

It is difficult to study the effect of egg weight or size on hatching success and of hatching weight on survival of young in the field. Factors such as female age, laying sequence, laying date, and clutch size, which are sometimes associated with egg weight, may counteract or intensify the effect of egg weight on breeding success.

The association between egg weight and female age has been observed in some species. In general, egg size increases with age up to a point (Davis 1975, Mills 1979, Richdale 1955). Brakhage (1965) found egg size in Canada geese (*Branta canadensis*) was also related to female age and that 5-year-old birds laid the largest eggs.

The relationship between egg weight and laying sequence was demonstrated by Cooper (1978) in Canada geese, who found that egg weight within a clutch increased from the first egg to the second and decreased afterward, by Mills (1979) in red-billed gulls (*Larus novaehollandiae scopulinus*), by Syroechkovsky (1975), who reported that egg weight in lesser snow geese (*Chen caerulescens*) decreased according to laying sequence, by Pinkowski (1975) in eastern blue birds (*Sialia sialis*), and by Osborne and Bourne (1977), who found that
egg weight in wattled jacana (*Jacana jacana*) increased with laying sequence.

The association between egg weight and laying season also varies among species. The mean egg weight decreased as the laying season advanced was demonstrated by Brakhage (1965) in Canada geese. Mills (1979) found the largest gull eggs were laid in the early breeding period; the opposite was true in great tits (*Parus major*) (Perrins 1970).

Egg weight varied among clutch size. Jones (1973) indicated that clutch size increased at the expense of egg weight in great tits, Gibb (1950) found that the median clutch size had the heaviest mean egg weight in the same species, and Batt and Prince (1979) reported that eggs were heavier in larger clutches in mallards (*Anas platyrhynchos*). However, mean egg weight did not change with clutch size change in lesser snow geese (Ankney and Bisset 1976).

The importance of egg weight to survival of young from hatching to fledging has been demonstrated in many studies. Skoglund et al. (1952) found chicks hatched from heavier eggs had higher survival rate in domestic fowl (*Gallus domesticus*). A similar effect of egg weight on survival of young was found in herring gulls (Parsons 1970), black-headed gulls (*L. ridibundus*) (Lundberg and Vaisanen 1979), common terns (*Sterna hirundo*) (Misbet 1973), wood pigeons (*Columba palumbus*) (Murton et al. 1974), and lesser snow geese (Ankney 1980). However, the effect of egg weight on
hatching success was generally assumed less important and rarely studied. Few studies have shown that lighter eggs generally had lower hatching success (O'Connor 1979, Murton et al. 1974).

Egg weight and young hatching weight were reported to be highly correlated in many species (Batt and Prince 1979, O'Connor 1979, Schifferli 1973). The effect of hatching weight on survival of young was similar to that of egg weight. Moss et al. (1981) found that survival of red grouse (Lagopus lagopus scoticus) chicks was related to their hatching weight. Syroechkovsky (1975) noted that in lesser snow geese the smallest goslings, which usually hatched last within a clutch, had a high mortality. Ankney (1980) demonstrated that heavier goslings survived longer than lighter ones without food after hatching under a laboratory condition.

**Egg Weight and Quality**

The importance of yolk as a source of energy is well known. Kear (1965) indicated that newly hatched mallard ducklings depended on their body fat reserves to survive. Thus, the larger the yolk within an egg, the higher the survival of the young can be expected to be. Carey et al. (1980) noted that the continuum from altricial to precocial species of developmental maturity at hatching of eggs was correlated with increases in yolk, solids, and caloric contents and a decrease in water content. In waterfowl,
which are precocial, Lack (1968a) found that the mean percentage of yolk in eggs among different species was slightly over 40%, which was higher than for many other precocial species.

The quality and quantity of yolk also varies within species. Romanoff and Romanoff (1949) showed the proportion of albumen in leghorn chicken eggs increased slightly when egg weight increased, whereas the proportion of yolk decreased slightly. A similar relationship was also found in starlings (Sturnus vulgaris) (Ricklefs 1977), white pelicans (Pelecanus onocrotalus) (Jones 1979), and herring gulls (Parsons 1970). Howe (1978) further demonstrated in common grackles (Quiscalus quiscula) the same proportion of yolk within clutches but different proportions between clutches of different females. However, Vangilder (1981) showed that yolk size in mallard eggs varied in direct proportion to increasing egg size.

Laying and Hatching Sequence

In Canada geese, females either do not incubate until their clutches are completed, or start to incubate after some eggs are laid (Brakhage 1965, Collias and Jahn 1959, Cooper 1978). Thus the first eggs laid might have a higher chance of being destroyed by predators, frozen and cracked by freezing temperature, or broken by females. Cooper (1978) showed that the first-laid eggs of all clutches of giant Canada geese had a comparatively lower hatching
success than that of the remaining eggs.

For the production of young, hatching sequence is as important as laying sequence. In nidicolous species, early hatched nestlings usually have a better chance to survive (Gibb 1950, Howe 1976, 1978, Knopf 1979). However, few studies have been done on the effect of hatching sequence on the survival of newly hatched chicks in nidifugous birds, probably because it is thought to be of less importance. Furthermore, the difficulties of determining hatching sequence in nidifugous young and of determining individual fate after young leave their nests have prohibited studying the relationship between hatching sequence and survival of young.

If obtaining data on hatching sequence is difficult, information on laying sequence can be used to study the relationship between hatching sequence and survival of young if there is some correlation between the hatching and laying sequences. A positive relationship between hatching sequence and laying sequence was found in several nidifugous birds such as lesser snow geese (Cargill and Cooke 1981) and mallards (Prince et al. 1969). However, no such relationship was found in Canada geese (Cooper and Hickin 1972).

Clutch Size and Brood Size

The causes of clutch size variation within a species have drawn much attention (Johnsgard 1973, Lack 1967, 1968b,
Ryder 1970). Yet studies on the effect of clutch size on egg hatching success are few. Several workers have reported that an increase of clutch size resulted in a decrease of hatching success (Hanson and Browning 1959). Others found that nests with an above average clutch size were more successful than those with below average size (Choate 1967). Within a species, larger clutches might limit the effectiveness of parental care and subsequently lower the hatching success (Johnsgard 1973). On the other hand, females with smaller clutch size should physically be capable of incubating eggs easily and thus have higher hatching success. However, no studies have clearly demonstrated this in waterfowl. The difficulties of studying the relationship between clutch size and hatching success are due to the fact that clutch size is correlated with female age in Canada geese (Brakhage 1965, Cooper 1978, Kossack 1950) and with laying date in geese and many other species (Barry 1962, Brakhage 1965, Batt and Prince 1979, Cooch 1961, Cooper 1978, Dane 1966, Dijkstra et al. 1982, Howe 1978, Kossack 1950), which also might affect egg hatching success.

The importance of studying clutch size and its effect on production of young is to know not only how many young hatch but also how many survive after hatching. Cooch (1961) showed that lesser snow goose goslings hatched from eggs laid late in large clutches survived less well. Dane
(1966) found that blue-winged teal (Anas discors) ducklings hatched from larger clutches suffered higher loss than those from smaller clutches. Hilden (1964) mentioned that Aythya hens experienced difficulties in keeping the larger broods intact when threatened by an enemy and when brooding in cold weather, and that higher mortality occurred in the larger brood. Eygenraam (1957) said that larger broods of mallards were reduced at a relatively faster rate than those of normal size and that survival rate likely was lower in those broods. Brown (1978) reported that more young were lost in larger broods than in smaller broods in purple martins (Progne subis). Howe (1978) observed that pairs of common grackles with below average brood size at hatching succeeded in raising them all but that those with above average size suffered some loss.

**Laying and Hatching Date**

The importance of laying and hatching date on egg hatching success and survival of young was recognized and studied by many researchers. Bengtson (1972) showed that the hatching success of clutches declined with advancing season in duck populations and survival of young was higher in early hatched ducklings. Davis (1975) indicated that hatching success in herring gulls was highest in the first laying period and lowest in the last laying period. Livezey (1981) reported nesting success in ducks was highest for nests initiated in May, lowest in June, and intermediate in
July. Perrins (1966, 1970) found a higher proportion of early young of Manx shearwaters (Puffinus puffinus) survived than of those hatched later in the season. Harvey (1971) found that most of the egg loss in blue geese (Chen caerulescens) came from the late nests. Newton and Kerbes (1974) found the early nests of greylag goose (Anser anser) were most successful. In some cases both breeding date and clutch size were important; Nickelson (1973) indicated that in early seasons large clutches produced more young than small clutches, whereas in late seasons the opposite was true. Eisenhauer and Kirkpatrick (1977) considered between-year difference instead of within-year difference and reported that 5-egg clutches of emperor goose (Anser canagicus) produced the most young in late nesting years and 6-egg clutches produced the most young in early nesting years. Newton and Kerbes (1974) reported that the breeding success in greylag geese was higher in early breeding years. However, in most of the studies the authors did not separate the possible age effect from laying and hatching date on breeding success. Older geese and other waterfowl females nested earlier (Brakhage 1965, Choate 1967, Cooch 1961, Grice and Rogers 1965, Lemieux 1959) and had higher breeding success (Raveling 1981), and clutch size was correlated with laying date (Brakhage 1965, Cooper 1978).

**Female Age**

The effect of female age on breeding success is well
known. Nelson (1966) found older gannets (Sula bassana) laid larger eggs, nested earlier, and had higher hatching success than did younger females. Brown (1978) showed that adult purple martins laid larger clutches and had higher hatching success but had lower fledging success than did subadults. Perrins and Moss (1974) reported that the breeding performance of female great tits improved progressively up to age 3 or 4 years and declined thereafter. Coulson (1966) reported that breeding success in kittiwakes (Rissa tridactyla) increased with female age and previous breeding experience. Grice and Rodgers (1965) found the productivity of wood duck (Aix sponsa) yearlings was less than that of adults. Older female Canada geese had larger clutch size and higher hatching success (Brakhage 1965) and raised broods of above average size more successfully (Baveling 1981) than younger birds did. The higher breeding success in older birds was thought to be due to their being more physically capable of breeding or to having more experience in breeding. Beside the effect of experience gained from age on breeding success, egg weight (Brakhage 1965, Bichdale 1955), clutch size, and breeding date might also confound the outcome of the effect of age on breeding success.

**Predation on Goslings**

Besides goose fitness, predation is generally the most
important factor that affects gosling production—the number of eggs hatched and goslings surviving. The number of eggs hatched is determined by the number of successful nests among all nests (nest success) and hatching rate among those successful nests (hatching success). Choate (1967) found nesting cover, predation, and human disturbance were related to nesting success. Newton and Kerbes (1974) found predation was the main cause of nest failure of greylag geese (Anser anser). Geis (1956) reported that over 90% of the destruction of goose nests was by common ravens (Corvus corax). Mickelson (1975) reported that predation accounted for 65.8% of the total eggs destroyed in his goose study. MacInnes and Misra (1972) further demonstrated that the increase in egg predation by predators resulted from the ability of learning of predators to follow biologists in the field.

Causes of gosling mortality vary from freezing temperature to road kill, but the major cause is predation. Mickelson (1975) found that most brood losses were the result of predation mainly from glaucous gulls (Larus hyperboreus). MacInnes et al. (1974) found herring gulls (L. argentatus) were the major predators preying on goslings. Other avian predators such as great horned owls (Bubo virginianus) were also reported to feed on goslings (pers. comm.). In addition to birds, mammals such as red foxes (Vulpes vulpes), minks (Mustela vison), and raccoons
(Procyon lotor), fish such as pike (Esox lucius), and reptiles such as snapping turtles (Chelydra serpentina) were all documented to prey on waterfowl (Coulter 1957, Klopman 1958, Sargeant 1972, Solman 1945).

**METHODOLOGY OF ESTIMATING GOSLING PRODUCTION**

Many techniques are developed to estimate gosling production. However, according to the degree of bird handling, there are generally 2 approaches—capture and non-capture methods. The capture approach is to count the number of goslings caught during roundup just before fledging as gosling production. It is used in many goose management areas such as Killdeer Plains State Wildlife Area, Mosquito Creek State Wildlife Area, and Ottawa National Wildlife Refuge. The non-capture approach is to observe the change of brood size within a given time and calculate the ratio of change as gosling mortality or to count total number of goslings directly to calculate gosling mortality. It is generally used in studies of non-management areas. The capture approach is costly, yet it is generally considered more useful than the non-capture count, because goslings captured are readily available for banding and are subsequently used by the U. S. Fish & Wildlife Service to estimate population dynamics of geese at continental level. On the other hand, brood exchange and mix make brood counts difficult and often biased in the non-
capture count. To improve the estimation in the non-capture counts, marked pairs were used to study the change of brood size (Zicus 1981) or marked broods were used to correct the brood count (Geis 1956). However, the question of the accuracy of estimates of gosling production by direct capture was not studied.
STUDY AREA

This study was conducted at The Killdeer Plains State Wildlife Area, which is administered by the Ohio Division of Wildlife, primarily as a Canada goose management area. This 3489-hectare (8622-acre) wildlife area lies in the grain farming country of northcentral Ohio, 13 km south of Upper Sandusky and 3.2 km west of Harpster (Fig. 1). It is situated in a natural basin of about 12,138 hectares of flat, poorly drained soils formerly covered by wet prairie sloughs. The wet prairie was drained, with varying degree of success, by ditching and tiling and converted to agricultural land for corn and soybean production. The Wildlife Area was acquired by the State of Ohio in the early 1950's. A 688-hectare waterfowl refuge was established in 1956 to provide nesting and resting habitat for geese and other waterfowl.

Approximately two-thirds of the Wildlife Area is in cropland and meadow. The other one-third is divided almost equally between woods and shrubby coverts, and water. The water areas include more than 324 hectares of marsh, a 115-hectare upground reservoir, and 69 ponds ranging in size from less than 0.5 hectare to 20 hectares. The 587 hectares of cropland are planted with corn (223 ha), buckwheat (202 ha), and wheat (162 ha) by farmers under a share-cropping program, plus 40 hectares of corn planted by the wildlife employees each year to provide food for Canada geese and
other wildlife in the area. Beside crop production, the meadows are mowed twice a month from May to August each year to maintain short, succulent plants for goose consumption. The common wetland plants found in this area are presented in Table 1.

About 350 tub nest structures have been established in the Wildlife Area to attract a local breeding flock that originated from 30 pairs of captive giant Canada geese (*Branta canadensis maxima*) in 1956. The main study site was in the refuge where more than 70% of available nest structures were located (238/333 in 1979, 242/338 in 1980, and 262/370 in 1981).
Fig. 1. The Canada goose study area, Killdeer Plains State Wildlife Area, 1979-81.
Table 1. Common wetland plants found at the Killdeer Plains State Wildlife Area, 1979-81.

<table>
<thead>
<tr>
<th>Scientific Name</th>
<th>Common Name</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acalypha rhomboidea</td>
<td>three-seeded mercury</td>
</tr>
<tr>
<td>Alisma plantago-aquatica</td>
<td>European waterplantain</td>
</tr>
<tr>
<td>Asclepias incarnata</td>
<td>swamp milkweed</td>
</tr>
<tr>
<td>Bidens cernuus</td>
<td>nodding bur marigold</td>
</tr>
<tr>
<td>B. connatus</td>
<td>swamp beggarticks</td>
</tr>
<tr>
<td>B. frondosa</td>
<td>devils beggarticks</td>
</tr>
<tr>
<td>Boehmeria cylindrica</td>
<td>smallspike false sedge</td>
</tr>
<tr>
<td>Calamagrostis canadensis</td>
<td>bluejoint reedgrass</td>
</tr>
<tr>
<td>Carex frankii</td>
<td>Frank's sedge</td>
</tr>
<tr>
<td>C. vulpinoidea</td>
<td></td>
</tr>
<tr>
<td>Cyperus erythrorhizos</td>
<td>redroot flatsedge</td>
</tr>
<tr>
<td>C. esculentus</td>
<td>chufa flatsedge</td>
</tr>
<tr>
<td>C. ferruginescens</td>
<td>ferruginous flatsedge</td>
</tr>
<tr>
<td>C. strigosus</td>
<td></td>
</tr>
<tr>
<td>Daucus carota</td>
<td>wild carrot</td>
</tr>
<tr>
<td>Echinochloa crusgalli</td>
<td>common barnyardgrass</td>
</tr>
<tr>
<td>E. pungens</td>
<td></td>
</tr>
<tr>
<td>Eleocharis obtusa</td>
<td>blunt spikerush</td>
</tr>
<tr>
<td>Epilobium glandulosum</td>
<td>glandular willow-herb</td>
</tr>
<tr>
<td>Erechites hieracifolia</td>
<td>American burnweed</td>
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</table>
Table 1. (Continued)

<table>
<thead>
<tr>
<th>Scientific Name</th>
<th>Common Name</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eupatorium perfoliatum</td>
<td>boneset joe-pye-weed</td>
</tr>
<tr>
<td>Festuca sp.</td>
<td>fescue</td>
</tr>
<tr>
<td>Juncus acuminatus</td>
<td></td>
</tr>
<tr>
<td>J. dudleyi</td>
<td></td>
</tr>
<tr>
<td>J. effusus</td>
<td>common rush</td>
</tr>
<tr>
<td>J. tenuis</td>
<td>poverty rush</td>
</tr>
<tr>
<td>Leersia oyszoides</td>
<td>rice cutgrass</td>
</tr>
<tr>
<td>Lemna minor</td>
<td>common duckweed</td>
</tr>
<tr>
<td>Lippia lanceolata</td>
<td>frog fruit</td>
</tr>
<tr>
<td>Lophotocarpus calycinus</td>
<td></td>
</tr>
<tr>
<td>Ludwigia alternifolia</td>
<td>seedbox</td>
</tr>
<tr>
<td>L. palustris</td>
<td>common marshpurslane</td>
</tr>
<tr>
<td>L. polycarpa</td>
<td>many fruited seedbox</td>
</tr>
<tr>
<td>Lycopus americanus</td>
<td>American bugleweed</td>
</tr>
<tr>
<td>Lythrum dacotanum</td>
<td>swamp loosestrife</td>
</tr>
<tr>
<td>Mimulus ringens</td>
<td>monkeyflower</td>
</tr>
<tr>
<td>Panicum sp.</td>
<td>panicum</td>
</tr>
<tr>
<td>Penthorum sedoides</td>
<td>ditch stone crop</td>
</tr>
<tr>
<td>Phalaris arundinacea</td>
<td>reed canarygrass</td>
</tr>
<tr>
<td>Phragmites communis</td>
<td>common reed</td>
</tr>
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<td>Pilea pumila</td>
<td>Canada clearweed</td>
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</table>
Table 1. (Continued)

<table>
<thead>
<tr>
<th>Scientific Name</th>
<th>Common Name</th>
</tr>
</thead>
<tbody>
<tr>
<td>Polygonum coccineum</td>
<td>marsh knotweed</td>
</tr>
<tr>
<td>P. hydropiper</td>
<td>marshpepper smartweed</td>
</tr>
<tr>
<td>P. pensylvanicum</td>
<td>Pennsylvania smartweed</td>
</tr>
<tr>
<td>P. persicaria</td>
<td>spotted ladysthumb</td>
</tr>
<tr>
<td>P. sagittatum</td>
<td>arrowleaf tearthumb</td>
</tr>
<tr>
<td>Populus sp.</td>
<td>cottonwood</td>
</tr>
<tr>
<td>Potamogeton nodosus</td>
<td>pondweed</td>
</tr>
<tr>
<td>Rorippa palustris</td>
<td>marsh cress</td>
</tr>
<tr>
<td>Sagittaria latifolia</td>
<td>common arrowhead</td>
</tr>
<tr>
<td>Salix sp.</td>
<td>willow</td>
</tr>
<tr>
<td>Scirpus atrovirens</td>
<td>dark green bulrush</td>
</tr>
<tr>
<td>S. cyperinus</td>
<td>woolgrass bulrush</td>
</tr>
<tr>
<td>S. fluviatillis</td>
<td>river bulrush</td>
</tr>
<tr>
<td>S. validus</td>
<td>softstem bulrush</td>
</tr>
<tr>
<td>Scutellaria epilobiifolia</td>
<td>common skullcap</td>
</tr>
<tr>
<td>S. lateriflora</td>
<td>sideflowering skullcap</td>
</tr>
<tr>
<td>Setaria sp.</td>
<td>bristlegrass</td>
</tr>
<tr>
<td>Solanum dulcamara</td>
<td>bitter nightshade</td>
</tr>
<tr>
<td>Solidago spp.</td>
<td>goldenrod</td>
</tr>
<tr>
<td>Spartina pectinata</td>
<td>prairie cordgrass</td>
</tr>
<tr>
<td>Stachys hispida</td>
<td>hedgenettle</td>
</tr>
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</table>
Table 1. (Continued)

<table>
<thead>
<tr>
<th>Scientific Name</th>
<th>Common Name</th>
</tr>
</thead>
<tbody>
<tr>
<td>Typha angustifolia</td>
<td>narrowleaf cattail</td>
</tr>
<tr>
<td>T. latifolia</td>
<td>common cattail</td>
</tr>
<tr>
<td>Verbena hastata</td>
<td>blue vervain</td>
</tr>
</tbody>
</table>

\(^a\) According to Scott and Wasser (1980).
METHODS

The methods are divided into 3 parts according to the study objectives. The first part includes factors such as egg weight, egg composition, laying date and sequence, clutch size, gosling weight, hatching date and sequence, brood size, and female age that might affect hatching success and gosling survival. The part also included information on goose breeding biology such as presence of nest down, length of incubation, nest related activities and hatching success (including nest utilization, egg and nest success, hatching success, causes of nest loss and egg failure, and renest), and movement. These egg and nest variables are presented in a chronological order from egg laying to gosling fledging. The second part describes methods used in identifying the causes of mortality from predation. The third part, including tagging and tag loss, roundup and roundup efficiency, and estimation of gosling survival, addresses the methods of estimating gosling survival or techniques related to it. Finally, several important statistical methods used for data analyses to study the effect of different factors on hatching success and gosling survival are presented.

Time was spent more or less evenly during the 2 main breeding stages—nesting and brooding. From March to late May during the regular nesting stages, nest structures were checked once per week from an all-terrain vehicle, a
'Bombardier'. With this vehicle, from 80 to 200 nesting structures could be visited a day, depending on how many active nests were found and how much time was spent at each nest in obtaining data needed. Active nesting structures found were visited 1-3 more times per week if possible from a boat or on foot to obtain information such as hatching sequence.

From late May to mid-July during the regular brooding stages, broods were identified and followed, and their activities were recorded to obtain information on gosling survival and factors related to estimating gosling survival.

**NESTING ACTIVITIES RELATED TO GOOSE FITNESS**

**Egg Weight**

Eggs found in nests were weighed with a spring scale to the nearest gram and the length and breadth of the eggs were measured with a vernier caliper to the nearest millimeter to estimate egg volume. Because an egg loses weight through water evaporation after being laid (Bahn and Ar 1974), and egg volume stays the same through time (Romanoff and Romanoff 1949), to estimate the original egg weight I made an egg weight and volume regression from weights of 122 fresh laid eggs to estimate the weight of other eggs from their volume. The egg volume was then calculated from the equation (Hoyt 1979):

\[ \text{Volume} = K_v * L * B^2 \]
where $K_v = a$ species-specific constant for the shape of the egg, $L =$ length, and $B =$ breadth. The constant for the shape of goose eggs estimated by Manning (1978) from 3 Canada goose subspecies is 0.5121 which is similar to the constant 0.51 provided by Hoyt (1979) and was used here to estimate egg volume. To study egg weight loss through incubation, I recorded weight changes of eggs every 3 to 4 days from laying to hatching.

**Egg Composition and Energy**

Forty-seven eggs were collected in 1979 and 1980 from Killdeer Plains State Wildlife Area ($N=39$) and Magee Marsh ($N=8$) to compare composition of eggs from these 2 Areas. The eggs were hard-boiled for easy separation of components and were analyzed for water, protein, and lipid contents. The components, yolk, albumen, and shell, were weighed with a balance to the nearest 0.001 g. Shell was put into an oven at 60 °C for at least 24 h and weighed several times until no further weight changes could be detected. The final weight was recorded as dry shell weight. Yolk and albumen were dried in a freeze-dryer for at least 48 h and weighed several times until no further weight change occurred. The water content of each component was estimated by subtracting dry weight from original egg weight. The amount of protein in yolk or in albumen was determined by Kjeldahl nitrogen determination (A.O.A.C. 1975) in the Animal Science Laboratory, The Ohio State University.
lipid content in yolk was estimated by chloroform extraction (Fogerty et al. 1971) in the Wildlife Biology Laboratory, Department of Zoology, The Ohio State University. The lipid fraction in dry albumen was negligible in chickens (Naber 1979) and was assumed unimportant in geese and therefore not analyzed. Similarly, the carbohydrate in yolk and albumen, generally less than 1.5% in chickens (Cook and Briggs 1977), was also assumed unimportant in geese and was not measured.

Using the information that a gram of lipid yields 9.5 Kcal, protein 4.5 Kcal, and mixed carbohydrate 4.0 Kcal (Bartholomew 1977), I calculated energy content of each egg. Because no carbohydrate was measured, the amount of carbohydrate was obtained by subtracting the protein and lipid weight from total dry weight (excluding shell). To evaluate the validity of this approach in estimating egg energy, I did a gross energy determination with a Parr adiabatic bomb calorimeter on dry yolk and albumen (n=4 each). A regression analysis was then used to study the relationship between egg weight and energy content.

**Nest Down**

Most birds form a brood patch to incubate their eggs. To do this, Canada geese pluck and place breast down in the nests. As a consequence, the presence of down in nests serves as a thermal protective material to the eggs (Cooper 1978). The date and amount of first appearance of down in each nest was recorded to study the relationship between the
female readiness for incubation and variation among clutch sizes.

**Laying Date, Laying sequence, and Clutch Size**

The laying period of the population, defined as the time interval between the first and last egg laid in the breeding population, was estimated for the Killdeer goose population. Due to the difficulty of knowing the exact date that a particular egg was laid, I used a 3-day interval instead of a daily basis to describe the relationship between egg laying frequency and laying period. Furthermore, the date of completion of each clutch during the laying period was estimated for each nest. A regression analysis was used to study the relationship between mean egg weight of a clutch and clutch completion date in the laying period.

Nests chosen for studying laying sequence were visited 3 to 5 times per week during the laying period. Eggs found in nests were numbered with a grease pencil to keep track of the sequence. Due to a limited sample size of nests with completely known laying sequence, I used a clutch size of 6, which occurred most frequently, to study the relationship between laying sequence and egg weight using a regression analysis.

Clutch size was determined by counting the number of eggs found in the nest, including those missing and broken. The overall mean clutch size was calculated by dividing all
eggs laid by all nests found. The overall mean active clutch size was calculated only from those eggs in the successful nests, i.e., nests with at least 1 gosling hatched, and the number of those successful nests.

To study the association between clutch size and the date of completion (laying date), I performed a regression analysis using laying date as an independent variable and clutch size from active nests as the dependent variable. The difference of mean egg weight in different clutch sizes was also studied from an ANOVA analysis.

Length of Incubation

A few nests were selected to observe the length of the incubation period. The starting of incubation was judged by the appearance of heavy down in the nest, the presence of the female in the nest, and the warmness of eggs in the nest. The terminating of incubation was determined by the time of hatching of the last viable egg in the nest.

Nest Related Activities and Hatching Success

The percentage of nesting structures used by breeding pairs and the number of ground nests found in the Area were recorded. The overall hatching success was determined by calculating the percentage of eggs hatched in the successful nests. Data collected from successful nests were used to study the effects of egg weight, laying date, clutch size, and age on hatching success. The overall egg success,
defined by Cooper (1978) as the percentage of the eggs hatched in all nests, was calculated. The nesting success of the Killdeer population was also estimated by comparing the successful nests and numbers of total nests found in the Area. Whenever possible, the causes of nest losses and fates of eggs were recorded. I observed neck-collared breeding females to study possible renesting activity if they lost their first clutch.

**Gosling Weight**

When clutches were about to hatch, the nests were visited 2 to 3 times a day. Artificial food colors (0.5 cc) were injected into the eggs during pipping to ensure that I could match goslings with the eggs for determining the relationship between egg and gosling weight. Goslings hatched were weighed to the nearest gram. Because goslings lost weight constantly after hatching until they left nests to feed and were not hatched at the same time, the weights of earlier hatched goslings were underestimated when I weighed all the goslings in a nest at a given visit. To avoid such a bias, I tried 2 practical approaches. First, egg weight was compared to gosling weight for 55 goslings known to be just hatched and was found to be highly associated with gosling weight and could be reliably measured. I either substituted egg weight for gosling weight or used the relationship between egg weight and gosling weight to estimate the gosling weight. The second
approach was to ignore the bias if it was very small. To assess the degree of the underestimation of gosling weight, I weighed the same gosling (n = 30) at least 1 more time from 3 to 51 h after hatching and made a multiple regression to study the effects of original gosling hatching weight and time span after hatching on gosling weight loss.

**Hatching Date and Hatching Sequence**

The population hatching period, defined as the time span between the first and last gosling hatched in the breeding population, was recorded. Successful nests were divided into early and late nests according to their hatching or laying date to study the effect of season on hatching success and gosling survival. Laying and hatching dates were used interchangeably because the incubation period is usually rather constant in Canada geese at 28 days (Brakhage 1965, Collias and Jahn 1954, and Hanson and Eberhardt 1971). Also, in this study only 2 of 24 nests studied during the incubation period were more than 1 day from the mean 28-day incubation. So in most cases, a clutch laid earlier would hatch earlier, and one laid later would hatch later.

When I separated early from late nests by dividing the hatching period into equal halves, a few nests hatching very late in the season prolonged the length of the whole breeding season. To avoid such outliers, I chose the period when 95% of the successful nests were hatched as the
'regular breeding season' and then divided this 'season' into equal halves, early and late periods. Using this criterion, May 5 and 6 in 1979, May 6 and 7 in 1980, and May 2 and 3 in 1981 separate the early and the late nests.

Hatching sequence among goslings within a nest was determined by direct observation during hatching if possible. In some cases, the physical appearances of newly hatched goslings, such as the dryness of down and the bulge of the yolk sac, was helpful in determining hatching sequence. Furthermore, different food color markings on down of newly hatched goslings aided study of the relationship between laying and hatching sequence for those goslings for which hatching sequence was determined indirectly.

**Brood Size and Time of Death of Goslings**

Brood size of a clutch is the number of goslings hatched from that clutch. To study the brood size change from hatching to fledging stage, I tagged goslings (see tagging for detail) when they were still in nests. After goslings left their nests they were led by their parents to a brooding ground. The brood size and individual goslings were recorded by identifying their tag numbers with the aid of a 20-30x spotting scope. A systematic searching route was developed for visiting each of the important brooding grounds (Fig. 1) at least once a day to record and identify the number of broods seen during the brooding season (late
April to early July). The mixed-brood or gang brood phenomenon (Warhurst 1974), a change of brood size due to brood mixing, was judged by observing goslings within a brood that were wearing tags with different numbers or by identifying goslings that differed in plumage or body size.

To study the temporal changes in gosling mortality, I observed only the tagged broods to avoid counting goslings that might have come from other broods. The number of goslings that died each day was estimated directly from a daily count if possible. However, in many cases a brood observed one day might not be observed again for a week or more when it might have missing goslings. It was difficult to determine when the missing goslings died. Under such circumstance, I assumed the probability of death of the missing goslings was equal in each day during the missing period of the brood, and calculated the fraction of death of the dead goslings on a weekly basis. For example, if a brood with 7 goslings which was observed at the third day of the second week reappeared at the sixth day of the third week with 2 goslings missing, thus 2 goslings disappeared within 9 days (4 days in the second week, 5 days in the third week), so the probability of a gosling dying each day was 2/9. The number of dead goslings was calculated as 8/9 (=4*2/9) for the second week and 10/9 (=5*2/9) for the third week for that brood.

**Female Age**
From 1978 to 1980 laminated vinylite blue neck collars (6.5 cm in height and 4.5 cm in diameter) with routed white letters and numbers were placed on 241 adult females, which had been leg-banded during annual summer roundups in the past years, at Killdeer Plains State Wildlife Area. The neck collars were used to identify the breeding success of individual females. The age of the female was then determined by checking the banding records to see if the bird was leg-banded in the year of hatching. However, many birds were banded as adults and their exact age could not be ascertained.

Nine marked females whose first year of breeding was known were selected to study the effect of experience on breeding performance by comparing their first year breeding with their second year.

To see the effect of female age on egg weight, laying date, and clutch size, I used a multivariate analysis, treating age as an independent variable and egg weight, laying date, and clutch size as dependent variables.

Movement

Movements of families from nesting ground to brooding grounds within the Wildlife Area were recorded. Observations were also made around the perimeter of the Wildlife Area, and local residents who lived within 2 km of the Area were contacted to see if they observed any tagged or non-tagged goslings outside the Area.
PREDATION

Predation on eggs or goslings was determined by direct observation and indirect evidence such as signs, tracks, gut remains, pellets, and droppings. Eggs destroyed by predators were determined by the signs or tracks that animals left within or near nests. Goslings preyed by predators were determined by looking bone remains from goslings and tracks from predators on ground. Furthermore, 3 snapping turtle traps were set up from late May to mid June in 1979. Turtles caught were sacrificed and their viscera were taken back to the laboratory to examine for gosling remains. Fox dens and great horned owl nests found were checked each year to see if there was any tag or skeletal remain from goslings.

METHODS USED AND TECHNIQUES RELATED TO ESTIMATING SURVIVAL

Tagging and Tag Loss

Goslings hatched in nests were marked on both wings with patagial streamers (Warhurst 1974). Both streamers of the pair had the same identification number written in black vinyl paint. The major purpose of tagging was to identify the fate of individual goslings and to estimate gosling survival in the population. The loss of tags from goslings before roundup could exaggerate the estimation of gosling mortality and affect the conclusions of the fate of individual goslings. To estimate tag loss, I compared the
ratio of tagged and non-tagged goslings after hatching with the ratio obtained from roundup.

**Roundup and Roundup Efficiency**

Roundup is the routine procedure to catch and band all the geese in the Wildlife Area during summer when geese are flightless and is carried out each year by the state wildlife employees. The number of goslings captured in the roundup is usually considered a good estimation of the total production. Furthermore, comparing the number of goslings captured during roundup with the number hatched from the early nesting survey permits an estimate of the gosling survival rate. However, because the geese are spread over a large area, all of them might not be caught during roundup, resulting in an underestimation of goose production and survival rate. To assess this problem, I estimated a roundup efficiency by comparing the numbers of neck-collared breeding females observed before roundup with the number captured in the roundup.

In 1980, all wing-tagged goslings captured in the roundup were further marked with blue neck collars, allowing an independent estimation of roundup efficiency by comparing the numbers of goslings having both patagial wing tags and neck collars with goslings having only patagial wing tags.

**Estimating Gosling Survival**

The fate of a tagged gosling was determined by its
presence or absence during roundup in this study except for
goslings found dead before roundup. The absence of a tagged
gosling during roundup did not mean it was dead. To
minimize the bias of my estimation I tried to assess factors
that might affect the presence or absence of a tagged
gosling during roundup. Three problems that might have
cased an underestimation of gosling survival were
considered: 1) emigration of tagged goslings before
roundup, 2) tag loss before roundup, and 3) failure to
capture goslings during roundup.

Gosling survival rate was estimated by either of the
formulae:

(1) \[ SR = \frac{(TGC / RE)}{TGH} \]
where \( SR \) = survival rate of goslings, \( TGC \) = total goslings
captured during roundup, \( RE \) = roundup efficiency, and \( TGH \) =
total goslings hatched, or:

(2) \[ SR = \frac{(TTGC / TE)}{TTGH} \]
where \( TTGC \) = total tagged goslings captured during roundup,
\( TE \) = tagging efficiency, and \( TTGH \) = total tagged goslings at
hatching.

**Statistical Analyses**

Whenever possible, any single factor that might affect
or associate with the outcome of hatching success or gosling
survival was analyzed separately while all the other factors
were held constant to avoid any possible confounding effect
with that factor. However, for the purpose of prediction of the outcome of the effects of several factors on breeding success in goose management, a multiple regression with logistic transformation (SAS 1980) was used to analyze the effect of egg weight, laying sequence, and laying date on egg hatching success within clutch; a regression technique was used to study the effect of mean egg weight, laying date, and clutch size on egg hatching success; a multiple regression with logistic transformation was used to analyze the effect of egg weight, hatching sequence, and hatching date on gosling survival within broods; and a multiple regression analysis was used to study the effect of mean egg weight, hatching date, and brood size on gosling survival between broods. A regression analysis with data converted to logarithms was used to study the allometric relationship between egg weight and each egg component (yolk, albumen, shell, etc.).
RESULTS

The presentation of results follows the format of the methods section, i.e., 3 major headings refers to 3 objectives. The first heading, nesting activities related to goose fitness, includes egg weight, egg composition, nest down, laying date, laying sequence, clutch size, gosling weight, hatching date and sequence, brood size, female age and general information on goose breeding such as nest down, length of incubation, nest related activities and hatching success (including nest utilization, egg and nest success, hatching success, causes of egg and nest failure, and renest), temporal change of gosling mortality, and movement. They are presented in a chronological order. Furthermore, the results from statistical analyses about the effects of egg weight, laying date, clutch size, and laying sequence on hatching success and the effects of egg weight, hatching date, brood size, and hatching sequence on gosling survival are presented at the end of this section.

The second heading, predation, includes the findings of both egg predators and gosling predators. The final section, methods used and techniques related to estimating survival, covers the findings of tagging and tag loss, roundup and roundup efficiency, and gosling survival.

NESTING ACTIVITIES RELATED TO GOOSE FITNESS

Egg Weight
From 1,975 eggs measured, the mean breadth was 59.2 mm ±1.7 (SD), the mean length was 85.8g ±3.3, and the calculated mean volume was 154.0 cm³ ±12.3. The egg weight and volume were highly correlated ($R^2 = 0.93$, $N = 122$, Fig. 2). The mean egg weight estimated from the weight-volume regression (weight = 0.129 +1.063 volume) was 163.8 g ±13.1 ranging from 121.0 to 202.9 (2 eggs were abnormal—one weighed 79.3 g, the other weighed 103.9 g).

The mean egg weight loss during a 28-day incubation was 12.5%, estimated from the regression equation (percent of egg weight loss = 1.1720 + 0.4063 day, $R^2=0.51$, $P<0.001$, Fig. 3).

**Egg Composition**

Because there was no difference (Hotelling t-test, $P>0.30$) among egg weight and components from eggs collected at Killdeer ($X=166.5g$ ± 2.0 SE, $N=39$) and Magee Marsh ($X=163.2g$ ± 3.6, $N=8$), the data were lumped to present a general description of egg composition. The mean egg weight of these 47 eggs was 165.9 g (Table 2). The 3 major components, shell, yolk, and albumen, comprised 12.1%, 40.5%, and 47.4%, respectively, of the fresh egg weight. The overall dry mass in an egg was 38.2% and the other 61.8% was water. The protein and lipid contents in an average egg were approximately equal (protein 12.0% and lipid 12.8%).

Most of the egg components were positively correlated with egg weight except the water content in the yolk (Table
Fig. 2. The relationship between egg volume and weight in the Killdeer Plains goose population, 1979-81.

\[ Y = 0.129 + 1.063X \]

\( r^2 = 0.93, P < 0.001, N = 122 \)
Fig. 3. The relationship between percent of egg weight loss and days in incubation, Killdeer Plains goose population, 1979.
Table 2. Characteristics of major components in Canada goose eggs (N=47), Killdeer Plains goose population, 1979-81.

<table>
<thead>
<tr>
<th></th>
<th>Shell (g)</th>
<th>Yolk (g)</th>
<th>Albumen (g)</th>
<th>Total (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$\bar{X}$</td>
<td>$\text{SD}$</td>
<td>$\bar{X}$</td>
<td>$\text{SD}$</td>
</tr>
<tr>
<td>Wet weight</td>
<td>20.0772</td>
<td>2.1441</td>
<td>66.9848</td>
<td>5.8190</td>
</tr>
<tr>
<td>Dry weight</td>
<td>18.3549</td>
<td>1.9120</td>
<td>34.1017</td>
<td>2.7945</td>
</tr>
<tr>
<td>Protein weight</td>
<td>—</td>
<td>—</td>
<td>10.9791</td>
<td>0.8939</td>
</tr>
<tr>
<td>Lipid weight</td>
<td>—</td>
<td>—</td>
<td>21.2615</td>
<td>2.0207</td>
</tr>
</tbody>
</table>

a Includes 8 eggs from Magee Marsh State Wildlife Area.
Table 3. Statistics for the regression of each egg component on egg weight \((N=47)\), Killdeer Plains goose population, 1979-81.

<table>
<thead>
<tr>
<th>Component</th>
<th>Intercept</th>
<th>Slope</th>
<th>SE</th>
<th>(R^2)</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shell weight</td>
<td>2.3113</td>
<td>0.1071</td>
<td>0.0206</td>
<td>0.37</td>
<td>0.001</td>
</tr>
<tr>
<td>Yolk weight</td>
<td>32.5085</td>
<td>0.2078</td>
<td>0.0637</td>
<td>0.19</td>
<td>0.005</td>
</tr>
<tr>
<td>Albumen weight</td>
<td>-34.8198</td>
<td>0.6852</td>
<td>0.0590</td>
<td>0.75</td>
<td>0.001</td>
</tr>
<tr>
<td>Shell water</td>
<td>0.0231</td>
<td>0.0102</td>
<td>0.0045</td>
<td>0.10</td>
<td>0.050</td>
</tr>
<tr>
<td>Yolk water</td>
<td>21.0008</td>
<td>0.0716</td>
<td>0.0457</td>
<td>0.05</td>
<td>0.124</td>
</tr>
<tr>
<td>Albumen water</td>
<td>-32.7199</td>
<td>0.6067</td>
<td>0.0608</td>
<td>0.69</td>
<td>0.001</td>
</tr>
<tr>
<td>Dry shell</td>
<td>2.2882</td>
<td>0.0968</td>
<td>0.0183</td>
<td>0.38</td>
<td>0.001</td>
</tr>
<tr>
<td>Dry yolk</td>
<td>11.5078</td>
<td>0.1362</td>
<td>0.0273</td>
<td>0.36</td>
<td>0.001</td>
</tr>
<tr>
<td>Dry albumen</td>
<td>-2.1000</td>
<td>0.0785</td>
<td>0.0185</td>
<td>0.29</td>
<td>0.001</td>
</tr>
<tr>
<td>Yolk lipid</td>
<td>4.6602</td>
<td>0.1000</td>
<td>0.0196</td>
<td>0.37</td>
<td>0.001</td>
</tr>
<tr>
<td>Yolk protein</td>
<td>5.5648</td>
<td>0.0326</td>
<td>0.0097</td>
<td>0.20</td>
<td>0.005</td>
</tr>
<tr>
<td>Albumen protein</td>
<td>-1.8554</td>
<td>0.0652</td>
<td>0.0164</td>
<td>0.26</td>
<td>0.001</td>
</tr>
<tr>
<td>Dry weight</td>
<td>11.6960</td>
<td>0.3115</td>
<td>0.0250</td>
<td>0.78</td>
<td>0.001</td>
</tr>
<tr>
<td>Water weight</td>
<td>-11.6960</td>
<td>0.6885</td>
<td>0.0250</td>
<td>0.94</td>
<td>0.001</td>
</tr>
</tbody>
</table>
3). But the total water content in the fresh egg contributed 94% of the variation of the egg weight, and most of the variation came from the albumen water. If the changes in the components of the egg were due only to the overall reduction in egg weight, one might expect that the weight of each egg component would also be reduced in proportion to the reduction in egg weight. I found that yolk weight reduced in proportion, albumen weight increased in proportion, and relative shell weight did not change as the egg weight increased (Table 4).

The dry weight of each component (yolk, albumen, and shell) also held the same relationship when the egg weight increased. However, the yolk lipid proportion did not change as egg weight increased. In general, the total dry weight of the egg decreased proportionately when egg weight increased, and the amount of water, on the contrary, increased.

The energy value (Kcal) of 100 g dry yolk or albumen calculated from the energy values of protein, lipid, and mixed carbohydrate was slightly higher than that of direct measurement by bomb calorimetry (Table 5). However, the total energy value of an average egg was only 1.1% different in the 2 estimations, suggesting that the calculation technique gave a good estimate of caloric value. Using this indirect method, I calculated the mean energy content of an egg that produced a live gosling as 298.5 Kcal ± 19.2 (SD,
Table 4. Statistics for the regression of the logarithm of each egg component on the logarithm of egg weight, Killdeer Plains goose population, 1979-81. A slope different from 1 indicates that the proportion of a component changes with egg weight (N=47).

<table>
<thead>
<tr>
<th>Component</th>
<th>Intercept</th>
<th>Slope</th>
<th>Slope 95% Confidence limits</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shell weight</td>
<td>-0.6140</td>
<td>0.8628</td>
<td>0.5203-1.2053</td>
<td>0.001</td>
</tr>
<tr>
<td>Yolk weight</td>
<td>0.6386</td>
<td>0.5344</td>
<td>0.2216-0.8472</td>
<td>0.005</td>
</tr>
<tr>
<td>Albumen weight</td>
<td>-1.2729</td>
<td>1.4272</td>
<td>1.1778-1.6766</td>
<td>0.001</td>
</tr>
<tr>
<td>Shell water</td>
<td>-1.6459</td>
<td>0.8438</td>
<td>0.0267-1.6876</td>
<td>0.050</td>
</tr>
<tr>
<td>Yolk water</td>
<td>0.6824</td>
<td>0.3749</td>
<td>-0.0506-0.8304</td>
<td>0.105</td>
</tr>
<tr>
<td>Albumen water</td>
<td>-1.4474</td>
<td>1.4765</td>
<td>1.1740-1.7790</td>
<td>0.001</td>
</tr>
<tr>
<td>Dry shell</td>
<td>-0.6414</td>
<td>0.8576</td>
<td>0.5229-1.1923</td>
<td>0.001</td>
</tr>
<tr>
<td>Dry yolk</td>
<td>-9.3502</td>
<td>0.6902</td>
<td>0.4299-0.9505</td>
<td>0.001</td>
</tr>
<tr>
<td>Dry albumen</td>
<td>-1.6696</td>
<td>1.2178</td>
<td>0.6387-1.7969</td>
<td>0.001</td>
</tr>
<tr>
<td>Yolk lipid</td>
<td>-0.4563</td>
<td>0.8031</td>
<td>0.5032-1.1030</td>
<td>0.001</td>
</tr>
<tr>
<td>Yolk protein</td>
<td>-0.1122</td>
<td>0.5189</td>
<td>0.2305-0.8073</td>
<td>0.001</td>
</tr>
<tr>
<td>Albumen protein</td>
<td>-1.8512</td>
<td>1.2604</td>
<td>0.6281-1.8927</td>
<td>0.001</td>
</tr>
<tr>
<td>Dry weight</td>
<td>-0.0059</td>
<td>0.8143</td>
<td>0.6826-0.9460</td>
<td>0.001</td>
</tr>
<tr>
<td>Water weight</td>
<td>-0.4631</td>
<td>1.1144</td>
<td>1.0340-1.1948</td>
<td>0.001</td>
</tr>
</tbody>
</table>
Table 5. Protein, lipid, and caloric density of yolk and albumen from 47 eggs collected at Killdeer Plains State Wildlife Area, 1979-81.

<table>
<thead>
<tr>
<th></th>
<th>Protein (g)</th>
<th>Lipid (g)</th>
<th>Energy (Kcal)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dry yolk (100g)</td>
<td>32.23</td>
<td>62.32</td>
<td>759.01</td>
</tr>
<tr>
<td></td>
<td>1.36</td>
<td>2.23</td>
<td>22.24</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>753.59</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>3.37</td>
</tr>
<tr>
<td>Dry albumen (100g)</td>
<td>81.87</td>
<td>—</td>
<td>441.00</td>
</tr>
<tr>
<td></td>
<td>2.13</td>
<td>—</td>
<td>9.59</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>426.33</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>35.42</td>
</tr>
</tbody>
</table>

\(a_{N=4}\).
N=170) and of an egg that produced a dead gosling as 289.3 Kcal + 26.3 (N=227).

Nest Down

No down was found in any nest when the first egg was laid (Table 6). Down first appeared in 9.5% of the nests studied when the second egg was laid. It occurred most frequently when the third (38.1%) and fourth (34.5%) eggs were laid. The timing of down appearance was related to the clutch size (Fig. 4). The greater the clutch size, the later the down appeared. In clutch size 6, down first appeared in 50% of nests when the third egg was laid, and in clutch size 7, in 48.1% of nests down first appeared when the fourth egg was laid. Appearance of first down when the fifth egg was laid was more frequent in clutch size 7 than in clutch size 6 (Fig. 4).

Laying Date, Laying Sequence, and Clutch Size

The laying period was estimated to be about 59 days, from March 19th to May 17th in 1979; 57 days, from March 16th to May 12th in 1980; and 63 days, from March 6th to May 8th in 1981. The peak laying period was around late March to early April each year (Fig. 5). Within the last week of March and the first week of April, about 60% of the total eggs laid during the breeding season were found (63.4% in 1979, 66.5% in 1980, and 58.2% in 1981). The laying patterns in these 3 years were basically similar, i.e., the
Table 6. First appearance of nest down in the egg laying period of Canada geese at the Killdeer Plains State Wildlife Area, 1979-81.

<table>
<thead>
<tr>
<th>Egg number</th>
<th>Number of nests</th>
<th>Percent</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>2</td>
<td>8</td>
<td>9.5</td>
</tr>
<tr>
<td>3</td>
<td>32</td>
<td>38.1</td>
</tr>
<tr>
<td>4</td>
<td>29</td>
<td>34.5</td>
</tr>
<tr>
<td>5</td>
<td>14</td>
<td>16.7</td>
</tr>
<tr>
<td>6</td>
<td>1</td>
<td>1.2</td>
</tr>
</tbody>
</table>
Fig. 4. The relationship between first appearance of goose down in the nest and number of eggs laid, clutch size 3 to 9. Killdeer Plains goose population, 1979-81.
Fig. 5. Number of eggs laid per 3 day-period, from March 5 to May 18, Killdeer Plains goose population, 1979-81.
production of eggs increased sharply before the peak laying period and declined slowly after peak period. Few eggs were laid very late in the season. However, in 1981 egg production increased slowly. A similar pattern was found between clutch completion dates and laying period (Fig. 6). When the breeding season advanced, the late clutches had smaller mean egg weight than the early clutches had (mean egg weight = 171.2890 - 0.3432X, where X = days from the first completed clutch, N=261, P<0.005, Fig. 7).

Egg weight changed with laying sequence in a certain pattern. Among 6-egg clutches (N=25), the first egg laid was usually smaller than the second one (Fig. 8). The second egg was usually the largest and egg weight decreased from then on. The last laid egg was usually the smallest within a clutch (ANOVA, P<0.12). Clutch size varied from 2 to 11 eggs. However, clutch size was between 5 and 7 in 84% of the nests, and clutch size 6 occurred most frequently (36.2%) followed by clutch size 7 (26.7%) and 5 (21.1%) (Fig. 9).

There was a negative association between clutch size and laying date. As the laying date advanced, the clutch size became smaller (clutch size = 6.4983 - 0.0243X, where X = laying period, N=261, P<0.005, Fig. 10).

Mean egg weight changed among different clutch sizes; as the clutch size increased from 3 to 5 the mean egg weight increased from 153.8 to 163.7 g (ANOVA, P<0.10). Though
Fig. 6. Date of clutch completion of each nest during egg laying period, Killdeer Plains goose population, 1979-81 (3 late nests not shown).
Fig. 7. The relationship between mean egg weight of clutch and clutch completion date during laying period, Killdeer Plains goose population, 1979-81.
Fig. 8. Mean egg weight (± SE) according to laying sequence in 6-egg clutches
(N=25, P<0.12), Killdeer Plains goose population, 1979-81.
Fig. 9. The occurrence of different clutch sizes, Killdeer Plains goose population, 1979-81.
Fig. 10. Relationship between clutch completion date and clutch size, Killdeer Plains goose population, 1979-81.
clutch size of 7 seemed to have the highest mean egg weight (165.8 g), there was no significant difference between clutch size 5, 6, 7, and 8 (Fig. 11). The mean egg weight of clutch sizes larger than 8 (9, 10, and 11) was smaller than those of clutch sizes 5, 6, 7, and 8. However, due to the limited sample size, no statistical analysis could be performed.

**Length of Incubation**

At Killdeer, incubation time varied from 26 to 33 days for 24 successful nests during the 3-year study period. The average length was 28 days (1 nest = 26 days, 6 = 27 days, 13 = 28 days, 3 = 29 days, and 1 = 33 days). For nests that failed to hatch due to the clutches containing infertile eggs or dead embryos the females spent more than 28 days in nests. In 2 extreme occasions, females were observed staying in nests 49 and 51 days.

**Nest Related Activity and Hatching Success**

Though most of the pairs still used the tub structures, there was a decline from 90.7% in 1979 to 77.0% in 1981. About 86% nests found were from tub structures within 3 years. Use of the available tub nests by breeding pairs declined from 46.85% in 1979 to 26.22% in 1981 (Table 7). On the other hand, the number of ground nests found nearly doubled from 16 in 1979 to 29 in 1981.

Nesting success was higher in 1980 (77.86%) than in
Fig. 11. Mean egg weight (± 1 SD) according to clutch size, Killdeer Plains goose population, 1979-81 (N = number of clutches).
Table 7. Utilization by Canada geese of nesting sites and hatching success of the tub and ground nests at the Killdeer Plains State Wildlife Area, 1979-81.

<table>
<thead>
<tr>
<th></th>
<th>1979</th>
<th>1980</th>
<th>1981</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Available tub nests</td>
<td>333</td>
<td>338</td>
<td>370</td>
<td>1041</td>
</tr>
<tr>
<td>Utilized tub nests</td>
<td>156</td>
<td>114</td>
<td>97</td>
<td>367</td>
</tr>
<tr>
<td>Successful tub nests</td>
<td>110</td>
<td>91</td>
<td>56</td>
<td>257</td>
</tr>
<tr>
<td>Ground nests found</td>
<td>16</td>
<td>17</td>
<td>29</td>
<td>62</td>
</tr>
<tr>
<td>Successful ground nests</td>
<td>9</td>
<td>11</td>
<td>23</td>
<td>43</td>
</tr>
<tr>
<td>Nest success (%)</td>
<td>69.19</td>
<td>77.86</td>
<td>62.70</td>
<td>69.93</td>
</tr>
</tbody>
</table>
1981 (62.70%). Egg production also decreased from 898 in 1979 to 656 in 1981 (Table 8). As a consequence, the number of goslings hatched was also reduced from 573 in 1979 to 366 in 1981.

The causes of nest loss of the 123 unsuccessful nests studied were: no incubation (30.89%), desertion (incubation begun) (37.40%), nest failure (incubation carried out for normal time period) (13.01%), flooding (4.88%), predation (9.8%), and human disturbance (4.07%). The fate of 145 eggs that failed to hatch was as follows: 30.34% broken, 7.59% missing, 15.86% infertile, and 46.21% with a dead embryo.

Renesting at Killdeer was not important. Only 1 of 84 positively identified individual breeding females was found to renest when the original clutch was lost.

Gosling Weight

The relationship between egg weight and gosling hatching weight was positively correlated (P<0.001, R² = 0.84, N = 55, Fig. 12). The average gosling weight calculated from the regression equation (gosling hatching weight = -8.047 + 0.7553X, where X = egg weight) was 116.8 g using the mean egg weight from all hatched goslings.

Goslings always stayed in the nest for a day or more after hatching. During this stage, they lost weight consistently by metabolic consumption and loss of water through the evaporation from wet down. The weight loss of 30 goslings studied from hatching to the time of leaving the
Table 8. Clutch size and hatching success of Canada geese at the Killdeer Plains State Wildlife Area, 1979-81.

<table>
<thead>
<tr>
<th></th>
<th>1979</th>
<th>1980</th>
<th>1981</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of eggs</td>
<td>898</td>
<td>754</td>
<td>656</td>
<td>2308</td>
</tr>
<tr>
<td>Number of nests</td>
<td>172</td>
<td>131</td>
<td>126</td>
<td>429</td>
</tr>
<tr>
<td>Mean clutch size (overall)</td>
<td>5.22</td>
<td>5.76</td>
<td>5.21</td>
<td>5.38</td>
</tr>
<tr>
<td>Mean clutch size (active)</td>
<td>5.79</td>
<td>6.25</td>
<td>5.90</td>
<td>5.98</td>
</tr>
<tr>
<td>Goslings hatched</td>
<td>573</td>
<td>503</td>
<td>366</td>
<td>1442</td>
</tr>
<tr>
<td>Egg success(%)</td>
<td>63.81</td>
<td>66.71</td>
<td>55.79</td>
<td>62.48</td>
</tr>
<tr>
<td>Hatching success(%)</td>
<td>83.16</td>
<td>78.96</td>
<td>78.54</td>
<td>80.44</td>
</tr>
</tbody>
</table>

*a* Calculated from all nests.

*b* Calculated from successful nests.
Fig. 12. The relationship between egg weight and gosling weight, Killdeer Plains goose population, 1979-81.
nest was positively correlated with the time span that a gosling stayed in the nest after hatching (P<0.001, \( R^2 = 0.87 \)). The predicted weight loss of an average weight gosling, estimated from the multiple regression equation (gosling weight after hatching = 25.6222 * 0.7258 gosling hatching weight - 0.3708 h in nest), was 2% of its body weight within the first 6 h after hatching and about 8% for the first day of life.

**Hatching Date and Hatching Sequence**

The hatching period lasted for 36 days (April 22 to May 27) in 1979, 38 days (April 23 to May 30) in 1980, and 50 days (April 12 to May 31) in 1981. The peak hatching period was around late April to early May each year with the amazing coincidence that the modal hatching date each year was May 1st. The hatching was more synchronous in 1979 and 1980 than in 1981. However, the pattern of few nests hatching very late in the season was found all 3 years (Fig. 13).

The laying and hatching sequences were positively correlated (\( R^2 = 0.21 \), P<0.001, Fig. 14). The last laid eggs in clutch sizes 6 and 7 were usually hatched last or second to the last (\( X^2 \) test, P<0.05), but the last laid eggs in clutch size 5 were not (P>0.10).

**Brood Size and Time of Death of Goslings**

As expected, large clutches usually produced large
Fig. 13. Number of clutches hatched each day during hatching period, Killdeer Plains goose population, 1979-81.
Fig. 14. The relationship between laying and hatching sequence of eggs in a clutch, Killdeer Plains goose population, 1979-81.
broods (P<0.001, Fig. 15). Brood size decreased as season progressed. However, on a few occasions, broods tended to mix together when they met on a brooding ground. Parents of one brood might lose some or all of their goslings to other parents. Thus, an apparent increase in brood size as the season advanced was noticed. The largest mixed broods found in Killdeer were 13 in 1979, 11 in 1980, and 9 in 1981. The other mixed broods usually had a size of 4 to 7 goslings.

The overall proportion of mixed broods at Killdeer was thought to be small, but no quantitative analysis was made.

The gosling age with the greatest mortality was the first week after hatching. Of 209 tagged goslings found dead or missing in their first 8 weeks of life, 28.9% died in the first week, 18.7% died in the second week, 12.2% died in the third week, and less than 10% each week afterward (Fig. 16).

**Female Age**

From the multivariate analysis, there was no significant effect of age of female on mean egg weight, laying date, and clutch size (Hotelling t-test, P>0.80).

Of 9 females (6 two years old and 3 three years old), whose first year of breeding was known there was no difference in clutch size with or without previous breeding experience. However, females with previous breeding experience had a higher hatching success and gosling survival (P<0.10, X² test) than they did in their first year.
Fig. 15. Relationship between clutch size and brood size at hatching, Killdeer Plains goose population, 1979-81. The numbers of observations are in circles.
Fig. 16. Number of tagged goslings that died during their first 8 weeks of life after hatching, Killdeer Plains goose population, 1979-81.
of breeding (Table 9).

Movement

Once goslings left nests, they were soon led by their parents to the brooding grounds, usually open meadows around ponds or marshes (Fig. 1). Geese nesting at Pond-3 and the Refuge tended to let their broods stay in the nearby meadows. Geese nesting in other ponds tended to lead their broods from pond to pond in the early brooding stage. During that early brooding period, fewer broods (3-5) using a brooding ground were very common and more brooding grounds were occupied by those broods. As brooding season advanced, more broods (10-20) were observed concentrating on fewer brooding grounds. In late June and early July each year, about 90-95% of the total geese were observed either in the south and west meadows around the Refuge (80%) or in Pond-3 meadow (10-15%) when a large body of open water was readily accessible to geese.

Three broods were observed to have a maximum moving distance 5-7 km in a day. However, they nearly always stayed in the Wildlife Area except feeding occasionally in the nearby agricultural fields as sometimes many other broods did. Emigration of goslings from the Wildlife Area to the surrounding areas was rare. In the 3 years of study, only 1 tagged brood was seen on a pond outside the Wildlife Area.

Effects of Mean Egg Weight, Laying Date, and Clutch Size on
Table 9. Comparison of breeding success of the same females (N=9) with and without previous breeding experience, Killdeer Plains goose population, 1979-81.

<table>
<thead>
<tr>
<th></th>
<th>Breeding for the first time</th>
<th>Breeding with previous experience</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eggs laid</td>
<td>56</td>
<td>54</td>
</tr>
<tr>
<td>Mean clutch size</td>
<td>6.2</td>
<td>6.0</td>
</tr>
<tr>
<td>Goslings hatched</td>
<td>40</td>
<td>46</td>
</tr>
<tr>
<td>Goslings survived</td>
<td>18</td>
<td>30</td>
</tr>
<tr>
<td>Hatching success (%)</td>
<td>71.4</td>
<td>85.2</td>
</tr>
<tr>
<td>Gosling survival (%)</td>
<td>45.0</td>
<td>65.2</td>
</tr>
</tbody>
</table>

*P<0.10, χ² test.
**Hatching Success**

Medium clutches (5, 6, and 7) had the highest hatching success (81.8%) and larger clutches had the lowest hatching success (67.1%) (Table 10). Mean egg weight of hatched eggs (165.1g ± 12.4 SD, N=1262) was 3.2 g heavier than unhatched eggs (161.9g ± 14.7, N=229, t-test, P<0.001). The early hatched nests had a higher hatching success than that of late nests (85.9% vs 81.8%, P<0.05, X² test). Due to the limited sample size for smaller and larger clutches, only clutch sizes 5, 6, and 7 were used in the multivariate analysis. From a univariate view, as the mean egg weight increased hatching success increased (P<0.05). This was also true for clutch size: clutch size 7 had the highest hatching success and 5 had the lowest hatching success (P<0.05). However, the reverse trend was true for laying date --hatching success was higher for early laid eggs than for late laid eggs (P<0.001). When all these factors were considered simultaneously, the same relationship still held, i.e., the heavier, earlier laid eggs within a larger clutch had a higher hatching success (P<0.001).

**Effect of Laying Sequence on Hatching Success**

The effect of laying sequence on hatching success was studied using a clutch size of 6. The first laid eggs within clutches had the lowest hatching success (52.2%, 12/23), the fourth laid eggs had the highest hatching success (91.3%, 21/23), and the remainder lay between 69.6
Table 10. Effect of clutch size on hatching success, Killdeer Plains goose population, 1979-81.

<table>
<thead>
<tr>
<th>Clutch Size</th>
<th>Small (&lt;5)</th>
<th>Medium (5,6,7)</th>
<th>Large (&gt;7)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of Clutches</td>
<td>28</td>
<td>247</td>
<td>18</td>
</tr>
<tr>
<td>Eggs Laid</td>
<td>100</td>
<td>1508</td>
<td>146</td>
</tr>
<tr>
<td>Hatched (%)</td>
<td>75.8</td>
<td>81.8</td>
<td>67.1</td>
</tr>
<tr>
<td>Range (%)</td>
<td>53.3-85.1</td>
<td>79.9-84.3</td>
<td>62.5-71.9</td>
</tr>
</tbody>
</table>
and 73.9%. It seemed that laying sequence did affect hatching success, but there was no significant difference between these two \( (X^2 \text{ test, } P>0.10) \).

**Effects of Mean Egg Weight, Hatching Date, and Brood Size on Gosling Survival**

From a univariate statistical analysis, egg weight and hatching date both affected gosling survival. Goslings that survived to roundup were hatched from eggs \( (N=59, \ X=165.5 \text{ g } \pm 1.7 \text{ SE}) \) that were 4.1 g heavier \( (P<0.05, t\text{-test}) \) than those eggs \( (N=74, \ X=161.4 \text{ g } \pm 1.4) \) that gave rise to goslings that died before roundup. Goslings hatched earlier \( (N=108) \) has a 25.4% (92.6% vs 67.2%) higher survival rate than those hatched later \( (N=134) \). The same relationship was also demonstrated in the multivariate analysis: clutches with a higher mean egg weight had higher gosling survival \( (P<0.05) \) and goslings hatched from early nests had a higher survival rate \( (P<0.01) \). However, brood size had no significant effect on gosling survival in both analyses.

**Effect of Hatching Sequence on Gosling Survival**

Six goslings, usually from the larger clutches (6-8) with known hatching sequence (4 first- and 2 last-hatched), were found dead in nests or near the nests. It was thought that the early or late hatches within a large clutch might have higher gosling mortality, yet no significant difference was found between hatching sequence and gosling survival.
(P>0.30).

**Predation**

Predation on eggs was rather light at Killdeer. Less than 4% of the total eggs produced were destroyed by predators. Raccoons were the main predators. They were seen in tub structures several times and their hairs and droppings were found with broken egg shells in many formerly active nests. Besides raccoons, crows (*Corvus brachyrhynchos*) were also seen near goose nests. Eggs from 1 nest were destroyed by crows.

No quantitative study was made of gosling predation. Predators such as foxes, raccoons, great horned owls, and snapping turtles were frequently seen in the wildlife area. No direct evidence of a gosling eaten by predators was observed. But indirect evidences were many. Within the refuge, a raccoon was seen chasing a pair of geese and their 2 goslings on May 17, 1979. On May 24, fresh raccoon and goose tracks were seen together along the central dike of the refuge. Two skeletal remains with tags were found along with raccoon tracks on the shore of a small pond near the refuge on June 14. Besides raccoons, tags and skeletal remains were found in a tub structure with great horned owl pellets in early June, 1980. About 3-4 active owl nests were found near goose tubs and brooding grounds each year. So some of the goslings were probably eaten by those owls. From the gut remains of 8 snapping turtles, no down or
feathers could be found. However, the sudden disappearance of a gosling from the water surface observed in May 1980 could be an evidence of turtle predation. Two active fox dens were found near goose brooding grounds, but no tags or gosling remains were found in them.

**METHODS USED AND TECHNIQUES RELATED TO ESTIMATING SURVIVAL**

**Tagging and Tag Loss**

In the 3-year study, 738 goslings were tagged with patagial wing markers (125 in 1979, 364 in 1980, and 249 in 1981). Loss of both tags was common in the first year, affecting 62.5% of the goslings tagged. In 1980, about 23.4% of the tagged goslings lost both tags. Only 1.7% lost both tags in 1981. The overall loss of both tags in the 3 years was 22.4%.

**Roundup and Roundup Efficiency**

In 1979, 368 birds were captured during roundup (33 adult males, 103 adult females, 98 juvenile males, and 134 juvenile females). Of 16 neck collared females with successful nests observed during breeding season, 9 were captured during roundup. The estimated roundup efficiency was thus 56.3% ± 24.3 (95% confidence interval).

In 1980, 484 birds were captured during roundup (96 adult males, 98 adult females, 121 juvenile males, and 169 juvenile females). Of 30 neck collared females observed, 21 were captured during roundup. The estimated roundup
efficiency was 70% ± 16.4.

In 1981, 347 birds were caught (76 adult males, 90 adult females, 100 juvenile males, and 81 juvenile females). The roundup efficiency was 61.9% ± 14.7 (26 caught from 42 observed birds).

There were 146 wing-tagged goslings with neck collars and 7 goslings with only patagial wing tags observed within 2 weeks after roundup in 1980. That indicated a 95% roundup efficiency of the neck-collared goslings.

**Gosling Survival**

Within 3 years, 709 goslings were captured (232 in 1979, 296 in 1980, and 181 in 1981) during roundup. The estimated gosling survival rate calculated from either formula was 71.9% in 1979, 84.1% in 1980, and 79.9% in 1981. The overall survival rate for the 3 years was 78.2%.

The gosling survival rate estimated from the roundup efficiency that derived from the second approach, i.e., ratio between tagged goslings with neck collars and without in 1980, was 62.0%.
DISCUSSION

The presentation of discussion follows the format of results to answer the corresponding problems in the objectives in the following order: 1. which nesting activity or factor related to goose fitness and how important was it in comparison with other factors? 2. was predation really important in determining gosling survival at Killdeer? and 3. was the procedure used in estimating gosling production appropriate? if not, what is the alternative way to measure gosling production? Before answering each of the questions at the end of each section, the findings of each topic were discussed with the findings of other studies. In addition to discussion, a section of recommendations for management was devoted to addressing the findings of the study in relation to future goose management.

NESTING ACTIVITIES RELATED TO GOOSE FITNESS

Nest Related Activities and Hatching Success

The low utilization of tub structures was mainly caused by decreasing numbers of initial breeding pairs. The reason for such decrease was unknown. However, some experienced females harvested during hunting seasons might contribute to some extent to the problem of fewer nest initiations. The marked increase in the number of ground nests in 1981 was due to changing the location of tub nest sites from a
uniform evenly distributed pattern to a linear clump pattern to save time in nesting survey within refuge before nest initiation in 1981. Many old birds preferred nesting on nearby ground, where the old tubs had been located, to the tub structures established in the new places.

The overall nest success (69.93%) was similar to other studies of giant Canada geese (Bellrose 1978). The mean overall clutch size (5.38) was slightly higher than Bellrose (1978) reported (5.22).

The high desertion rate could be due to the greater proportion of young females that bred at the first time. Nests destroyed by flooding were rather few (4.88%), because 85.55% of the breeding pairs nested in tub nest structures which were nearly always high enough to avoid being flooded except in 2 occasions.

Female Age

Because mean egg weight, clutch size, and laying date, were not associated with female age and did not affect female breeding success in the Killdeer goose population, any effect of age on breeding success there could be attributed to the greater breeding experience gained by older females. Raveling (1981) found that a successful 2-4-year-old was 3 times more likely to be successful the next year than was an unsuccessful bird of the same age. In this study, a similar trend, that young birds (2 and 3 years) improved their breeding success (20% in hatching
success and 14% in gosling survival) after they had bred once, was observed.

Besides breeding experience of females, the age of male is also important in determining breeding success in many birds. Coulson (1966) observed that the relative age of male kittiwake gulls influenced the date of egg laying and breeding success of the females. He further demonstrated that a female paired with a new male had a lower breeding success than one that had paired with her old mate. Bruggers and Jackson (1981) suggested that courtship inexperience of yearling males may be in part a reason for the reduced productivity noted for anatids that breed in their first year. Males with different degrees of alertness and aggressiveness were observed during the egg laying and brooding period in the Killdeer goose population. The loss of mate during hunting seasons was also rather common. However, due to the limited time and manpower, the important effect of male age and mate retention on female breeding success was not studied.

Movement

Movement from nesting ground to brooding ground in waterfowl is very common. Munro and Bedard (1977) observed that female common eiders (Somateria mollissima) took their brood to rearing areas up to 13 km from nesting areas. In Canada geese, the distances between the nest locations and the centers of the marshes that were first used for brood
rearing ranged from 0.7 to 8.4 km in Zicus' (1981) study, from 9.6 to 16.1 km in Geis' study (1956), and 10 to 15 km in MacInnes and Lieff's study (1968). On the contrary, Dismick (1968) reported goose broods at Jackson Hole, Wyoming, remained on the nesting ground for several weeks. The causes of such variation of movement (0-16.1 km) in different populations are hard to specify. It seems that food plays a very important role in determining the movement of broods (Geis 1956). Besides food, the accessible water present on the brooding ground also seem to be a necessity. Furthermore, tradition or learning might also affect pairs in choosing their brooding grounds. Zicus (1981) observed that pairs raised young on the same brooding grounds in 2 years.

Most of the favorable common brooding grounds at Killdeer were meadows that were mowed at least 1-3 times and were close to open water. The aggregation of broods near open water in the late brooding period could be due to (1) less food intake was needed for the nearly full grown goslings, so that food probably no longer was a limiting factor separating different broods, and (2) temperature became higher as summer began, which kept geese in the water for a longer time.

The movement of broods had some survival value to goslings. The choices of brooding grounds from parents in terms of food, cover, chance of predation, and human
disturbance were all directly or indirectly related to gosling survival. However, due to the limited time and manpower effects of spatial heterogeneity resulting from movement of broods on gosling survival were not studied.

Emigration was rare at Killdeer probably because there was no standing water in the corn and soybean fields that surrounded the Wildlife Area. This made traveling to reach the few ponds in a far distance outside the Wildlife Area more difficult for the flightless geese.

**Effect of Laying Sequence on Hatching Success**

Cooper (1978) reported that the first laid egg in Canada geese clutches had a lower hatching success (85.4% vs. 93.4% of other eggs). In this study, a similar trend was established though no statistical difference was found. Females started incubation after the third or the fourth eggs were laid, according to the appearance of down found in nests in this study and others (Brakhage 1965, Collias and Jahn 1959, Kossack 1950), so the lower hatching success of the first laid eggs could be due to their having been left unattended for the longest time period, no down protection, and having the highest probability of physical or environmental damage to the eggs or embryos.

The unexpected finding that the fourth laid eggs tended to have the highest hatching success could be also explained by the fact that they had the least probability of being damaged by environmental or physical factors prior to
incubation. One might expect to find that eggs laid after the fourth egg should also have the highest hatching success. In fact, in 6 instances, the last laid eggs or next to last laid eggs in large clutches (>6) were not hatched but had fully developed embryos that were 0.5-2 days away from hatching. On another occasion, I transferred an unhatched last laid egg from a nest (parents had already taken the brood away) to a clutch that was about to hatch and found the egg hatched the next day. Synchronized egg hatching has been demonstrated in some precocial species (Vince 1964, 1968) and is generally thought to be true in Canada geese. However, this transfer experiment demonstrated the imperfection or the limitation of such mechanism, i.e., if the development of an embryo is far behind due to late laying, it is going to die.

No statistical analysis was tested to investigate the effect of laying sequence on hatching success between large and small clutches. From the observation on egg transfer experiment I suspect that the effect of hatching sequence on hatching success if exists, is more prevalent in large clutches than that of small clutches.

Effect of Egg Weight on Hatching Success

Egg weight affecting hatching success was demonstrated in several studies, yet the underlying mechanism was not clear. Murton et al. (1974) reported that heavier woodpigeon eggs (>20 g) hatched more successfully than light
eggs (18-20 g) and none weighing less than 16 g hatched. O’Connor (1979) found European swift, clutches of 2 or 3, in which all eggs hatched successfully, averaged slightly heavier than clutches in which one or more eggs failed to hatch. He suggested that the low hatching success of lighter eggs might be due to such eggs being formed during food shortage and resulting in poor quality, or having larger surface-volume ratio that might cool more rapidly than those of larger eggs during parental absence and subsequently affecting the survival of embryos.

Because there was no significant difference in protein and lipid contents between different egg sizes (large or small) in this study, the unhatched eggs had 3.2 g lower in weight than hatched eggs in geese is probably not due to the poor quality as was suggested by O’Connor. The possibility of detrimental effect of temperature on developing embryos was probably higher in species with larger surface-volume ratio such as European swift eggs (4 g) and woodpigeon eggs (20 g) than in species with lower surface-volume ratio such as Canada goose eggs (165 g). So the relative smaller difference of surface-volume ratio between larger and smaller eggs in Canada geese could not fully explain why smaller eggs had lower hatching success.

Besides heat loss, different proportion of water loss due to different surface-volume ratio between large and small eggs could be the cause of low hatching success of
small eggs. However, Rahn et al. (1979) found that, regardless of egg mass or incubation time, the typical egg will lose 15% of initial mass during natural incubation. Ar and Bahn (1980) further stated that during incubation, water loss was mandatory if the relative water content of an egg at the end of incubation was to remain essentially the same as at the beginning because of increasing metabolic water production during development and decreasing dry matter content during metabolism.

Egg laying and incubation behavior of the female that depends on her energy reserve demonstrated in many recent studies might reveal some light in explaining the mechanism of egg weight on hatching success. Krapu (1981) found that lipid reserves were utilized to meet energy requirements during laying and incubation in mallards. Incubating geese depended on stored reserves and were near starvation weight by the time their eggs hatched or sometimes even starved to death before the incubation was completed (Ankney and MacInnes 1978, Raveling and Lumsden 1977, Raveling 1979). Geese without enough energy reserves to carry out incubation could have other options, i.e., abandon the nest or leave the nest to feed. It was generally believed that females with larger nutrient reserves laid larger clutches than did females with smaller nutrient reserves (Ankney and MacInnes 1978). However, I suspect that the smaller eggs also could be produced by those females with lower energy reserves. As
a consequence, those females might leave nests to feed late in the incubation period because of their reduced energy reserves to sustain a full term of incubation and thus expose their eggs to possible environmental stress or to predators. One would expect that males would guard against predators as females leave the nest to feed. On the contrary, Harvey (1971) reported that female lesser snow geese were accompanied by their mates if they left their nests during incubation and such behavior was also observed in this study. Furthermore, the tolerance of embryos to temperature stress declined with age (Drent 1970), and the leaving of the female to feed during the late incubation period would leave the more susceptible embryos to environmental stress, and the degree of susceptibility would further be intensified as a result of a relatively small egg. Thus, the lower hatching success of the smaller eggs found in this study could be attributed to the combined effects of high surface-volume ratio of the eggs and inability for full term incubation by the female with less energy reserve under the assumption that smaller eggs were laid by those 'energy poor' females.

Effect of Laying Date on Hatching Success

The higher hatching success of early nests found in this study were comparable to other waterfowl studies (Harvey 1971, Newton and Kerbes 1974). Perrins (1970) suggested that food requirements for laying females probably
predetermined the laying date of some altricial females. However, in Canada geese food was acquired before birds reached the breeding grounds at northern latitudes. The entire breeding period of nest initiation was relatively short in comparison with other species. MacInnes et al. (1974) found that the first and the last laid eggs of Canada goose (*B. c. hutchinsii-parvipes*) populations at McConnell River and Cape Churchill were between 10 and 20 days. The highly synchronized breeding activities found in these populations were probably due to the intensive selective pressure exerted on breeding females resulting from the harsh environment in the high arctic. In this case, early or late nests were separated by just a few days. Bellrose (1978) described studies in different latitudes and demonstrated that the breeding period of goose populations decreases from southern to northern latitudes. At Killdeer the geese began to nest in March and the laying season extended over a period of 50 to 60 days. Thus the difference between the early and late nests could be several weeks.

The low hatching success (4.1% different from early nests) in late nests could be due to the lack of incubation experience from young females which started nests late, but no correlation was found between female age and laying date. Birds that nested late could be bothered by an increase of predatory activities, as observed at Killdeer as the season
advanced, resulting in a poor hatching success of those late nests. Alternatively, the early nesters would expose their eggs more often to freezing temperature than late nesters would. One should expect that early nests have a lower hatching success. However, at Killdeer the weather was rather mild (average temperature in March 40.6°F, April 51.8°F, and May 60.8°F) compared to weather farther north and the impact of cold stress was probably rather small.

**Effect of Clutch Size on Hatching Success**

I have no explanation for the increased hatching success as the clutch size increased from 5 to 7. Other factors that might affect hatching success were taken into account in this study, so I cannot attribute the higher hatching success of the larger clutch size to its association to laying date and egg size that was found in other studies (Brakhage 1965, Cooper 1978). The causes of such change have to be in clutch size itself, i.e., the numbers. Norton (1970) found that the cooling constant of dunlin (*Calidris alpina*) eggs when positioned in the typical packed mass of 4 in the nest was significantly lower as compared to the isolated egg or packs of less than 4. Though he did not show what happened when the pack of eggs was more than 4, it seemed less likely that the thermal advantage will change much when the clutch size changes from 5 to 7. The low hatching success of smaller clutch size (3 and 4) found in this study could be attributed to the eggs
being more susceptible to cold due to the lack of thermal advantage.

Besides the possible thermal advantage which probably does not occur between clutch size 5 to 7, larger clutches could serve as a larger stimulus to attract more attention from the females in terms of incubation. Tinbergen (1951) reported that female oyster catchers (Haematopus ostralegus) preferred incubating giant dummy eggs to their own. On the other hand, there was a dilemma that, for increase of clutch size up to certain number, females might be either physiologically unable to produce more eggs due to the constraint of their energy reserves or physically unable to incubate those eggs. Though no adjustment was made for other factors that might associate with larger clutch sizes (8-11), hatching success in larger clutches was significantly lower than in clutch sizes 5 to 7 combined. I suspect that the females' incapability of incubation would still be the main cause.

The higher hatching success of clutch size 5 to 7 could account for the frequent occurrence (around 85%) of this clutch size. It was evident that they were favored by natural selection. Cooper (1978) found that clutch size had no influence on the ability of geese to heat their eggs adequately. If this is true in females with a rather large clutch, other factors may become critical in determining hatching success. There is usually a tradeoff that when the
clutch size increases the early laid eggs might have a greater chance of being broken by the female or frozen by low temperature if she chose to incubate after clutch completion, or run the risk of leaving eggs unhatched due to incomplete embryonic development if she chose to incubate eggs before the last eggs were laid.

The high hatching success (81.8%) of clutch size 7, its high frequency of occurrence (26.7%, next to clutch size 6), and the larger than average clutch size (5.98 at Killdeer) made the clutch size 7 the optimal size in terms of hatching success.

**Effect of Hatching Sequence on Gosling Survival**

Hatching sequence in nidicolous young is critical to their survival. Because a young hatched earlier gets fed earlier and develops earlier, it nearly always outgrows or outcompetes its smaller siblings that hatch later. As a consequence, it should have a higher survival rate than those that hatched later, especially when the food supply is critical. On the other hand, in nidifugous birds food seems not to be a limiting factor in terms of young survival. Results from this study demonstrated no advantage of hatching earlier. However, the earlier hatched goslings within a brood were more active than those hatched later. If the brood was attacked by a predator the earlier hatched goslings would probably have the edge over the later hatched goslings in escaping from the predator. However, most
broods stayed in nests for at least 24 h after hatching, and after such period the slight advantage of the earlier hatched goslings is probably no longer held.

Because hatching sequence was determined by the timing of female incubation. From the first appearance of down found in nests (Fig. 4), the negative association between nest attentiveness and clutch size was demonstrated in the study, i.e., females with larger clutches start to incubate eggs later than females with smaller clutches. As a consequence, the eggs laid late (last or second to last) were usually hatched last. No such relationship was found in clutch size 5 perhaps due to the egg hatching synchronization expected in many precocial species (Vince 1964, 1968).

From the above observation, again as suspected in the differential effect of laying sequence on hatching success between different clutch sizes, the effect of hatching sequence on gosling survival will probably exist among large clutches, but will not find in small clutches.

Effect of Mean Egg Weight on Gosling Survival

Young hatched from larger eggs have a higher survival rate than that of young hatched from smaller eggs, a finding in this and many other studies. However, most of the studies were of species that usually stayed in the nests and depended on their parents for food (Lundberg and Vaisanen 1979, Murton et al. 1974, Wisbet 1973). The relationship
between egg weight and survival of the young can be readily studied by regularly visiting the nests. The few studies found of nidifugous species were done with captive birds (Ankney 1980, Moss et al. 1981). This study demonstrated that in natural condition goslings hatched from larger eggs had the selective advantage over goslings hatched from smaller eggs. Kear (1965) suggested that mallard ducklings without food for the first 2 days depended on their body fat reserves. It is reasonable to suspect that the lipid content in goose eggs provides the energy source for goslings to survive during the first few days after hatching. Though the yolk weight decreased as the egg size increased (Table 3), the amount of lipid had no significantly proportional change in large eggs (Table 4). It is known that the metabolic rate of a homeotherm is negatively associated with its body size. Thus, a larger gosling normally from a larger egg would use proportionally less energy per unit time than a smaller gosling would use. With no significant difference in proportion of lipid content (Table 4) and a slower metabolic rate in a larger gosling, the advantage of a larger gosling to survive longer during unfavorable conditions during the early days after hatching is rather prominent.

Larger eggs had more energy content than did smaller eggs. Yet the underlying mechanism that caused differential survival of the young was unknown. Larger eggs might
produce larger young or young of the same size but in advanced developmental stage or with more energy reserve. Larger young might outcompete siblings of smaller size for food or have faster growth rate that enhances their survival. Or, being rich in energy reserves, larger young might have a better chance to survive under unfavorable conditions than those with lower energy reserves. Ricklefs et al. (1978) found that variation in water, lipid, and nonlipid dry matter of eggs in newly hatched chicks of laughing gulls and Japanese quail was related to variation in egg size. O'Connor (1975) found that large day 0 blue tit and house sparrow chicks had a faster growth rate during the first week as nestlings. He also found that larger chicks of European swifts hatched from larger eggs, and heavy chicks had significantly shorter nestling periods than light chicks. Studies of newly hatched gulls and Japanese quail showed that chicks hatched from the larger eggs were not only large in size but also differed in the size of certain organs or constituents (Parsons 1970, Ricklefs et al. 1978). Ankney (1980) reported that body weight and tarsus and culmen lengths of newly hatched goslings were positively correlated with the fresh egg weight in lesser snow geese. It is probably also true in Canada geese though no measurements were made in this study.

Goslings with larger body size hatched from larger eggs. The positive correlation between egg weight and
gosling hatching weight found in this study (Fig. 12) was also demonstrated in many nidicolous species (Howe 1976, 1978, Jones 1973, Schifferli 1973). The weight loss for the first few days after hatching found in this study was due to the facts that no feeding was observed and the yolk and body lipid reserve of the young was depleted during this period (Kear 1965, Marcstrom 1966). Positive correlation between egg size and gosling hatching weight was found in this study. However, the correlation between egg weight and body weight soon vanished between 3 and 4 weeks (Ankney 1980). Being grazers and living in an environment of abundant food, goslings did not compete for food, and growth rates did not favor large goslings. Thus the advantage of being a large gosling was probably not the ability to compete for food among siblings or the ability to grow faster and decrease the chance of being attacked by the predators, but was probably the greater energy reserves found in larger goslings. And such an advantage would probably last only for the first few days after hatching, when the young were dependent on the reserves (Kear 1965). Bellrose (1978) reported that most of the goslings that did not survive to adulthood died in their first week of life. Zicus (1981) found most Canada goose goslings died during the first 12 days after hatching. Findings in this study were similar that among all goslings found dead from hatching to roundup, about 1/3 of them died at the first week. It seemed that
even such an advantage was short-lived, yet biologically significant.

**Effect of Hatching Date on Gosling Survival**

In northern latitudes goslings hatched late had a distinctive disadvantage, because they did not have enough time to molt and gain flight and subsequently froze to death (Barry 1962, Cooch 1961). However, weather at Killdeer was rather mild, and weather alone was probably not the main driving force that caused a higher gosling mortality in the late hatches (25.4% higher). Newton and Kerbes (1974) reported that growth of young grass became evident in March/April at the Loch Druidibeg National Nature Reserve, Outer Hebrides, was greatest during May/June, less during July, and slight thereafter. They found on average the young greylag goslings from the first 24% of nests completed their growth within the best grass growth period, those from 74% continued growth well into July, and from 2% into August, when little fresh grass was available. A similar growing pattern of grass was found at Killdeer except the growing season was longer and there was usually some new growth available in the late season due to the regular mowing of the Wildlife Area. Still the early hatched goslings (late April-early May) would have the distinct advantage of having fresh, tender grass available for food in their growing period, whereas those goslings hatched very late in the season (late May) might have less favorable food
in part of their growing period. Again the difference of the quality of grass and its impact on the differential survival of the early and late hatched goslings was unknown. If quality of grass did have some impact on gosling growth and survival, its influence probably wouldn't be enough to cause the differential mortality observed between early and late hatches. The differential survival rate between early (92.6%) and late hatches (67.2%) could be explained by the possible age difference between early and late nesters, because older geese nested earlier (Brakhage 1965) and raised larger broods than did younger geese (Raveling 1981). However, no such relationship was found at Killdeer.

The association between aggressiveness of breeding pairs and time of nest initiation, though not quantified, could be a possible cause for the higher success of early nesters. Strong territorial strife was observed between some tub nesting pairs in this study. Pairs that started to nest in a tub 20 m from another nesting tub were attacked and chased away by the gander of the nesting tub and the defeated pair was found a week later nesting 100 m away from the tub they intended to use. Thus, parents with high aggressiveness toward intruders might nest earlier and their aggressiveness might be applied more effectively to defending predators that may attack their goslings at the brooding ground than less aggressive pairs that nested later and defended predators less effectively.
Effect of Brood Size on Gosling Survival

In nidifugous young such as goslings that find their own food, and food is generally readily available, brood size probably makes little difference in terms of survival of the young, as was found in this study. Since the brood size used in the analysis was the size right after hatching, and the estimation of survival was conducted later in the roundup, there could be some difference between brood size and gosling survival that changes through time that was undetected. Large broods, like large clutches, might draw more attention from their parents and be defended more vigorously by the parents when the broods are attacked by predators. They might also be more likely to escape the attack from predators due to the confusion created by the large brood when the brood broke suddenly. On the other hand, small broods might be easy to control by the parents and lesser conspicuous to predators thus provide less chance for predators to attack. The subtle change through time, i.e., the larger brood suffered a higher mortality in the early period after hatching and had a higher survival at the later stage, could mask the effect of brood size on gosling survival. Some further studies are needed to see if this is true.

Comments on Nesting Activities Related to Goose Fitness

The fitness of a goose is defined as the number of goslings produced by a female that reach fledging stage and
survive until sexual maturity to reproduce. For geese, big, long-lived birds, natural enemies that could kill their goslings after those goslings reach fledging stage are very rare. Thus in this discussion, I will restrict the meaning of fitness of geese to the number of goslings produced by a breeding female that reach fledging stage. The number of fledged goslings produced by a female is determined by clutch size, hatching success, and gosling survival. The clutch size that determines the potential number of goslings produced should be one of the most important factors in determining goose fitness. Goose should be favored by natural selection for the number of egg she could produce up to a point that further increase of production would cause a proportionally higher tolls than usual on hatching success and gosling survival resulting from incapable of adequate incubation or depletion of its energy reserve resulting in nest desertion. In this study, clutch size 7, which produced 5.73 goslings (clutch size * hatching success = 7*81.8%), was most successful and followed by clutch size 8 with 5.37 goslings per nest (8*67.1%) among all the other clutches (<5.37). If this is true, the next question will be how much energy a female should invest for each egg laid. If a small change of egg weight has a distinctive effect on hatching success and gosling survival, would a smaller clutch with larger eggs have more advantage than a larger clutch with smaller eggs? In this study, egg weight
affected both hatching success and gosling survival. While the mechanism by which the 3-g difference in egg weight affected hatching success was not clear, it did show the importance of egg weight on hatching success. On the other hand, the 4-g difference in egg weight that affected gosling survival could be attributed to the 9-Kcal difference calculated from eggs that produced live (298.5 Kcal $\pm$ 19.2 SD, N=170) and dead goslings (289.3 Kcal $\pm$ 26.3, N=227). Though the difference is small, it might help those goslings with this edge to overcome the unfavorable conditions during very early life.

The exact upper limit of egg weight in terms of survival advantage was hard to study and not determined. However, goslings hatched from eggs more than 10 g above average weight had a similar survival rate to goslings hatched from eggs up to 10 g above average weight; this demonstrated that 10 g above average weight was probably the upper limit for weight selection. It seems that females should invest their energy in the eggs that are no more than 10 g above average weight. The mean egg weight in clutch size 7 (165.8 g) was found to be the highest among all clutches (Fig. 11). This and previous findings showed that clutch size 7 size is favored by natural selection on both clutch size and egg weight.

Besides clutch size and egg weight, laying date which subsequently determined the hatching date was important to
hatching success and gosling survival. The 4% difference in hatching success between the early and late nests was less important than the 25% difference in gosling survival between those early and late nests. On the other hand, the effect of laying and hatching sequence on hatching success and survival was insignificant, because only few early and late laid or hatched eggs were found dead in large clutches.

Finally, females with breeding experiences improving hatching success by 20% and gosling survival by 14% (Table 5), were probably the most important factor in determining goose fitness. Other related factors such as body condition of females, behavior, and genetics of parental birds could be also very important to goose fitness but were not studied.

PREDATION

The low nest predation (4%) in comparison with other studies (Klopman 1958, MacInnes et al. 1974) was probably due to the fact that the majority of geese nested on elevated tub structures which discouraged predators such as foxes with no climbing skill from preying on eggs. Furthermore, by applying "tangle foot" grease to the posts that support nest structures, subsequently preventing raccoons, the major egg predators, from climbing to the nest structures, their predation on eggs was probably reduced a great deal. In fact, those nests destroyed by raccoons were either ground nests or tub nests with little
or no grease.

No real quantitative studies of predators feeding on goslings or ducklings could be found. However, many authors attributed predation as the major factor to gosling mortality (Brakhage 1965, Mickelson 1975, Newton and Kerbes 1974).

Comments on Predation on Goose Production at Killdeer

Survival rate calculated from roundup captures was rather low. About half of the total hatched goslings (43-60%) disappeared before roundup, presumably from predation. However, the survival rate calculated from roundup efficiency (62.0-84.1%) was much higher than that from roundup captures. From that calculated mortality, even if I assumed all gosling deaths were from predation, i.e., predation=mortality, the estimated gosling loss due to predation was no more than 20-38% which is not unusual in the natural environment (62.5% of gosling survival from Zicus 1981, 64-80% from Brakhage 1965). Thus, predation at Killdeer probably is not as important as thought to be.

Methods Used and Techniques Related to Estimating Survival

Tagging and Tag Loss

Warhurst (1974) found that patagial wing tags were near perfect for tagging goslings. Very few of his tagged goslings lost their tags. However, in this study the massive loss of patagial wing tags from the goslings in 1979
was mainly due to the inexperience of the tagger. Because the knobby rivets used to attach the streamers were put on the leading edge of the patagium (away from bones), it was easy for goslings to peck them out. Scars on the wings of a few goslings could still be seen during roundup. The vast improvement in the second year (<25% loss in the tagged population) was due to the placement of knobby rivets at the center of the patagium (equal distance from outer edge of skin and bones). Because I still had a great tag loss in the second year and a few birds that had their knobby rivets on their central inner patagium had both wing tags intact and normally developed wings, I decided to place knobby rivets on the central inner patagium (near bones) of gosling wings at the third year. This resulted in a low tag loss (1.7%).

Roundup and Roundup Efficiency

The roundup efficiency estimated from the neck-collared breeding females tended to be biased, because there was a possibility for any of the marked females to leave the Wildlife Area before roundup. As a consequence they would have been missed regardless of roundup efficiency, resulting in a smaller sample size in calculating the roundup efficiency. As the sample size decreased, the reliability of estimating roundup efficiency decreased. The sample size decreased from 42 females in 1981 to 19 in 1979, and the 95% confidence interval increased from 14.7% in 1981 to 24.3% in
Another method of estimating roundup efficiency, by comparing the numbers of goslings having both patagial wing tags and neck collars with goslings having only patagial wing tags during post-roundup observation, tended to be an overestimation. Because birds with neck collars were easier to spot from a distance than birds with patagial wing tags (which were probably covered by wings when goslings were nearly full grown after roundup), a higher proportion of neck-collared goslings with patagial wing tags and a lower proportion of goslings marked only with wing tags probably would be spotted by an observer. Both methods had some bias: the first method used breeding females to estimate roundup efficiency and the second method used goslings to estimate roundup efficiency. One tended to underestimate and another overestimate the efficiency. Thus, the true value of roundup efficiency probably lay between 70 and 95% in 1980.

**Estimating Gosling Survival**

Many methods have been used to estimate gosling survival. Williams and Marshall (1938) estimated gosling mortality by recording the frequency of brood size encountered each day to calculate the rate of change of brood size through time. A similar technique was used by Nickelson (1975), who observed the gosling size changes of different broods and calculated the brood size change as
gosling mortality. He found the brood size decreased 12.9% (from 4.2 to 3.7) from hatching to F-stage in cackling geese (*Branta canadensis minima*). Hanson and Eberhardt (1971) found that gosling survival from hatching to about 3 weeks old was 86% by counting the change of brood size. Because the brood mixing phenomenon was fairly common in many studies, there was a bias that tended to underestimate the gosling mortality; some broods gained size and some broods lost all their goslings to other broods that were unnoticed. MacInnes et al. (1974) observed brood size change of neckbanded females to obtain specific information on size change in each brood. They found that the survival of goslings from 6 days before hatching to approximately 7 days after hatching ranged from 64.7 to 87.3%, and from 7 days up to 35 days it ranged from 91.9 to 99.3%. Zicus (1981) also used marked pairs to study the change of brood size at Crex Meadows, Wisconsin, and reported that the overall gosling survival rate was 62.5%.

Gosling survival was determined in other studies by comparing total goslings hatched with the goslings surviving to a certain time. The gosling survival estimated by such method ranged from 16 to 78% in Michigan (Sherwood 1966) and from 64 to 80% in Missouri (Brakhage 1965). Besides total visual count of goslings, Geis (1956) used some marked broods to correct her direct count in Montana, and found gosling survival varied between 80 and 84%. However, the
method of direct count might result in underestimation of gosling survival unless all the goslings in the study area were accurately counted or captured.

In this study the estimated gosling survival rate (62.0-84.1%) was comparable to that of other studies. The 2 methods, one using all goslings (first approach) and another using tagged goslings (second approach) to estimate gosling survival, yielded the same results. However, each of the approaches has some advantages over the other. The first approach needs fewer assumptions. The only requirement is that the figures of the total hatches and total catches be accurate. In goose management areas with tub structures, such as Killdeer Plains State Wildlife Area, where geese are accustomed to tub structures and those structures are easy to locate, the accurate estimation of the total hatches seems beyond doubt. The total catch will present a problem if no roundup efficiency is estimated. The second approach requires that goslings be tagged, which is time consuming, and the assumption that the tag loss is negligible. Otherwise, the tag loss should be estimated to compensate for the actual loss. Again, the roundup efficiency of tagged birds needs to be estimated. However, the advantage of this approach is that one does not need to know the exact number of goslings hatched.

The 2 different roundup efficiencies estimated in 1980 resulted in 2 different estimates of survival rate that
The real survival rate, I suspect, probably fell between 62.0 and 84.1%.

No attempt was made to compare estimates of gosling survival from total count and count of brood size change in this study. However, with the marked pairs one could follow the fate of individual broods to estimate gosling survival and thus decrease the bias of the possible brood-mix. Furthermore, if broods are individually tagged in addition to marked pairs and tag loss is negligible, one could probably achieve the perfection of estimation of survival in a large area.

Comments on Methods in Estimating Survival

The use of roundup efficiency to estimate gosling survival would certainly improve the accuracy of survival estimation. However, how much the improvement could be depends on how isolated the management area is. The more isolated the area, the less immigration and emigration would be. As a consequence, a more accurate roundup efficiency could be obtained due to the lower effect of movement to or from the area on population composition. Furthermore, the estimation is affected by the techniques chosen. The 2 techniques used in this study to estimate roundup efficiency from marked breeding females or double marked goslings are both deficient in some aspects. An increase in the number of marked birds will produce a higher reliability of both estimates. The double marking of goslings is a direct
method to estimate the roundup efficiency of goslings. Besides placing neck collars on goslings during roundup, the patagial wing tags need to be placed on goslings before they leave the nest. Patagial wing tags are very durable if attached properly and are easily spotted by observers when goslings are not fully fledged. Furthermore, no prominent adverse effect was observed on tagged birds during the study period. However, placing such tags on goslings is time consuming and requires extra attention to avoid separating goslings from their parents. Due to the enormous time involved, it is not applicable to general goose management practices except when detailed information on individual goslings is needed in addition to roundup efficiency.

The marking of breeding females is an indirect method to estimate roundup efficiency of goslings. The technique requires adult females to be neck collared. The tag is easily observed at any stage of life and tagging is less time consuming when the birds are tagged during annual roundup. However, the accuracy depends on the degree of association between marked females and their broods. From the 26 neck-collared breeding females captured with tagged broods in 1981, only 3 marked females had no goslings. This could be either because all the goslings died among these 3 broods or because goslings were attached to other broods that were not caught in roundup. Furthermore none of the tagged broods (N=16) were caught during roundup without
their parents. Due to the small possibility (no more than 3 of 46) of brood mix at Killdeer, I concluded that marking breeding females for estimating gosling roundup efficiency is valid.

The low gosling production at Killdeer Plains in comparison to those on other Ohio goose production areas in fact might have been no lower than that of the other areas. Evidence from this study indicated that the method used by the Division of Wildlife to estimate gosling survival, based upon the number of goslings caught at roundup, with no calculation of roundup efficiency, could have produced the low production figures.

Recommendation for Management

In goose management, ways that could increase gosling production and techniques that could accurately obtain information needed for management plans are very important. The methods used for estimating roundup efficiency in this study could be readily applied to any goose management area where roundup is an annual routine. If brood mixing occurs frequently in the area, the direct double marking techniques probably should be applied. If brood mixing is not a problem, then the roundup efficiency could be easily estimated for the season to come by tagging adult females with neck collars. At Killdeer Plains State Wildlife Area, because brood mixing is not prevalent, I would recommend that marking females should be used as the method to
estimate roundup efficiency.

Factors associated with hatching success and gosling survival could be applied to increasing gosling production. Because the early laid eggs are often broken by females or cracked by freezing temperature and the late laid eggs are often left unhatched due to short of incubation time in large clutches (>7), it is feasible to take those early and late laid eggs and hatch them in incubator to increase hatching success under an intensive management plan. Furthermore, because older or experienced birds have higher breeding success, older birds (age obtained from leg banding information) could be marked with neck collars during roundup and hunters could be advised not to shoot collared birds. As a result, a higher proportion of older birds could be saved and possibly a better production could be achieved.
The study was conducted from March to July each year from 1979 to 1981 at Killdeer Plains State Wildlife Area, Harpster, Ohio, to study problems associated with low gosling production of giant Canada geese. Objectives of the study were: 1. to obtain background information on goose breeding and to study nesting activities that related to goose fitness, 2. to study predation on goslings, and 3. to study and evaluate the procedures of estimating gosling production.

In early March, before nest initiation, nest structures were checked on a regular basis from boat, on foot, or from a Bombardier. Eggs found in nests were numbered and weighed, and the length and breadth of the eggs were measured. First appearance of down found in nests was recorded. Nests were visited 2-3 times a day when the eggs were about to hatch. Artificial food colors were injected into the eggs during pipping to study hatching and laying sequence of individual eggs. Goslings hatched were weighed and marked with patagial wing tags. Adult females were also marked with neck collars. Observations of brood size changes from hatching to fledging were made after tagged goslings were released.

Gosling survival was estimated after they were caught during the early July roundup each year by either of the formulae:
\[ \text{SR} = \left( \frac{\text{TGC}}{\text{BE}} \right) / \text{TGH} \]

where \( \text{SR} \) = survival rate of goslings; \( \text{TGC} \) = total goslings captured during roundup; \( \text{BE} \) = roundup efficiency, which was estimated by the proportion of marked females captured during roundup and total marked females observed during incubation or by the proportion of remarked and marked goslings observed after roundup; and \( \text{TGH} \) = total goslings hatched, or:

\[ \text{SR} = \left( \frac{\left( \frac{\text{TTGC}}{\text{TE}} \right)}{\text{BE}} \right) / \text{TTGH} \]

where \( \text{TTGC} \) = total tagged goslings captured during roundup; \( \text{TE} \) = tagging efficiency, which was estimated by the proportion of tagged goslings caught during roundup and the proportion of tagged goslings after hatching; and \( \text{TTGH} \) = total tagged goslings at hatching.

Forty-seven eggs were collected and the components, yolk, albumen, and shell, were weighed with a balance to the nearest 0.001 g. Shell was oven-dried at 60 °C for 24 h and yolk and albumen were freeze-dried and weighed. The amount of protein in eggs was determined by Kjeldahl nitrogen determination (A.O.A.C. 1975) and the lipid content in yolk was estimated by chloroform extraction (Fogerty et al. 1971). Energy content of egg was calculated using the information that a gram of lipid yields 9.5 Kcal, protein 4.5 Kcal, and mixed carbohydrate 4.0 Kcal and a gross energy determination with a Parr adiabatic bomb calorimeter on dry yolk and albumen (n=4 each) was also performed.

From 1,975 eggs measured, the mean breadth was 59.2 mm.
1.7 (SD), the mean length was 85.8 ±3.3, and the calculated mean volume was 154.0 cm³ ±12.3. The mean egg weight estimated from the weight-volume regression (weight = 0.129 +1.063 volume) was 163.8 g ±13.1. The mean egg weight loss during a 28-day incubation was 12.5%. The timing of down appearance was related to the clutch size—the greater the clutch size, the later the down appeared. When laying period advanced, the mean egg weight of each clutch decreased (P<0.005). Egg weight changed with laying sequence in a certain pattern. Among 6-egg clutches (N=25), the first egg laid was usually smaller than the second one. The second egg was usually the largest and egg weight decreased from then on. Clutch size varied from 2 to 11 eggs. Clutch size 6 occurred most frequently (36.2%) followed by clutch size 7 (26.7%) and 5 (21.1%). There was a negative association between clutch size and laying date (P<0.005). Mean egg weight changed among different clutch sizes: as the clutch size increased from 3 to 5 the mean egg weight increased from 153.8 to 163.7 g (ANOVA, P<0.10). Though clutch size of 7 had the highest mean egg weight (165.8 g) among all clutches, there was no significant difference. The average incubation time was 28 days (26-33 days) for 24 successful nests. Use of tub nests by breeding pairs declined from 46.85% in 1979 to 26.22% in 1981. However, the number of ground nests found nearly doubled from 16 in 1979 to 29 in 1981. Nesting success was higher
in 1980 (77.86%) than in 1981 (62.70%). Egg production also decreased from 898 in 1979 to 656 in 1981. As a consequence, the number of goslings hatched was also reduced from 573 in 1979 to 366 in 1981. The causes of nest loss of the 123 unsuccessful nests studied were no incubation (30.89%), desertion (incubation began) (37.40%), nest failure (incubation carried out for normal time period) (13.01%), flooding (4.88%), predation (9.8%), and human disturbance (4.07%). The fate of 145 eggs that failed to hatch was as follows: 30.34% broken, 7.59% missing, 15.86% infertile, and 46.21% with a dead embryo.

Renesting at Killdeer was not important. The relationship between egg weight and gosling hatching weight was positively correlated (P<0.001, R² = 0.84, N = 55). The average gosling weight was 116.8 g. The weight loss of 30 goslings studied from hatching to the time of leaving the nest was positively correlated with the time span that a gosling stayed in the nest after hatching (P<0.001, R² = 0.87). The predicted weight loss of an average weight gosling was 2% of its body weight within the first 6 h after hatching and about 8% for the first day of life. The laying and hatching sequences were positively correlated (R² = 0.21, P<0.001). The last laid eggs in clutch sizes 6 and 7 were usually hatched last or second to the last (X² test, P<0.05), but the last laid eggs in clutch size 5 were not (P>0.10). Brood mixing at Killdeer was rare. The most
susceptible age on gosling survival was the first week (1/3 of total deaths) of life after hatching.

Females with previous breeding experience had a 20% higher hatching success and 14% higher gosling survival (P<0.10, X² test) than they did in their first year of breeding. In the 3-year study, 738 goslings were tagged with patagial markers. The overall loss of both tags in the 3 years was 22.4% (62.5% in 1979, 23.4% in 1980, and 1.7% in 1981). The estimated roundup efficiency was 56.3% ± 24.3 (95% confidence interval) in 1979, 70% ± 16.4 in 1980, and 61.9% ± 14.7 in 1981. The roundup efficiency estimated by mark-remarked technique was 95%. Within 3 years, 709 goslings were captured during roundup. The estimated gosling survival rate calculated from either formula was was 78.2% in 3 years (71.9% in 1979, 84.1% in 1980, and 79.9% in 1981). The gosling survival rate estimated from the roundup efficiency that derived from the mark-remark technique in 1980, was 62.0%. Mortality of goslings from predation was observed but not quantified.

The 3 major components, shell, yolk, and albumen, comprised 12.1%, 40.5%, and 47.4%, respectively, of the fresh egg weight. The protein and lipid contents were about equal (protein 12.0% and lipid 12.8%). Yolk weight reduced in proportion, albumen weight increased in proportion, and shell weight did not change in proportion as egg weight increased. However, the yolk lipid proportion did not
change as egg weight increased.

Clutch sizes 5, 6, and 7 were used in the multiple logistic regression analysis. As the mean egg weight increased hatching success increased (P<0.05). The reverse trend was true for laying date (P<0.001). There was also a significant positive relationship between clutch size and hatching success (P<0.01). Clutch size of 6 was used to analyze the effect of laying sequence on hatching success. The first laid eggs within clutches (N=23) had the lowest hatching success (52.2%), the fourth laid eggs had the highest hatching success (91.3%), and the remainder lay between 69.6 and 73.9%. Clutches with a higher mean egg weight had higher gosling survival (P<0.05) and goslings hatched from early nests had a higher survival rate (P<0.01). However, brood size had no significant effect on gosling survival, nor did hatching sequence (P>0.30).

The low gosling production at Killdeer Plains in comparison to those on other Ohio goose production areas in fact might have been no lower than that of the other areas. Evidence from this study indicated that the method used by the Division of Wildlife to estimate gosling survival, based upon the number of goslings caught at roundup, with no calculation of roundup efficiency, could have produced the low production figures. I recommend that marking adult females should be used as the method to estimate roundup efficiency at Killdeer Plains State Wildlife Area.


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