

**NESTING AND MIGRATION  
IN THE INTRODUCED CANADA GOOSE  
IN SWEDEN**

**Göran Sjöberg  
Umeå 1993**

Department of Animal Ecology  
University of Umeå  
S-90187 Umeå  
Sweden

**AKADEMISK AVHANDLING**

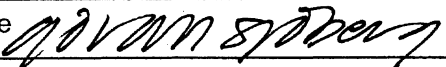
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Author	Göran Sjöberg		
Title	Nesting and migration in the introduced Canada goose in Sweden		
<p>Abstract</p> <p>The aim of the thesis was to document patterns in breeding and migration in Swedish Canada geese <i>Branta canadensis</i>, to explain these against the genetic and historical background of the population, and to test predictions of hypotheses pertaining to parental investment.</p> <p>The Canada goose population in Sweden was founded by the introduction of a few individuals in the 1930's. DNA fingerprint similarity between geese breeding in Sweden was on average at the same level as between inbred close relatives in other wild bird species. The genetic variability of the population appeared to be considerably reduced in comparison to that of Canada geese breeding in North America.</p> <p>Dispersal and migration patterns were studied using plastic neck-bands that could be identified at long distance. Most Canada goose females nested at the lake where they grew up. Males were more prone to disperse than females, although most of them still returned to breed close to their area of origin.</p> <p>Geese from three breeding areas in Sweden had different winter distributions, although wintering areas overlapped considerably. Individual geese tended to return to the same wintering area as they had used in previous years.</p> <p>The females' investment in the egg clutch was related to the migration distance from spring foraging areas to the nesting area, suggesting an energetic cost of migration for egg production. Within breeding seasons, clutch size decreased with later initiation of nesting, but only in years with early breeding. A probable reason for this decrease was that body reserves available for egg production were larger in early layers. In years with late breeding, clutch size did not decrease, most likely because late-nesting females could supplement their body reserves by foraging on fresh vegetation.</p> <p>Nest defence intensity was studied by recording the behaviour of the female geese when a human approached the nest. The results largely confirmed predictions for nest defence intensity extracted from parental investment theory.</p>			
<p>Key words</p> <p>Species introductions, DNA fingerprinting, natal dispersal, breeding dispersal, bird migration, wintering areas, clutch size, laying date, body reserves, nest defence, waterfowl, Canada goose, Anatidae, <i>Branta canadensis</i>.</p>			
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## Addendum

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*To my parents and my children*

O far far away  
in the far remote  
there is something nearby!  
Oh deep within me  
in the nearby  
there is something far remote  
something beyond-nearby  
on this side of the distant  
something neither nor  
in what is either or:  
neither cloud nor image  
neither image nor image  
neither cloud nor cloud  
neither neither nor nor  
but something else!  
The only existing  
is something else!  
The only existing  
in the existing  
is something else!  
The only existing  
in the existing  
is what in this  
is something else!

*From Absentia animi*  
G. Ekelöf 1945

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## List of papers

This thesis is a summary and discussion of the following papers, which will be referred to in the text by their Roman numerals:

- I. Tegelström, H. and Sjöberg, G. Introduced Swedish Canada geese (*Branta canadensis*) have low levels of genetic variation as revealed by DNA fingerprinting. - Submitted manuscript.
- II. Sjöberg, K. and Sjöberg, G. 1994. Natal and breeding dispersal in a migratory population of Canada geese in Sweden. - **Proceedings of the International Canada Goose Symposium 1991, Milwaukee**. In press.
- III. Sjöberg, G., Andersson, Å. and Sjöberg, K. Migration and wintering patterns in Swedish Canada geese. - Submitted manuscript.
- IV. Sjöberg, G. and Sjöberg, K. 1992. Geographical variation in reproductive investment in Canada Geese (*Branta canadensis*) in Sweden. - **Journal für Ornithologie** 133:403-412.
- V. Sjöberg, G. 1994. Early breeding leads to intra-seasonal clutch size decline in Canada geese. - **Ornis Scandinavica**. Accepted for publication.
- VI. Sjöberg, G. 1994. Factors affecting nest defence in female Canada geese *Branta canadensis*. - **Ibis** 136. In press.

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## Introduction

### Species introductions as large-scale experiments

On a long-term basis, changes of species distributions occur constantly. Thus, in four countries in northern Europe, the bird colonization rate was found to be 2.8 species and the loss rate 0.6 species per decade and country during the period 1850-1970 (Järvinen & Ulfstrand 1980). The great majority of the colonizing species were established spontaneously, often in natural environments (Järvinen & Ulfstrand 1980).

Even though animal and plant species continuously establish themselves spontaneously in new areas, man has had an overwhelming impact in affecting natural communities by more or less deliberate introductions. While beneficial to community ecologists by providing experiments that no scientist would have dared to suggest (Diamond & Case 1986), species introductions have contributed to a homogenization of the biosphere. In addition, introductions have been a threat, not only to individual species, but also to the persistence of entire ecological communities (Lodge 1993).

Many fields in ecology could gain much information from studies of species introductions. Thus, the study of species interactions in different kinds of communities, the study of the effect of different life history parameters for the survival and spread of populations, and the study of the stochastic processes affecting small populations, are all fields that have used species introductions as a source of knowledge (e.g. Zaret & Paine 1973, Stearns 1983, Moulton & Pimm 1986, Spencer *et al.* 1991).

### Evolution of reproductive investment

The idea of optimal trade-offs is basic for today's understanding of life-history variation. The number and size of offspring can be regarded as a result of physiological trade-offs under certain phylogenetic constraints (Stearns 1992). In iteroparous organisms as birds, a most important trade-off is the one between the investment in present and in future reproduction (Williams 1966). This trade-off includes a number of physiological and behavioural decisions - whether to produce gametes, whether to complete or suppress their development, how many offspring to produce, and whether to care for them oneself or not (Stearns 1992).

The costs of reproduction are manifested proximately in direct mortality or in negative effects on physiological condition of parents. Condition may, in its turn, influence parental survival and/or number or quality of future offspring. The decision of how great risk to take in the defence of offspring also depends on a trade-off between present and future reproduction (Montgomerie & Weatherhead 1988).

## Social transmission of behavioural traits

One area which has received only limited attention is the change of behavioral traits in introduced species. Some of these traits, e.g. bird song, display analogues in social transmission as described for genetical transmission, i. e. mutation, selection, and recombination (Baker & Jenkins 1987, Lynch *et al.* 1989).

In geese, the use of certain migration routes and wintering areas is socially transmitted (Owen 1980). Sometimes, changes occur in goose migration habits due to habitat changes, often induced by man's activities (Owen 1980, Syme 1989, Owen & Black 1991) or, alternatively, upon direct disturbance from hunting (Ebbinge 1991, Perco 1991). Migration route learning from foster-parents of other species has been made use of by managers for changing wintering areas of goose and swan populations (von Essen 1991, Baskin 1993).

The use of specific foraging areas during brood-rearing was transmitted socially between generations in barnacle geese (*Branta leucopsis*) (Larsson & Forslund 1992). The close resemblance in size between mothers and offspring was explained by Larsson & Forslund (1992) as a result of the exposure to a similar environment during growth.

## Aims of the thesis

The purpose of this thesis was to document patterns in breeding and migration in Swedish Canada geese (*Branta canadensis*), and to explain these against the genetic and historical background of the population. Some questions I set out to answer were: What are the genetical and ecological consequences of a limited number of founding individuals? Are recently developed migration and wintering patterns similar to those present since long time ago in other populations of the species? How is reproductive investment related to migration distance, and to between-year variation in breeding conditions? Finally, I wished to test the validity of hypotheses of parental investment on nest defence in Canada geese.

## The Canada goose

### Phylogenetic background

The genera *Branta* and *Anser* separated just prior to the speciation event producing the two species brant goose (*B. bernicla*) and Canada goose (*B. canadensis*), approximately 4 million years ago (Shields & Wilson 1988, Van Wagner & Baker 1990). Evidence from mitochondrial DNA suggests that the two main branches of Canada geese present today, large- and small-bodied, evolved about 1.2 million years ago (Shields & Wilson 1988, Van Wagner & Baker 1990). The present 9 or so subspecies of Canada geese are not older than 150 000 years (Shields & Wilson 1988, Van Wagner & Baker 1990). Electrophoretic analyses of proteins suggest that considerable nuclear genetic introgression has taken place between subspecies, presumably as a result of male-biased dispersal between breeding areas (Van Wagner & Baker 1986, 1990).

### General biology and present distribution

Together with swans, the true geese of the genera *Branta* and *Anser* form the tribe Anserini, morphologically distinct from other waterfowl by their large size, long necks and strong bills. In the Anserini, the sexes are alike in plumage, and few species are brightly coloured (Owen 1980). Both geese and swans are essentially monogamous with often life-long pair-bonds, and both parents stay with the young until the next breeding season (Owen 1980). Geese and swans are both mainly herbivorous, and they feed in shallow water or on land (Cramp *et al.* 1977)

The Canada geese vary considerably in size, habitat and life-history patterns. Female body mass at moulting varies between 1.2 and 4 kg, egg weight varies between 96 and 175 g, and clutch size between 4.2 and 5.3, between small and large subspecies (Owen 1980). Nevertheless, many characteristics are similar over the range of subspecies. The nests are most often placed on small islands (Bellrose 1978). The food is almost exclusively composed by plants, and in natural environments Canada geese feed mainly on leaves, seeds and tubers of monocots (Owen 1980).

The smaller subspecies breed in Alaska, western Greenland and the Canadian Arctic, and they winter in southern North America south to the Mexican coast. The natural breeding range of the larger subspecies is approximately from the Arctic Circle south to the central parts of the United States. The wintering areas of the large subspecies are mainly located within the United States (Bellrose 1978, Owen 1980).

The earliest records of Canada geese from Europe are from the park at Versailles, France, and from England, where they were held in parks in the 17th century (Cramp *et al.* 1977, Long 1981). Around 1930, the Canada goose was introduced to Sweden. After the establishment in two areas in southern and central Sweden, Canada geese were released at a large number of localities in this country, and later also in Norway and Finland (Heggberget 1991, Vikberg & Moilanen 1985). The wide distribution of the Canada goose in Sweden and the neighbouring countries is thus mainly due to intensive introductions (Madsen & Andersson 1990). The spontaneous expansion of the breeding range has been rather slow (Fabricius 1983 a). The taxonomic position of the Nordic Canada goose population is still unclear, but the body size is similar to that of the larger subspecies in North America (Cramp *et al.* 1977).

In addition to the populations in Britain and the Nordic countries, there are more or less free-ranging breeding populations in Belgium, Germany and Ukraina (Cramp *et al.* 1977, Madsen & Andersson 1990). The Canada goose has also been successfully introduced to New Zealand and reintroduced to areas in North America (Long 1981). Attempts to introduce the species to Western Australia and the Hawaiian islands were unsuccessful (Long 1981).

## Study areas

Four Canada goose breeding areas in Sweden were studied here (Fig. 1). In addition, blood samples were obtained from one breeding area in Ontario, Canada. The two main study areas, Härnösand and Kramfors, were located in the province of Ångermanland, on each side of a river mouth. These two areas were situated only approximately 20 km apart, and the data from these were sometimes pooled. The typical landscape there consists of bedrock ridges with mixed conifer forests, small agricultural fields, and oligotrophic lakes.

The third area, Öster-Malma, is situated in the province of Södermanland considerably further south. There, the landscape is somewhat similar to that of the two Ångermanland areas, although agricultural land is more abundant at Öster-Malma. The climate there is also more benign, with shorter winter season than in Ångermanland. In these three areas, nest surveys were performed during seven breeding seasons, and Canada geese were banded during six seasons.

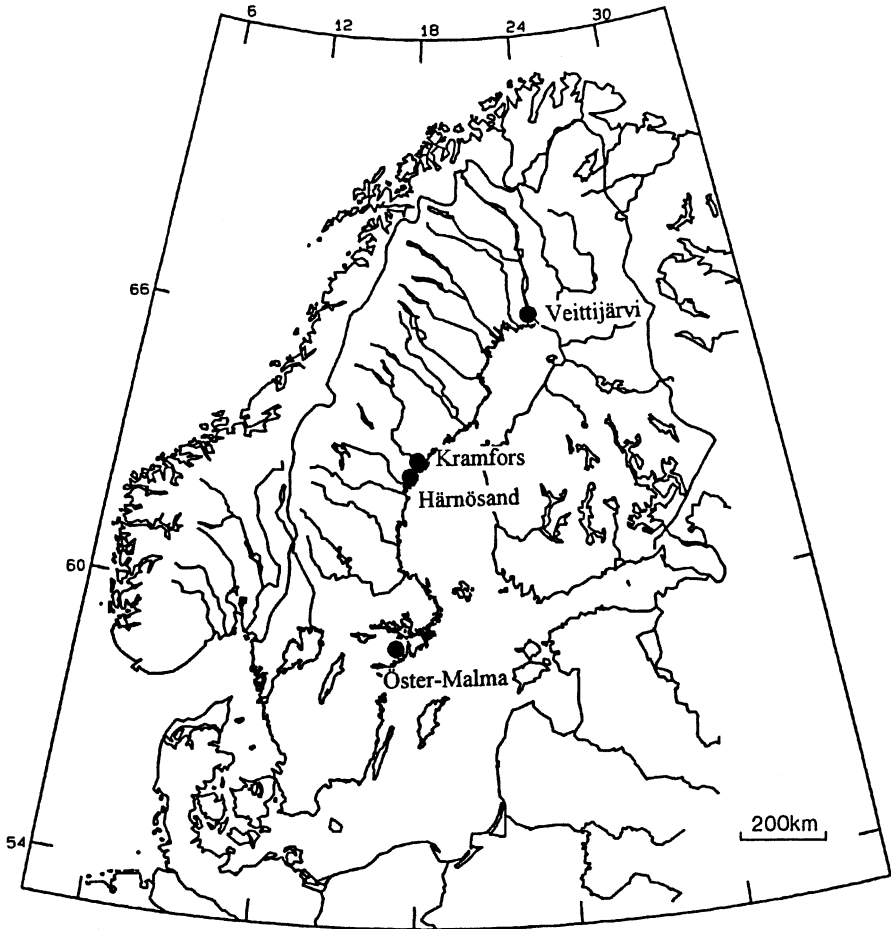


Figure 1. Breeding areas in Sweden where Canada geese were studied.

The fourth area is a small man-made lake, Veittijärvi, located in marshy pine forest in the province of Norrbotten, just south of the Arctic Circle in northern Sweden. Here, nest surveys were performed during eight years, but no banding was made.

Finally, a Canada goose population of different origin compared to the Swedish ones, in the Cambridge Highlands in southern Ontario, Canada, was used for collection of blood samples. In this area, Canada geese nested at ponds interspersed in an agricultural landscape with patches of deciduous forest (Seddon 1991).

The wintering areas of the Swedish Canada goose population are situated in areas around the southern Baltic (Timmerman *et al.* 1976). More specifically, the geese

banded in this study were mainly observed in the south-western part of the Swedish province of Scania, in the Danish islands of Mön and Lolland, and in Germany along the Baltic coast and at wetlands along the River Elbe. The geese generally roosted on the water (coast or river), and they were observed during daytime feeding in agricultural fields some kilometers inland.

During spring migration to breeding areas, Kramfors and Härnösand Canada geese were regularly observed to stop in feeding areas along the migration route, often for a week or more. Öster-Malma geese, on the other hand, returned to the breeding area early in spring without stopping at feeding areas along the route.

## General methods

The Canada geese were captured during July, when adults were moulting, and goslings were not yet fledged. The geese were herded from the water into a trap hidden in the shore vegetation. In addition, nesting birds could sometimes be taken by hand at the nest. Captured birds were weighed and measured. For identification of individuals, leg rings supplied by the Bird Banding Centre of the Swedish Museum of Natural History were used. Retrieved rings were received by the Centre which communicated all finding data. Neck-bands in blue plastic, with three-letter/digit codes engraved in white, were also used to facilitate identification at long distance.

Nest surveys were conducted with varying intensity between localities and years. In the two main study areas, Härnösand and Kramfors, nesting areas were generally visited several times each breeding season. The eggs were counted, measured, and individually marked with a pencil. They were also weighed in order to obtain an egg density index used for estimation of time remaining until hatching. The distance from the human visitor at which the incubating female left the nest was measured, and her subsequent behaviour was categorized.

When hatching time approached, eggs were scrutinized for gosling vocalization or signs of pipping. After hatching, broods were surveyed.

In 1989 and 1990, blood samples were collected from Canada geese in the Härnösand and Kramfors areas, and in 1990 from geese in the Ontario area. Blood samples were stored frozen in a citrate buffer. They were used for DNA fingerprinting, a genetic technique producing individually recognizable electrophoresis band patterns of DNA minisatellite fragments (Jeffreys *et al.* 1985 a,b, Burke 1989).

## Biology of an introduced species

### Effects of small founding populations (I)

The origin of the Swedish Canada goose population was five individuals introduced to two localities in the 1930's (Berg 1937, Heggberget 1991). Four of these birds were supplied by the Hagenbeck Zoo in Hamburg, and they were probably derived from the British population, founded in the 17th century (Fabricius 1983 a). One male was imported directly from North America (Berg 1937). The genetic basis of the Swedish Canada goose population is thus very narrow.

Isolated populations founded by small numbers of individuals are exposed to certain evolutionary forces. These forces include stochastic changes in gene frequencies, loss of alleles, increased levels of homozygosity and changes in genetic architecture (intra-genomic associations) (Berry *et al.* 1978, Berry 1986, 1992, Carson 1983, 1990). Rapid genetic change in combination with founding events can be the basis for what Berry (1986) called "instant subspeciation" (see also Johnston & Selander 1964, Baker & Moeed 1987).

The results of DNA fingerprinting for the Kramfors/Härnösand and the Ontario Canada geese indicate that the repeated founding events in the lineage of Swedish geese have severely depleted their genetic variability (I). The similarity between individual fingerprints of unrelated birds was approximately at the same level as that found between offspring in incestuous relationships in other bird species (Wetton *et al.* 1987). An increase in the level of homozygosity and a loss of alleles have most likely taken place in the European Canada geese. Introduced house sparrows (*Passer domesticus*) in Australia and New Zealand lacked alleles present in the British population, from which the founders had originated (Parkin & Cole 1985). Loss of genetic variability has led to a decrease in fertility as well as in disease resistance in many species (Allendorf & Leary 1986, O'Brien & Evermann 1988).

Nevertheless, Scandinavian Canada goose populations have shown to be viable and only few cases of what could be genetically caused deficiencies have been found (Madsen & Andersson 1990, Heggberget 1991). This should not be taken as evidence that waterfowl generally can increase and sustain population numbers from extremely small founding populations. Several waterfowl populations that have passed bottlenecks have not easily regained their former numbers despite intense managing efforts. The world population of the Laysan duck (*Anas laysanensis*) recovered after going through a bottleneck of about 10 individuals around 1910, and reached close to a number of 500 in 1979 (Moulton & Weller 1984). Survival of eggs and ducklings is still low, which could indicate inbreeding depression (Moulton & Weller 1984). The

wild population of the Hawaiian goose (*Branta sandvicensis*) was reduced to less than 30 individuals in the 1940s, then it increased to 1500 birds 30 years later after a release program, but then it decreased again to 350 individuals in 1990 (Owen & Black 1990).

As a result of the history of the population, the Canada geese released in Sweden were probably adapted to inbreeding as has been reported for certain mammal populations (Templeton 1987). During three centuries, the likely ancestors of Swedish Canada geese were held in small populations in parks in England (Parkin & McMeeking 1985), a condition likely to promote inbreeding. Previous adaptation to inbreeding can be an asset to species colonizing in small numbers (Gray 1986).

The original purpose for using DNA fingerprinting was to analyse parentage relations. This has been done successfully in many bird populations (e.g. Burke *et al.* 1989, Gyllensten *et al.* 1990, Gelter & Tegelström 1992). A prerequisite for the exclusion of potential parents is, however, that there is sufficient variation between individuals in fingerprint band patterns (cf. Faulkes *et al.* 1990). As this was not the case in the geese under study (Fig. 2), no maternity or paternity assignments were made from DNA fingerprints.

## Dispersal patterns (II)

Philopatry is pronounced in both sexes of Swedish Canada geese, although some male natal dispersal, i.e. between localities of birth and first breeding (Greenwood 1980), takes place (II, III). On the scale of local breeding areas, males showed greater natal dispersal than females. Thus, significantly more males than females dispersed from their lake of origin (II). Dispersing males were also found nesting at significantly longer distances from their lake of origin than dispersing females (II). A similar pattern was found in non-migratory Canada geese in England (Lessells 1985). Breeding dispersal, i.e. between consecutive breeding sites (Greenwood 1980), did not differ significantly between sexes neither within nor between breeding areas, for individuals changing mates in Swedish or English Canada geese (Lessells 1985).

Since the males of waterfowl generally disperse while the females show a stronger philopatry, this group differs from most other birds in their dispersal patterns (Greenwood 1980). Migratory Canada geese in North America have been considered to mate randomly within groups using the same wintering areas (MacInnes 1966, Van Wagner & Baker 1990). Consequently, dispersal between breeding areas should be strongly male-biased (Surrendi 1970). Such a male bias in natal and breeding dispersal has been best demonstrated in the lesser snow goose (*Anser caerulescens caerulescens*) (Cooke *et al.* 1975, Cooke & Sulzbach 1978).

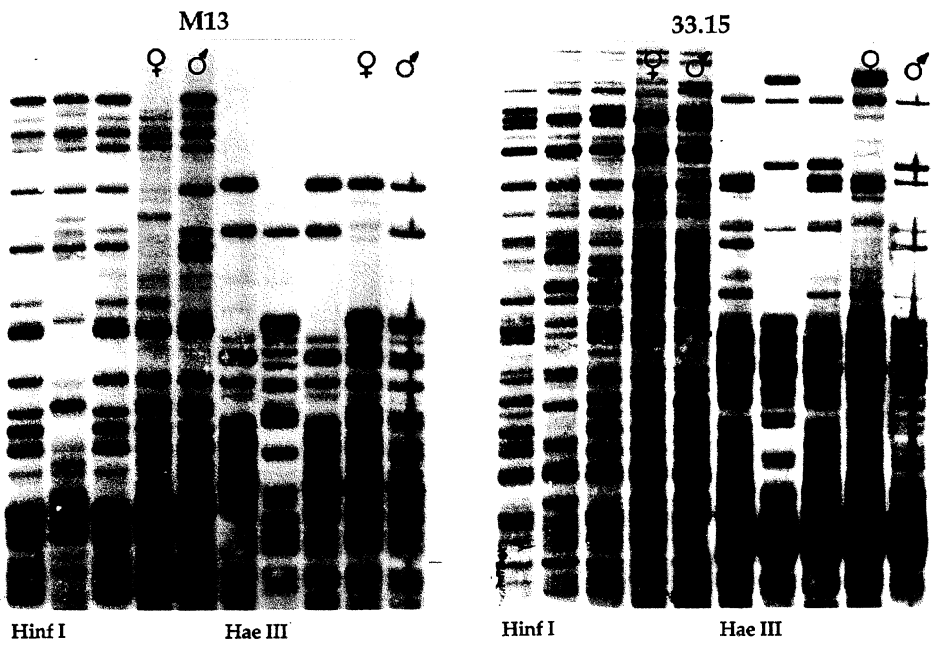


Figure 2. DNA fingerprints of a Swedish Canada goose family as revealed by two different probes (M13 and 33.15) hybridized to the same filter. DNA digested with restriction enzymes *Hinf* I and *Hae* III was run on the right and on left side, respectively. In each section, the DNA fragment patterns of the three offspring are shown to the left, and those of the parents to the right. Autoradiographs provided by H. Tegelström.

Dispersal has been suggested to result from selection against inbreeding in many mammals and birds (Greenwood *et al.* 1978, Hoogland 1982, Pusey 1987, Bollinger *et al.* 1993) and this may well be an important reason for male dispersal also in waterfowl (Ralls *et al.* 1986). If the ancestors of Swedish Canada geese were adapted to inbreeding by living in small isolated populations, then selection for male dispersal should be less intense compared to North American Canada geese. This scenario is consistent with the observed high frequency of mating within the breeding-area in the Härnösand and Kramfors Canada geese compared to that reported from North America (MacInnes 1966, Surrendi 1970).

### Social transmission of migration patterns (III)

The northern limit of wintering areas for Canada geese is set by the temperature (Lefebvre & Raveling 1967, Owen 1980), and in North European Canada geese these are situated close to the 0 °C isotherm (Timmerman *et al.* 1976). Within this constraint, the use of specific wintering and staging areas is largely learned by juvenile geese following adults during migration (Owen 1980). Changes in wintering areas of Canada geese populations may result both from a change in the winter habitat in individuals or from different mortality in parts of the population utilizing different areas (Hestbeck & Malecki 1989, Hestbeck *et al.* 1991).

Early in the history of Swedish Canada geese, southward winter migration occurred in cold winters, but no specific wintering areas were established (Fabricius 1983 b). As the size of local flocks increased in the beginning of the 1960's, migration took place annually, and migration distance increased until wintering areas were established at the Baltic and North Sea coasts (Fabricius 1983 a,b).

From the 1970's, the main wintering areas for migrating Swedish Canada geese have been located in southern Sweden, Denmark and northern Germany (Timmerman *et al.* 1976, Fabricius 1983 a, b, III). In severe winters Swedish Canada geese have been found also in the Netherlands (Timmerman *et al.* 1976, Fabricius 1983 a, b) and in England (Alerstam 1982). In some areas, however, especially in south-western Sweden, Canada geese have remained close to their breeding areas in winter (Nilsson 1976, Å. Andersson, pers. comm.).

The Kramfors, Härnösand, and Öster-Malma geese mainly used the same combination of wintering areas. The proportion of individuals using certain wintering grounds, however, differed between the three areas (III).

Individual geese generally remained faithful to their wintering areas. Still, the proportion of Öster-Malma geese that wintered in a specific area in Germany tended to increase during the study period. This could be a result of the lower hunting pressure in eastern Germany, as compared to southern Sweden, leading to higher survival rates for the groups of geese wintering in the German area.

During spring migration, Kramfors and Härnösand geese were observed at staging localities, many of which were visited repeatedly in different years. Very few observations were made of Kramfors and Härnösand geese during spring migration between the northern limit of autumn-sown wheat and barley and the breeding areas some 300 km northwards.

Öster-Malma geese were only occasionally observed along their migration route, but they ranged quite widely around their breeding area in spring. In this region of Sweden, there is abundant access to autumn-sown crops in spring. In the more

northern breeding areas, cereals are not sown in autumn, and furthermore, spring thaw is considerably later there. These differences with respect to food availability at the breeding areas should have important repercussions on the reproduction (Gauthier *et al.* 1992).

## Variation in clutch investment

### Geographical variation (IV)

In many species of waterfowl, stored reserves are important for reproduction (Alisauskas & Ankney 1992). Migrating Canada geese store large amounts of fat prior to leaving wintering areas or spring staging areas (Raveling 1979, Bromley & Jarvis 1993). During migration, a large part of the protein and fat previously accumulated by geese is consumed (Ebbinge 1989, Gauthier *et al.* 1992, Bromley & Jarvis 1993). If the female does not have substantial access to fresh vegetation, her body reserves remaining at arrival to the breeding area must suffice for both egg production and incubation. Egg production probably ceases when a lower threshold of body reserves is surpassed (Ankney & MacInnes 1978).

The Canada geese were recently established in all of the breeding areas studied. I therefore assumed that, unlike in North America, observed differences between breeding areas in clutch investment should be purely phenotypic and not reflect adaptations to different environmental conditions (cf. Dunn & MacInnes 1987). The body reserve threshold for cessation of egg production should not differ in a systematic way over the geographic gradient in Sweden. Many northern geese do not feed much in their breeding areas before egg-laying (e.g. Ankney & MacInnes 1978). Canada geese also face very poor feeding conditions in the Härnösand and Kramfors areas, at least during the early part of the egg-production period, and during this period breeding females spend only a small proportion of their time foraging (Åström 1993).

The egg volume per clutch was largest in the Öster-Malma area, and smallest in the Härnösand and Kramfors areas (IV). Clutch volume was thus related to the distance of migration between staging areas and breeding grounds. This result supports the hypothesis that body reserves determine clutch investment in the Canada geese studied. At Veittijärvi, the northernmost of the breeding areas studied, clutch volume was intermediate. Geese from this area, however, most likely migrate on the eastern side of the Gulf of Bothnia where autumn-sown cereals are available further north than on the western side. The choice of migration route is thus suggested to influence clutch volume through the position of the staging areas.

## Temporal variation (V)

In older Canada goose females in the Kramfors and Härnösand areas, the condition threshold for cessation of egg-laying appeared to be at a higher level compared to younger ones. Females also increased their clutch size between their first and second year of breeding. Older females thus accumulated more resources before breeding (cf. Aldrich & Raveling 1983).

The mean laying date differed significantly between years and also between individual females (V). Laying date differences between individuals could be the result of different individual tactics. Clutch size differed significantly between years in the pooled sample from Kramfors and Härnösand, but not in Veittijärvi. Clutch size and laying date in the Kramfors, Härnösand, and Veittijärvi areas were strongly negatively correlated within years with early laying, but not within years with late laying (V).

Partial consumption of body reserves during the delay between arrival and egg production could explain a seasonal clutch size decline (Ryder 1970, 1972, MacInnes & Dunn 1988). The mechanism behind the variation between years in seasonal decline is probably related to variation in the use of body reserves versus external resources for egg production. The year-to-year variation in the availability of vegetation for grazing should be crucial for which resource the females use for this purpose. In years with late breeding, there was a rapid plant growth in the end of the egg production period due to high temperature and long photoperiod. In late years, therefore, late nesting Swedish Canada geese could utilize fresh vegetation in the breeding area for egg production and thus compensate for loss of body reserves caused by a delay of breeding. Differences in resource use for egg production in waterfowl have been shown between populations and between individuals within years, as well as between years within populations (Krapu 1981, Mainguy & Thomas 1985, Bromley & Jarvis 1993, Young 1993).

Clutch size could also be influenced by costs of brood care. The investment in brood rearing is relatively small in waterfowl since the parents do not feed their young. However, both parents spend more time alert in large broods (Gautvik 1992). In Canada goose females with artificially enlarged brood size, weight at moult decreased, and the time of moult as well as next year's breeding was delayed (Lessells 1986).

## Nest defence intensity, a life history trade-off (VI)

Parental investment was defined by Trivers (1972) as "any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offspring".

The defence of offspring against predators is a case of parental investment. The intensity of offspring defence presents a trade-off between investment in present and future reproduction. This trade-off should be strongly influenced by the probability of survival to next reproduction in the parent and the offspring, respectively.

According to parental investment theory, the defence intensity should 1) increase with increasing effect of the parent's defence on the offspring's chance of surviving the attack, and 2) increase with increasing number and reproductive value of offspring, and 3) increase with decreasing residual reproductive value of the parent (Andersson *et al.* 1980, Wallin 1987, Redondo 1989, Wiacek 1992).

Specific predictions for nest defence in the Canada goose are listed in Table 1. These predictions were tested by studying the reactions to an approaching human in incubating goose females in the field (VI). Nest tenacity, a variable derived from leaving distance, and post-encounter behaviour were studied in Canada geese in the Kramfors and Härnösand areas.

Table 1. The result of testing predictions for nest defence [nest tenacity (NT) and post-encounter behaviour (PEB)] in Canada geese (VI). + = significant increase, 0 = no significant relationship, - = significant decrease.

Prediction for nest defence	NT	PEB
1. Increase with the female's age	0	+
2. Increase with the female's size	0	0
3. Increase with clutch size	+	0
4. Increase with earlier laying	0	-
5. Increase closer to hatching	+	0

Nest defence was found to increase with a) the female's age, b) clutch size, and c) proximity to hatching, as measured by either of the nest defence variables (Table 1). For one prediction (laying date) an opposite response to the prediction was obtained for post-encounter behaviour. In all other cases, no significant relationship was found. Both nest tenacity and post-encounter behaviour, however, always showed the same direction of response (VI).

Differences in nest defence between individuals were large, and they could not be fully explained by the variables included. The possible effects of nest location, distance to nearest neighbour, or nest site type were also studied but did not yield any additional explanation for variation in nest defence intensity.

### **Concluding remarks**

The fact that the Swedish Canada goose population was founded by a small group of individuals has had important consequences for its genetic configuration (I) and probably also influenced dispersal patterns (II). Effects of history on the development of migration were evident in the early phases after introduction, but migration routes and wintering areas of Swedish Canada geese have now been stabilized (III). Changes in wintering areas still occur, though, and may be the result of selection through hunting mortality on socially transmitted habits of wintering area use.

Swedish Canada geese, although genetically homogeneous, occur over a large range of breeding conditions, and with large variation in migration distance. Thus, Swedish geese offer interesting comparisons to the Canada geese in North America, where adaptations to local breeding conditions are expected to have occurred. The differences observed in clutch investment between areas as well as between years in Swedish Canada geese are believed to result from variation in the use of endogenous reserves vs. exogenous food resources (IV, V).

Few studies of nest defence in birds have been performed on long-lived species with nidifugous young. It is therefore of general interest to study whether predictions about nest defence intensity derived from parental investment theory are valid also for such birds. The results obtained for the Canada goose support the application of parental investment theory to nest defence intensity also in long-lived species (VI).

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