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A simulation model for the Greater Snow Goose population

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Abstract

The Greater Snow Goose population has recently undergone a rapid increase from 50 000 to more than 200 000. A mathematical model was developed to understand and simulate the growth of that population. Three parameters were used: the size of the population in spring, the percentage of juvenile geese in the fall flight, and the numbers of geese killed by hunters in the USA and Canada over the past 20 years. Those survey data were used to estimate a rate of non-hunting mortality as well as probabilities for rates of reproduction and hunting mortality. The stochastic discrete model reproduces well the recent history of the population and can be used to simulate scenarios for the future of the population. The model could be refined by developing and introducing other factors such as the carrying capacity of the range, annual variations in non-hunting mortality, and a function relating kill rates to population size and age structure. The model is available on diskette for interactive use on IBM PC microcomputers.

Introduction

The Greater Snow Goose (*Anser caerulescens atlanticus*) migrates between the northeastern Canadian Arctic and the mid-Atlantic coastal states of the United States and makes a major stopover on the St. Lawrence estuary near Quebec City. The history of the growth of the Greater Snow Goose population is noteworthy (*A Greater Snow Goose management plan* 1981). From 1860 to 1930, the population was barely maintained at a level of a few thousand. A year-round prohibition on hunting in the United States and an open season limited to the fall in Canada allowed the population to increase to 50 000 by 1967 and to more than 190 000 in the spring of 1978. Resumption of the hunt in the United States from 1975 seems to have slowed down the population increase.

The Snow Goose population is well suited to model simulations because of the tendency of Greater Snow Geese to gather in a limited area of the St. Lawrence estuary for several weeks each spring, thus permitting complete photographic censuses. Another characteristic of the species is the ease with which first-year juveniles can be distinguished from older birds in the fall; we can thus determine the percentage of juveniles among the total fall population and obtain an indication of reproductive success. These two parameters, spring population size and fall juvenile percentage, have been measured regularly for nearly two decades by the Canadian Wildlife Service (CWS) and the United States Fish and Wildlife Service (USFWS). A third parameter, the number of geese killed by sport hunters, has been estimated annually in Canada since 1967 and in the United States since 1975. We used these three parameters, which can be measured easily and relatively cheaply, to develop a stochastic discrete mathematical model to simulate the dynamics of the Greater Snow Goose population. Our aim was not to produce a sophisticated model, but rather to examine whether a simple, three-parameter model could accurately retrace or predict changes in a known population.

All three parameters, being established by survey, are subject to biases and errors. Although we discuss the possible sources of error for each type of survey, we have not undertaken the complex (perhaps impossible) task of establishing the magnitude of any such inaccuracies. Ultimately, the success or failure of the model to produce plausible results will provide information on the quality of the data.

The model is based on the change in the population from spring 1965 to spring 1984. The model's dependent variable is the spring population; random variables are the juvenile percentages and the Canadian and American hunting kill rates. An estimated rate of non-hunting mortality is also applied. The random variables are generated from probability distributions constructed from data published in *A Greater Snow Goose management plan* (1981) and Reed *et al.* (1981) and, for recent years, from unpublished CWS and USFWS data. By adjusting the non-hunting mortality rate and the random variables one can use the model to simulate population trends under various scenarios. The model is available as a program suitable for interactive use on an IBM PC microcomputer equipped with a graphics card and colour monitor.

Although a mathematical model does not generally have medium- or long-term predictive value (Levin 1984), it can help us to understand the data and identify features associated with population trends. We can thus anticipate the effects of actions that could modify these trends. The creation of models for animal populations is an iterative search for an approximate, realistic, and intelligible representation of a living entity that by its nature is too complex to be wholly described by a limited number of mathematical formulas.

Hunting of Greater Snow Geese has been a popular fall pastime in the St. Lawrence estuary since the seventeenth century.

Photo: A. Reed

Development of the model

1. Population surveys

Since 1950, aerial surveys have been conducted in midwinter on the wintering grounds in the US and, since 1965, in the spring and most falls in the St. Lawrence estuary (see Appendix 1). Aerial photography has been used to improve accuracy of flock counts since 1969 in the St. Lawrence (Heyland 1972; *A Greater Snow Goose management plan* 1981) and on the Atlantic coast since 1978. The spring census in the St. Lawrence since 1969 (Table 1) is the most accurate of the surveys because it involves almost complete photographic coverage at a time when the entire population is present within a relatively small, well-defined area. In early May a single flight is made over the staging area, and all flocks larger than 200–300 geese are photographed on 70 × 70-mm black and white film; for smaller flocks, visual estimates are made and a sample is photographed to establish correction factors (P. Dupuis, pers. commun.). The geese are counted directly from enlarged prints using a stereomicroscope, acetate overlay grids, and an automatic point counter. All geese are counted on each photograph, and the results are summed and added to the visual estimates for unphotographed flocks.

Up to 1980–81, few, if any, geese were missed on the spring survey because the areas used were well circumscribed. Since then, a longer stretch of the St. Lawrence has been used by the geese, and inland foraging flights have become more extensive. Those changes have increased the likelihood that some flocks were undetected, but this source of error is minor. Although it is not possible to quantify the accuracy of the survey, for all practical purpose it is a total count.

Before 1968, neither the US nor Quebec surveys benefited from aerial photography; we have used the more complete US winter data for 1964–68 (Appendix 1), along with the 1969–84 St. Lawrence spring counts, to construct a graph showing population growth (Fig. 1). The substantial increase between 1969 and 1978 is noteworthy.

2. Recruitment—percentage of juveniles

The goslings, born during summer in the Arctic, are grey when they take part in the fall migration. It is therefore possible to measure the percentage of juveniles in the population and thus estimate reproductive success (Lynch and Singleton 1964). However, several factors make it difficult to obtain an unbiased estimate of recruitment. First, the juvenile birds are not distributed uniformly within the population during fall migration. Some flocks are composed entirely of non-breeding adults (subadults and failed breeders), whereas others are groupings of individual families (containing juvenile birds and their parents) and still others contain a mixture of non-breeders and family units. There is considerable variation in the spatial distribution (habitats used, position within the flock) and temporal distribution (migration schedules, daily activity patterns) of family units in comparison with non-breeders (H. Boyd and A.R., personal observations). Second, juvenile geese, being more vulnerable, are shot at a greater rate than adult birds by hunters who are active throughout the fall survey period. Thus, the proportion of young birds in the population is decreasing while the

Table 1
Numbers of Greater Snow Geese counted in the St. Lawrence Valley, Quebec, during spring

Year	Number of geese
1969	68 800
1970	89 600
1971	123 300
1972	134 800
1973	143 000
1974	165 000
1975	153 800
1976	165 600
1977	160 000
1978	192 600
1979	170 100
1980	180 000
1981	170 800
1982	163 000
1983	185 000
1984	225 400

Table 2
Estimated percentages of juveniles in fall flights of Greater Snow Geese

Year	Canada	USA
1965	11.2*	2.8
1966	38.4*	37.0
1967	18.8*	12.4
1968	18.9*	12.5
1969	30.0	24.3
1970	45.6	46.8
1971	29.7	11.3
1972	0.0	0.4
1973	46.6	41.1
1974	6.4	2.0
1975	32.7	37.3
1976	12.6	9.8
1977	23.9	23.8
1978	20.1	14.7
1979	28.2	23.2
1980	40.1	36.4
1981	16.8	17.0
1982	25.1	23.8
1983	41.6	48.9
1984	37.6	27.4

*Value obtained by linear regression.

Figure 1
Greater Snow Goose spring populations, 1964–84

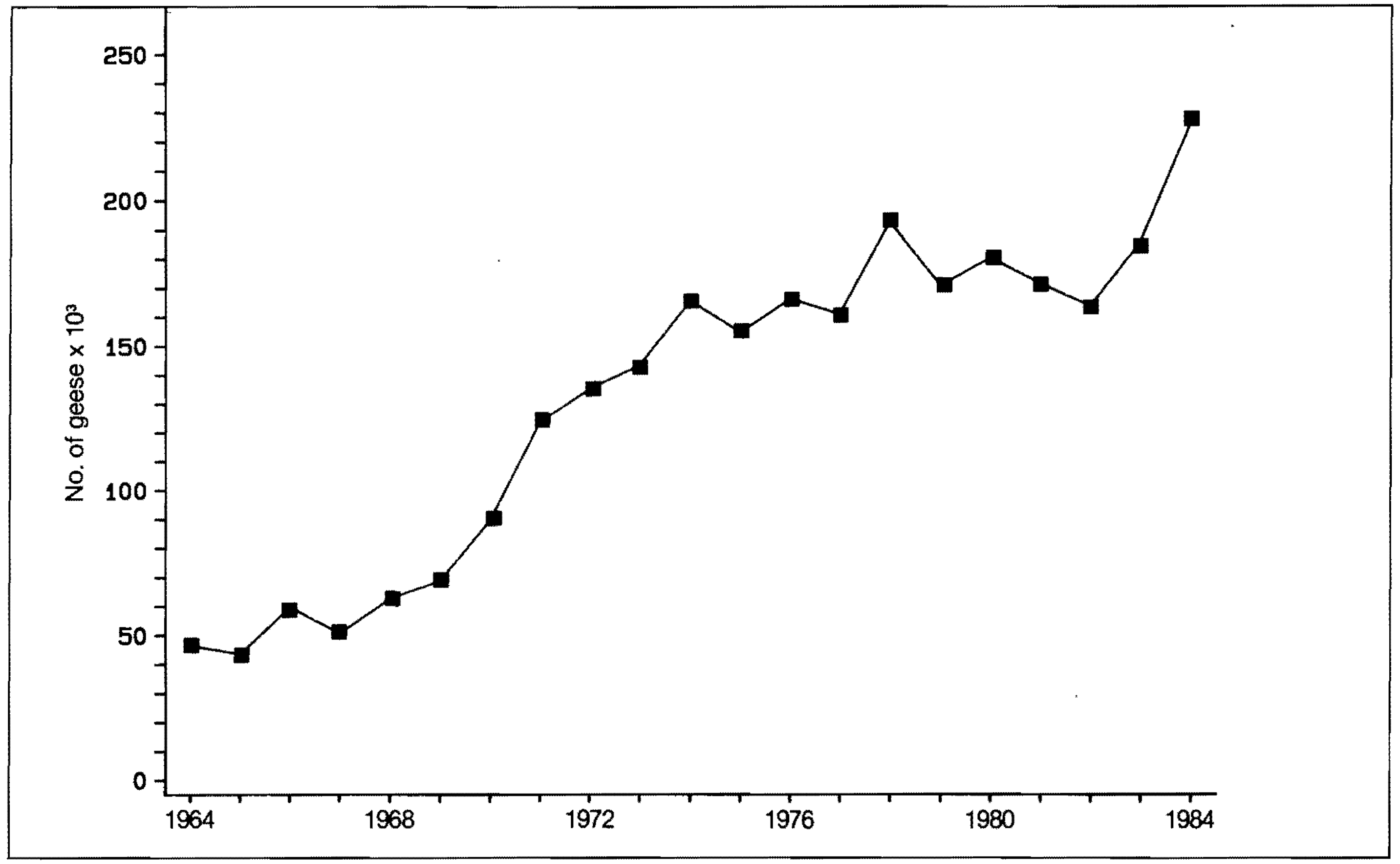
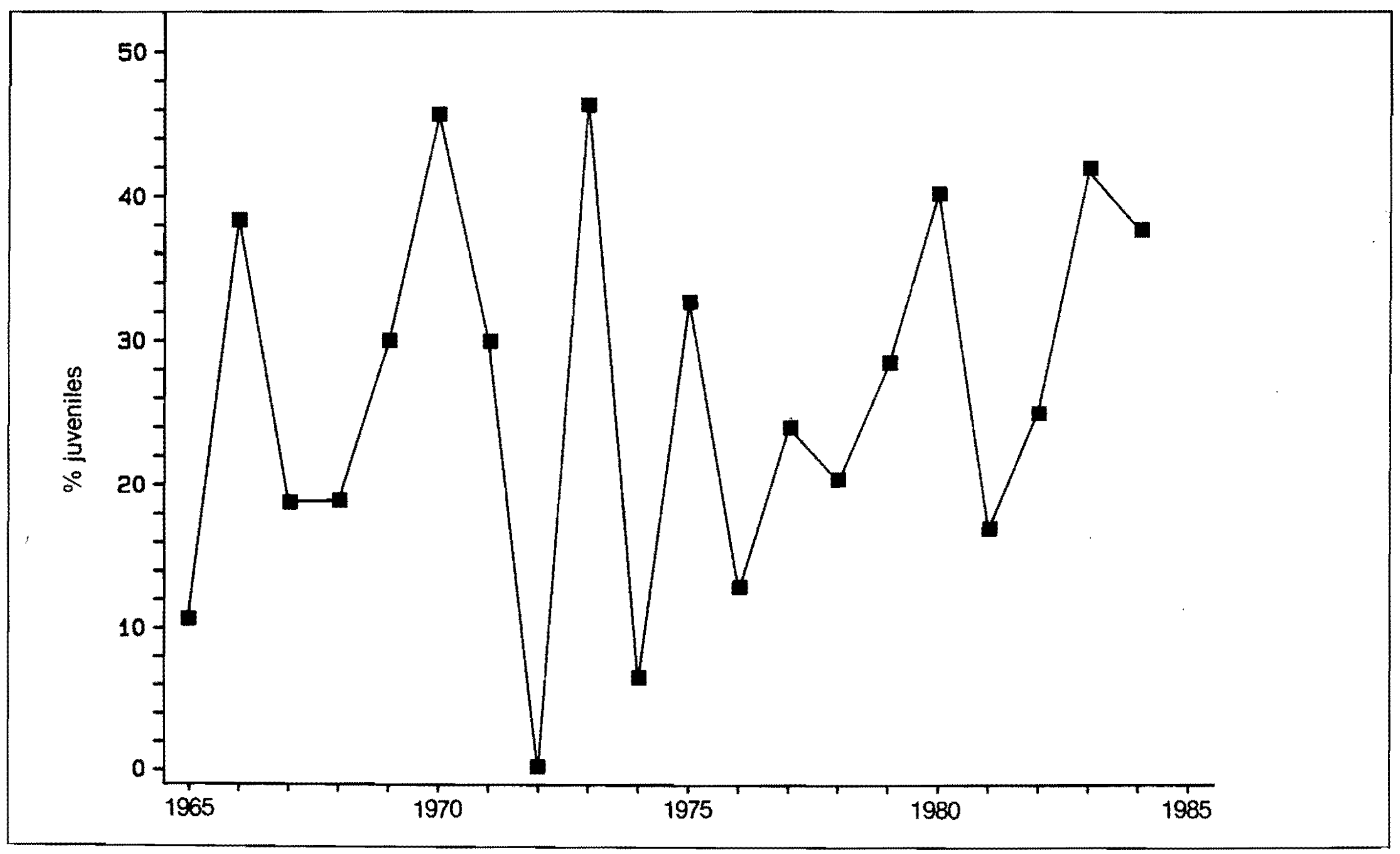


Figure 2
Percentages of juveniles in fall flights of Greater Snow Geese in Quebec



counts are being conducted. No satisfactory way of adjusting the data to account for the many sources of bias has been found. However, considerable effort has been made to reduce bias by collecting large samples distributed throughout the season, at different times of the day, and in all types of habitat.

The juvenile percentages recorded in the United States and Canada since 1965 are listed in Appendix 1. Two annual estimates of juvenile percentages are available for Quebec, one based on counts from aerial photographs, the other from ground counts. For modelling we have retained only the higher of the two annual Quebec values (Table 2) because the surveys appear to yield low estimates. The US values, generally derived from smaller samples, were used only to estimate values for the missing years 1965–68, from the linear regression:

$$\% \text{ juvenile Quebec} = 0.795\ (\% \text{ juvenile US}) + 8.95.$$

The Quebec values are plotted in Fig. 2, which shows that reproductive success fluctuates considerably from year to year and in an apparently random (in the mathematical sense) fashion.

3. Hunting kills

Hunting kills of Snow Geese are estimated annually in both countries in the course of national surveys designed for all migratory waterfowl species (see Boyd and Finney 1978). Greater Snow Goose kill areas are geographically restricted in both countries, which renders kill estimates less accurate than for other species that are hunted more widely. Some field biologists believe the national surveys overestimate the Greater Snow Goose kill (*A Greater Snow Goose management plan* 1981), but a special survey conducted in Quebec from 1978 to 1980 (Hyslop and Wendt 1982) suggested an underestimation. In earlier population modeling exercises (*A Greater Snow Goose management plan* 1981; Reed *et al.* 1981) it was judged that the national surveys provided acceptable estimates. For the sake of consistency we have taken the Canadian kill as that reported by the national survey for all Snow Geese (*Anser c. caerulescens, A. c. atlanticus*) in southern Quebec (zone 1) and the American kill as that of all Snow Geese for the Atlantic Flyway States (*A Greater Snow Goose management plan* 1981 and more recent CWS and USFWS unpublished data).

Table 3 gives estimates of hunting kills in Canada since 1967 and in the United States since resumption of the hunt in 1975. The total hunting kill has fluctuated considerably over the 18-year period, showing an increasing trend, especially since 1975. After a ban of more than 40 years, the US hunt was not great at the start, but built up rapidly as American hunters learned how and where to hunt Greater Snow Geese. American kill figures appear to be independent of juvenile percentages, perhaps because the young birds, having experienced the Canadian hunt, are less vulnerable to the gun when reaching the United States. The relationship between Canadian hunting kills and juvenile percentages is difficult to quantify, because the hunting kill is influenced by weather, the length of the flocks' stay, the birds' social behaviour, and other factors (Reed *et al.* 1981). In the absence of identifiable parameters that would help to explain the numbers of hunting kills, we assume in this study that hunting success is random.

Table 3
Estimated numbers of Greater Snow Geese killed by sport hunters in Canada and the USA

Year	Canada	USA	Total
1967	16 800	—	16 800
1968	2 700	—	2 700
1969	3 300	—	3 300
1970	25 300	—	25 300
1971	13 300	—	13 300
1972	6 100	—	6 100
1973	26 200	—	26 200
1974	9 000	—	9 000
1975	31 400	8 500	39 900
1976	25 100	12 300	37 400
1977	20 100	28 200	48 300
1978	41 200	21 600	62 800
1979	23 400	25 000	48 400
1980	54 400	27 300	81 700
1981	29 500	13 500	43 000
1982	40 700	21 700	62 400
1983	45 300	40 400	85 700

4. Annual population balance

Taking the spring population $P(k)$[1] as a reference and assuming a fixed mean annual natural survival rate m (i.e., accounting only for non-hunting mortality), we have developed the population balance chart shown in Fig. 3. The fall population can be written as:

$$PA(k) = \sqrt{m}P(k) + J(k)$$

where $J(k)$, the number of juveniles in the fall population, is calculated from the juvenile percentage $R(k)$ measured in the fall and $\sqrt{m}$ is the semi-annual survival rate, assumed to be the same in both halves of the year:

$$R(k) = \frac{100\,J(k)}{\sqrt{m}P(k) + J(k)}$$

from which we obtain the number of juveniles:

$$J(k) = \frac{R(k)\,\sqrt{m}P(k)}{100 - R(k)}$$

and then the fall population:

$$PA(k) = \frac{100\,\sqrt{m}P(k)}{100 - R(k)}$$

in terms of the juvenile percentage and the spring population. By subtracting Canadian and American hunting kills, $C(k)$ and $D(k)$, we obtain the US winter population:

$$PH(k) = \frac{100\,\sqrt{m}P(k)}{100 - R(k)} - C(k) - D(k)$$

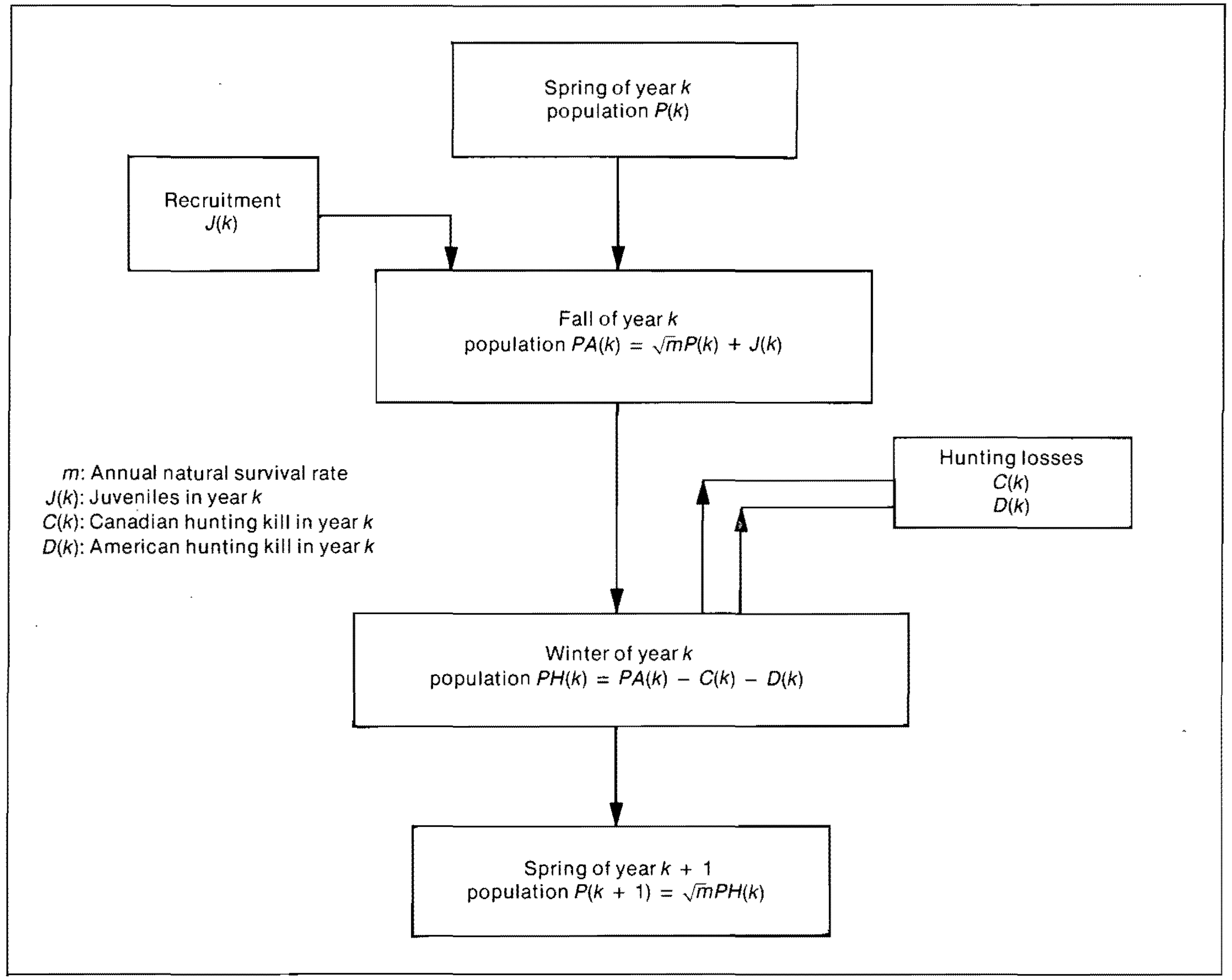
and finally the population for the following spring:

$$P(k + 1) = \frac{100\,mP(k)}{100 - R(k)} - \sqrt{m}\,[C(k) + D(k)] \qquad [1]$$

Formula [1] gives the population balance from one spring to the next taking into account reproduction, natural (non-hunting) mortality, and hunting kills.

[1] k designates the year: e.g., $P(k)$ = population, spring 1980; $PA(k)$ = population, autumn 1980; $PH(k)$ = population, winter 1980/81; $P(k + 1)$ = population, spring 1981

Figure 3
Annual population balance



5. Estimation of natural survival rate

The literature on Greater Snow Geese gives little information on individual longevity or the natural survival rate. The annual natural survival rate can be estimated by determining the value m that minimizes the sum of the standard deviations between the measured values for the spring population and those calculated using formula [1]:

$$\underset{m}{\text{minimize}} \sum_{k=1967}^{1980} \left[P(k+1) - \frac{100\, m^2\, P(k)}{100 - R(k)} + \sqrt{m}C(k) + \sqrt{m}D(k) \right]^2$$

where $P(k)$ is the spring populations from Table 1, $R(k)$ is the Canadian juvenile percentages from Table 2, and $C(k)$ and $D(k)$ are the Canadian and American hunting kills from Table 3. The problem is formulated only for the period starting in 1967, the first year for which hunting kill data are available. The minimization calculation, made using the SAS software PROC NLIN procedure, gives a result of $m = 0.895$ with a confidence interval of [0.812, 0.982]. This yields an annual mortality rate of 10.5%, with a confidence interval of [2.8%, 19.8%]. In an exceptionally detailed study involving resightings of individually marked Barnacle Geese (*Branta leucopsis*), on which there was no open hunting season, Owen (1982) estimated total annual mortality at 11.5% for adults and 16.8% for juveniles. Our estimate therefore seems plausible. Our large confidence intervals are not surprising in view of the imprecise nature of some of the raw data used in calculation of the mortality rate and the likelihood that the rate varies somewhat from year to year (Owen 1982). For the remainder of the study we assume that the population has a fixed annual survival coefficient of $m = 0.895$.

6. Correction of data

The population balance formula [1] can be used to detect anomalies in the data and make certain corrections. First, it is necessary to correct the spring population estimates for the years 1965–68, which are incompatible with the corresponding fall estimates. Because the American winter population estimates for the same years are consistent, the figures for the subsequent springs can be obtained by multiplying the US figures by the semi-annual survival coefficient $\sqrt{m} = 0.946$. This gives:

year k	spring population $P(k)$	hunting kills $C(k)$
1965	44 000	5 100
1966	41 000	20 100
1967	56 600	
1968	47 800	

where the hunting kills for 1965–66 are obtained by subtracting American from Canadian fall population values for the corresponding years.

Assuming that the spring population figures are fairly accurate, we must still verify the consistency of the juvenile percentages and hunting kills. Formula [1] can be used to calculate hunting kills from spring populations and juvenile percentages; this yields hunting kill figures that, in comparison with the established estimates, are doubtful. In particular, a number of negative values are obtained, suggesting that some juvenile percentages have been underestimated. On the other hand, using the same formula to calculate juvenile percentages from the other parameters, we obtain values that are fairly consistent with the observations from Quebec that were sometimes based on small fall samples. The observed (Table 2) and adjusted (Table 4) juvenile percentages are plotted in Fig. 4. The two chronological series are similar in appearance and, except for 1968, vary only in magnitude. The adjusted juvenile percentages $R(k)$ can be used to estimate the fall population in Canada with the formula:

$$PA(k) = \frac{100\,\sqrt{m}P(k)}{100 - R(k)} \qquad [2]$$

where $P(k)$ represents the spring populations. The estimated populations with those for the preceding springs are plotted in Fig. 5. The spring population net growth rates, calculated using the formula:

$$100\,[P(k+1) - P(k)]/P(k)$$

are plotted in Fig. 6.

Table 4
Hunting rates for Greater Snow Geese and adjusted juvenile percentages

	Hunting rates (% of fall population)			Adjusted juvenile percentage
Year k	Canada $S(k)$	USA $T(k)$	total	$R(k)$
1965	10.5	—	10.5	14.2
1966	25.2	—	25.2	51.4
1967	24.9	—	24.9	20.5
1968	3.6	—	3.6	40.0
1969	3.4	—	3.4	33.6
1970	16.3	—	16.3	45.5
1971	8.5	—	8.5	25.2
1972	3.9	—	3.9	18.9
1973	13.1	—	13.1	32.6
1974	5.2	—	5.2	9.0
1975	14.6	4.6	19.2	32.3
1976	12.2	6.8	19.0	24.1
1977	8.0	12.2	20.2	39.9
1978	17.0	10.7	27.7	24.9
1979	9.8	11.6	21.4	32.6
1980	20.7	13.1	33.8	35.1
1981	13.7	7.3	21.0	24.9
1982	15.8	10.0	25.8	40.2
1983	13.8	15.3	29.1	46.4
1984	—	—	—	37.6

Figure 4
Juvenile percentages of Greater Snow Geese, observed and adjusted

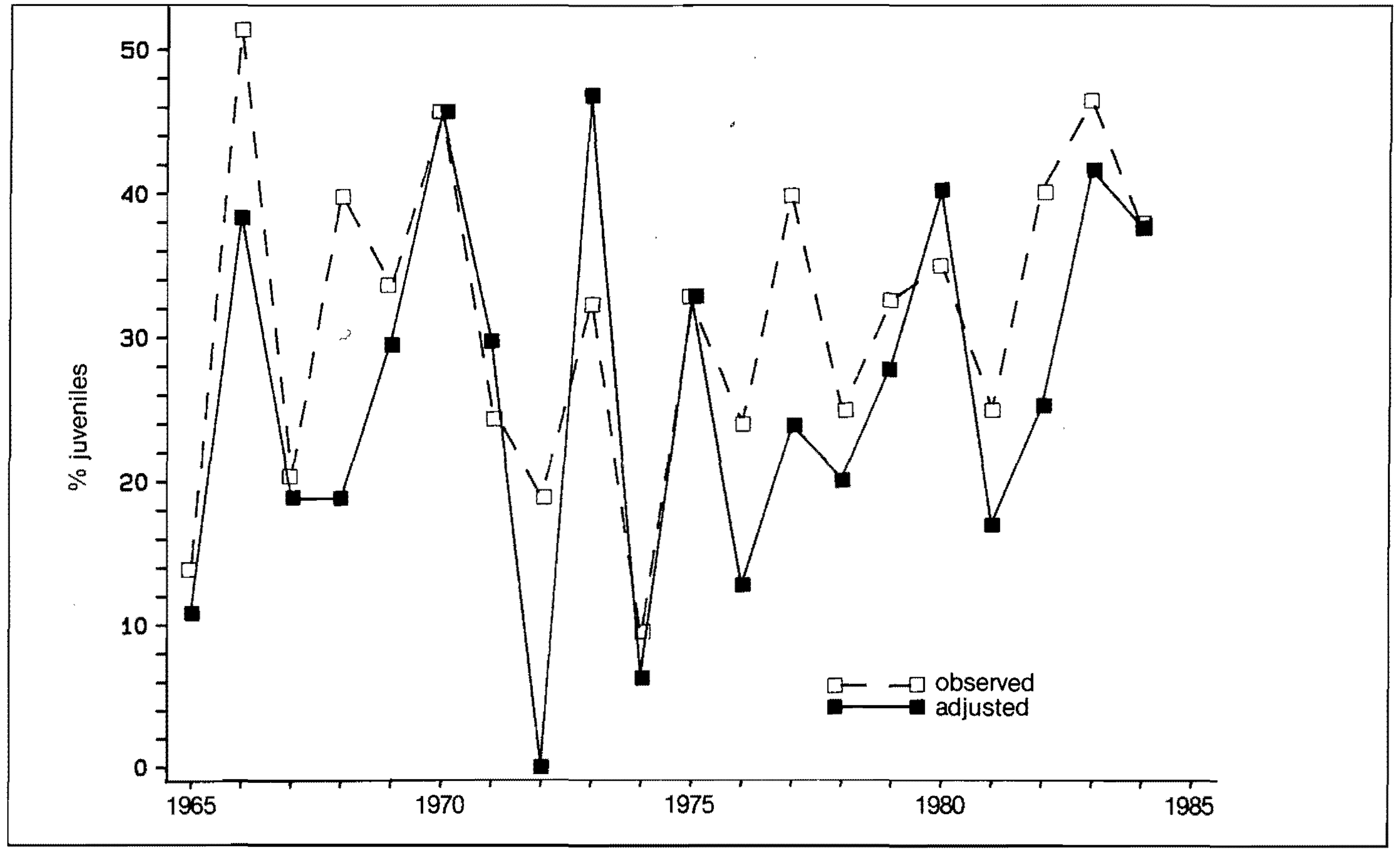


Figure 5
Adjusted estimates of Greater Snow Goose populations during spring and fall

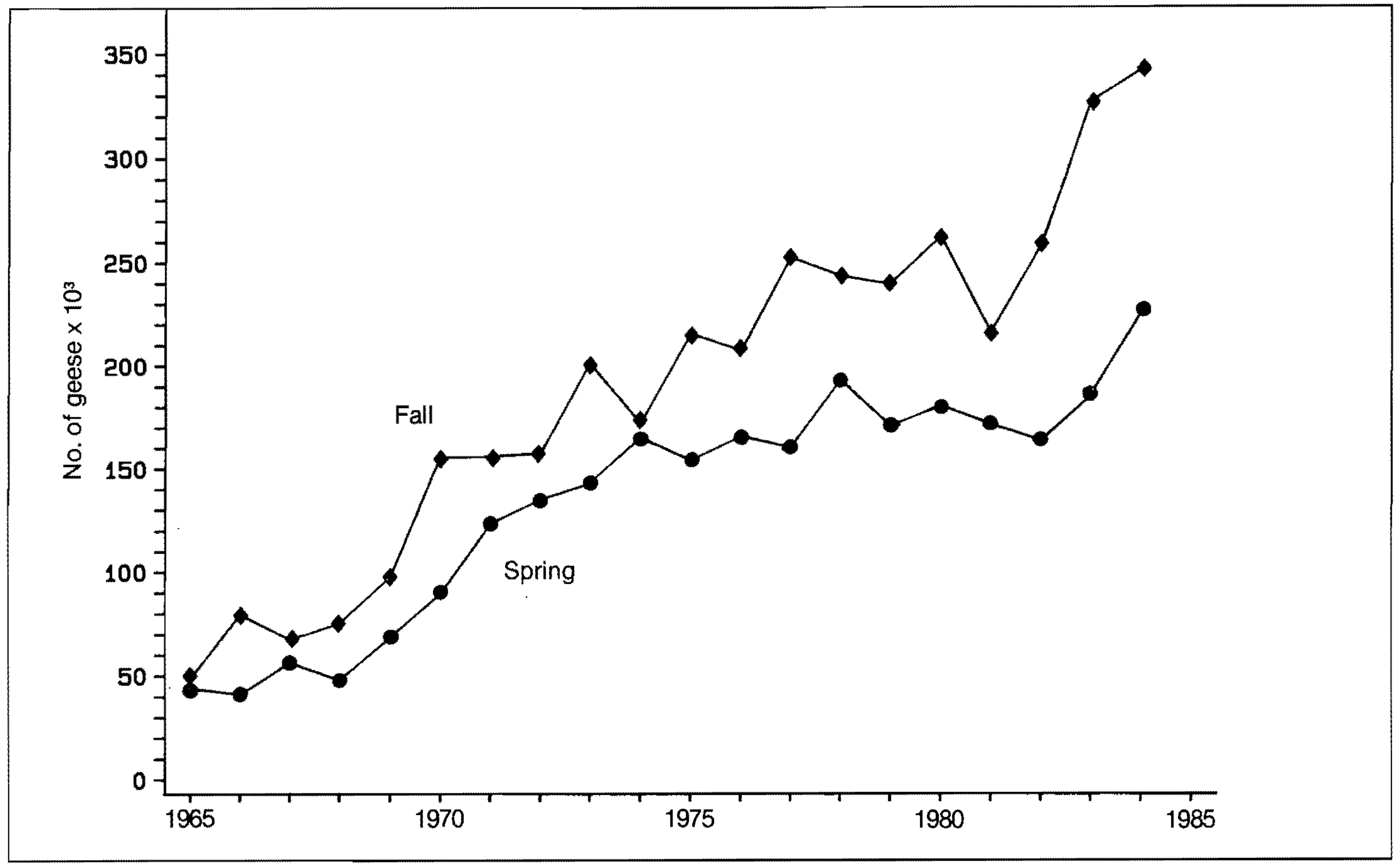
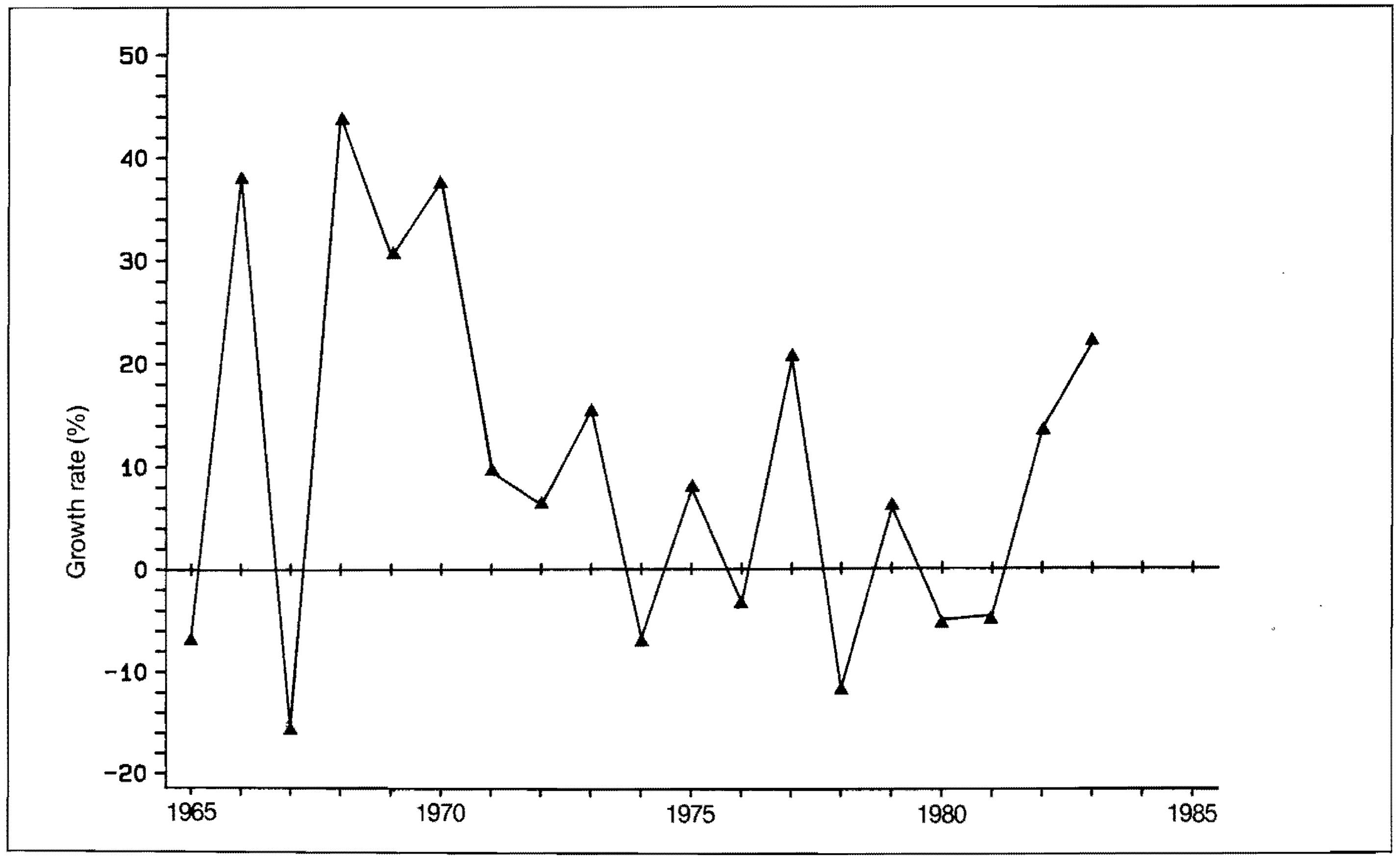


Figure 6
Greater Snow Goose spring-to-spring growth rates



7. Hunting rates

Because recruitment is expressed as a percentage, hunting kills must be represented in the same manner. The Canadian hunting rate is calculated using the formula:

$$S(k) = 100 \frac{C(k)}{PA(k)} \qquad [3]$$

where $C(k)$ is the size of the Canadian hunting kill and $PA(k)$ is the fall population in Canada derived from formula [2]. The American hunting rate, which must take into account the earlier Canadian hunt, is calculated from the formula:

$$T(k) = 100 \frac{D(k)}{PA(k) - C(k)} \qquad [4]$$

where $D(k)$ is the size of the American hunting kill. The calculated hunting kill rates appear in Table 4, which also shows the corrected juvenile percentages. The hunting rates are plotted in Fig. 7; they too vary, essentially at random. In 1968 and 1969 the juvenile percentages were very high and the hunting rates very low. In addition to contributing to an immediate population gain, the many juveniles from those years that did not fall victim to the hunt went on to form a large group of young breeders in 1971 and 1973. They thus ensured high juvenile percentages in subsequent years, accompanied in 1971, 1972, and 1974 by very low hunting rates. This explains the spectacular population increase between 1968 and 1975 and shows that a series of favourable chance occurrences can lead to rapid population growth. It also suggests that a series of unfavourable circumstances could cause a correspondingly steep decline in the population.

8. Model equations

From formulas [2] and [3] we can derive an expression for the Canadian hunting kill:

$$C(k) = \frac{S(k)\sqrt{m}\,P(k)}{100 - R(k)} \qquad [5]$$

From this formula, with [2] and [4], we can also represent American hunting kill:

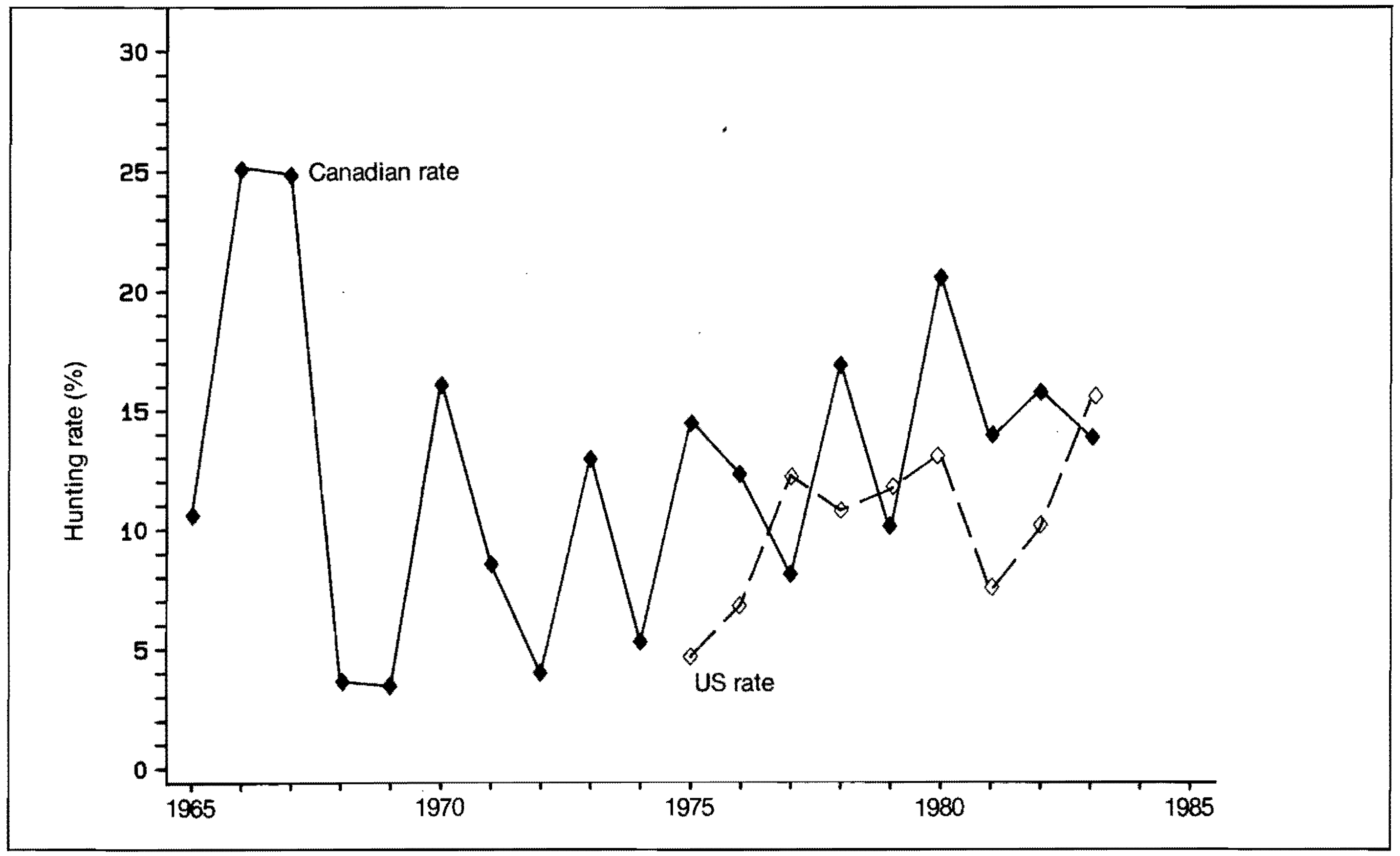
$$D(k) = \frac{\sqrt{m}\,P(k)}{100 - R(k)} \left[T(k) - \frac{S(k)\,T(k)}{100} \right] \qquad [6]$$

Insertion of these formulas for $C(k)$ and $D(k)$ into balance equation [1], after simplification, yields the relation:

$$P(k+1) = \frac{m\,P(k)}{100 - R(k)} \left[100 - S(k) - T(k) + \frac{S(k)\,T(k)}{100} \right] \qquad [7]$$

which gives the spring population in year $k + 1$ based on the natural survival coefficient m, the juvenile percentage $R(k)$, and the Canadian and American fall hunting rates $S(k)$ and $T(k)$ for year k. This recurrent relationship can be

Figure 7
Canadian and American hunting rates for Greater Snow Geese



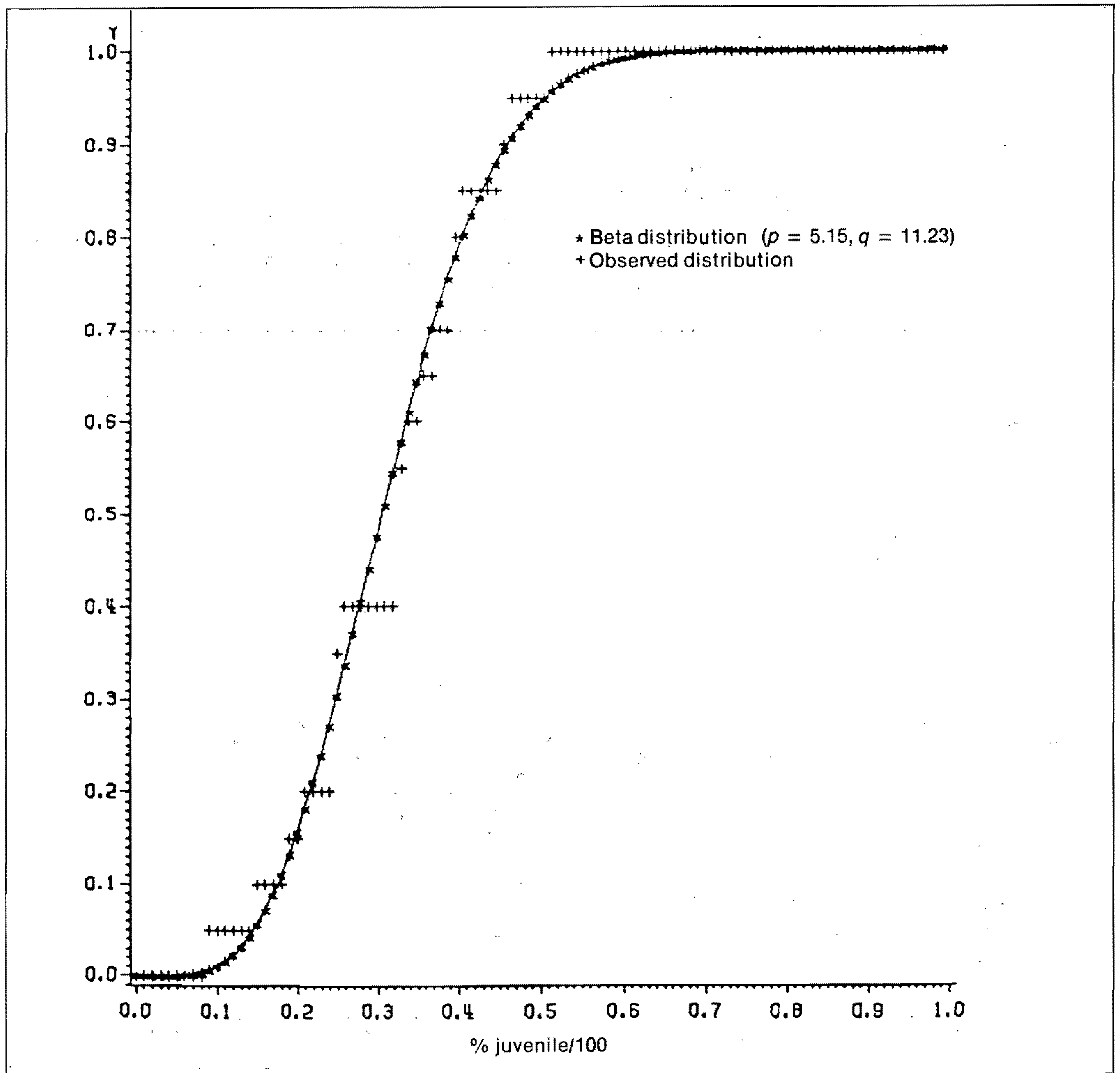
used as a model for population growth. The model, with discrete time periods, is too simple to have good theoretical properties. To improve it would require the addition of a function that, while taking into account the carrying capacity of the range, would link hunting rates to juvenile percentages and population levels while also compensating for hunting effort. However, Clark (1976, Ch. 7) showed that for models of this type any population $P(k)$ is at equilibrium, but the equilibrium is neither stable nor unstable. That is undesirable in a predictive model.

9. Probability distributions for percentages of juveniles and hunting rates

The corrected juvenile percentages listed in Table 4 and plotted in Fig. 4 are highly random from one fall to the next. For the purpose of the simulation, a probability distribution is estimated to reproduce this phenomenon. Examination of the juvenile percentages suggests that a Beta distribution may be suitable. If x is defined as the proportion of juveniles (%/100), $0 \leqslant x \leqslant 1$, a Beta distribution may be written as follows:

$$f(x; p, q) = \frac{1}{B(p, q)} x^{p-1} (1-x)^{q-1}$$

Figure 8
Probability distribution for juvenile percentages of Greater Snow Geese



where p and q are parameters that can be determined by the method of moments:

$$p/(p+q) = \bar{x} = 0.314$$
$$pq/(p+q)^2 (p+q+1) = s^2 = 0.0124$$

where $\bar{x}$ is the mean of the observed values and s^2 is the variance. Resolution of these two equations yields:

$$p = 5.15, \quad q = 11.23$$

To ensure that this probability distribution is acceptable, we conducted a Kolmogorov significance test, which consists of comparing the experimental distribution function:

$$F_n(x) = \frac{i}{n} \quad \text{if } x(i) \leqslant x \leqslant x(i+1)$$

$i = 1, \ldots, 19$, $x(0) = 0$, $x(20) = 1$, where $x(i)$ are observations, and the Beta distribution function:

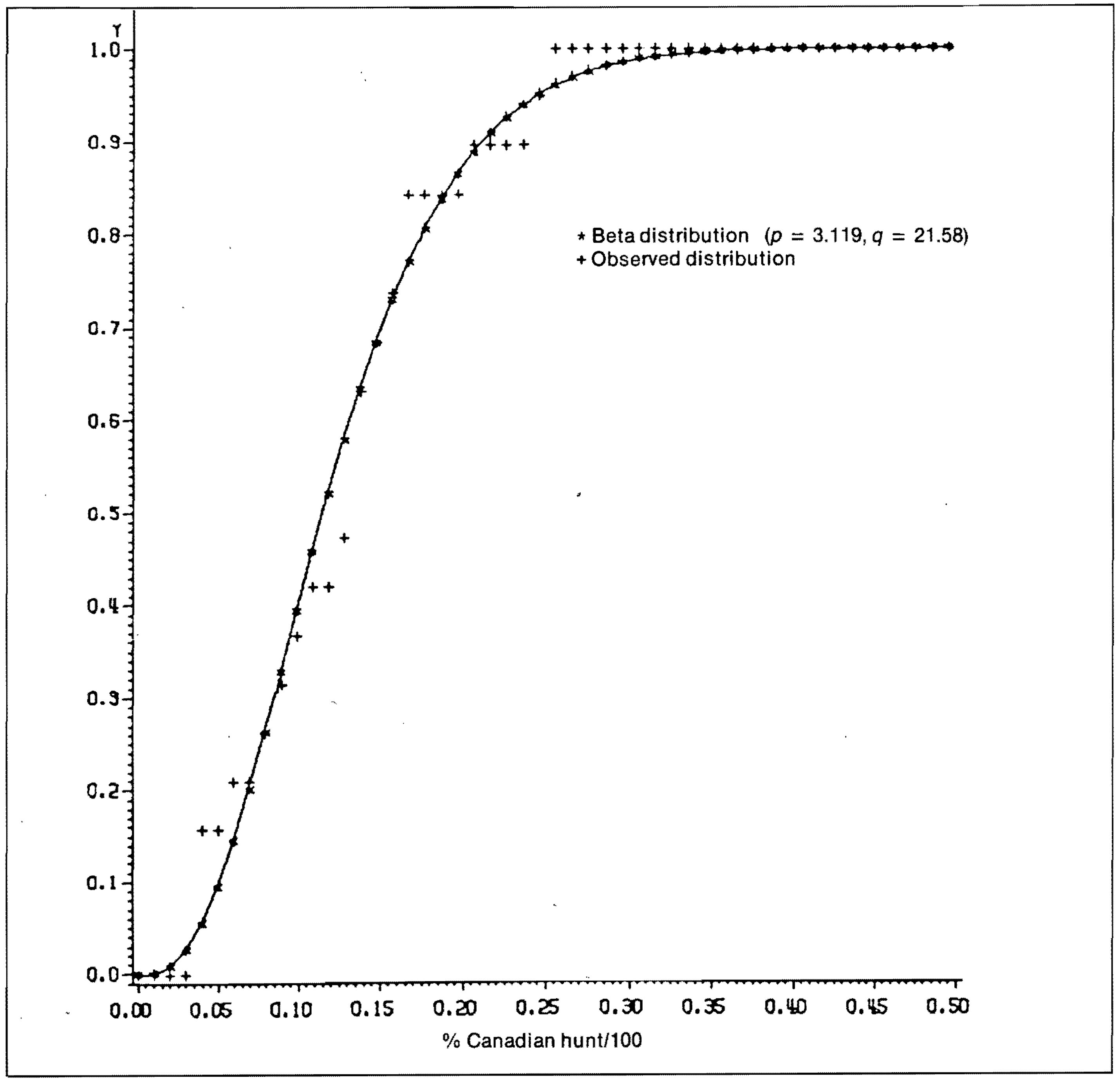
$$F(x; p, q) = \int_0^x \frac{1}{B(p, q)} y^{p-1} (1-y)^{q-1} \, dy$$

by measuring the maximum deviation:

$$D = \max_x |F_n(x) - F(x; p, q)|, \; x = 0.00, 0.01, \ldots, 0.79$$

The calculated maximum deviation was $D = 0.145$; the 5% rejection criterion is $D \geqslant 0.301$. The Beta distribution

Figure 9
Probability distribution for Canadian hunting rates for Greater Snow Geese



function $F(x; p, q)$ and experimental distribution function $F_n(x)$ are plotted in Fig. 8.

The Canadian hunting rates shown in Fig. 7 also appear to be highly random. Since the mean and variance of $S(k)/100$ are:

$$\bar{x} = 0.123, \ s^2 = 0.0048$$

a Beta function can be estimated with parameters:

$$p = 3.12 \text{ and } q = 21.5$$

The Kolmogorov test yields a maximum deviation of $D = 0.107$ between the Beta distribution function and the experimental distribution function in Fig. 9, making the probability distribution acceptable.

While we have few data on the American hunting rate $T(k)$, a fit can be obtained with a Beta distribution. The mean and variance of $T(k)/100$ being:

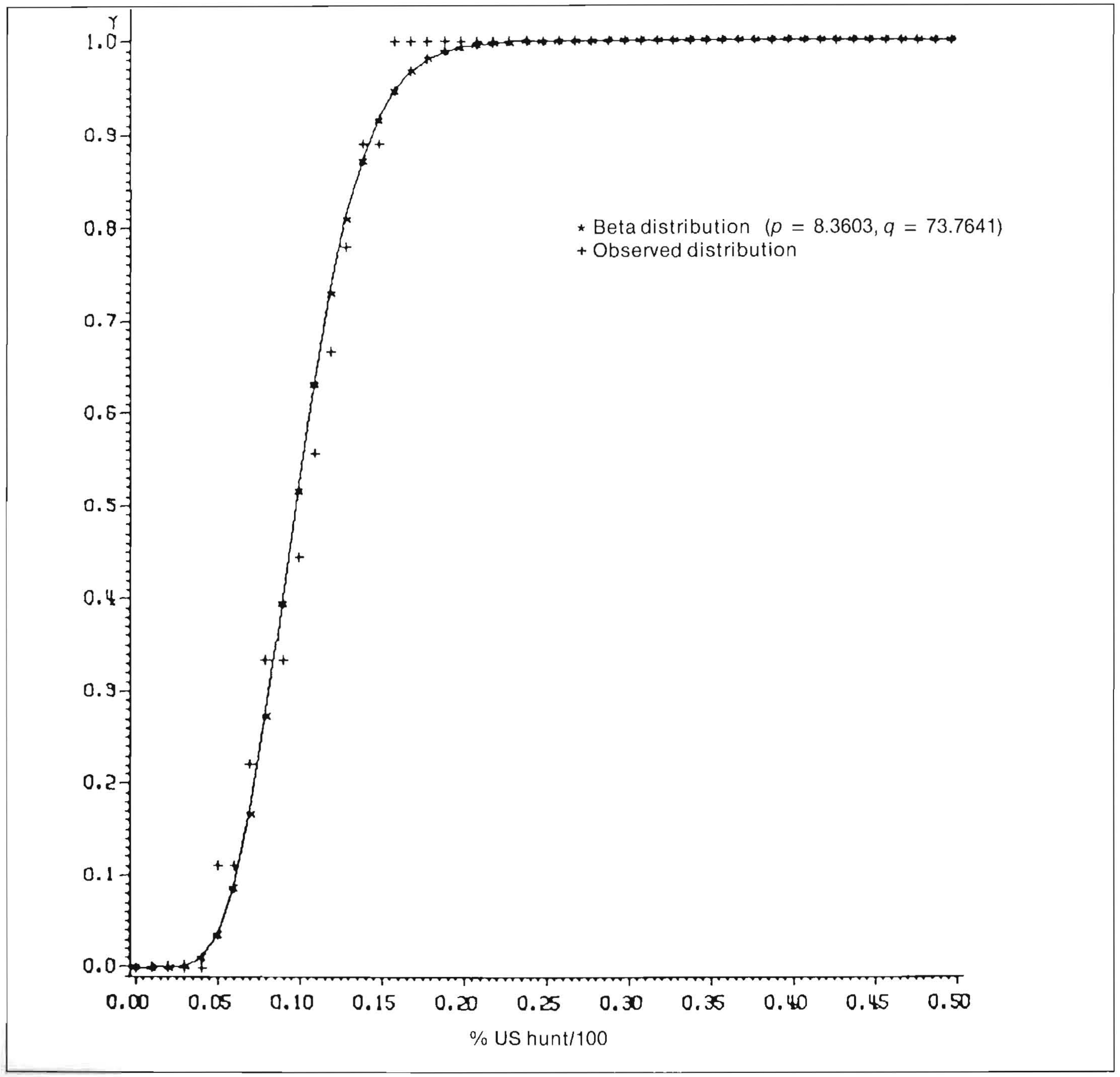
$$\bar{x} = 0.102, \ s^2 = 0.0011$$

the parameters are:

$$p = 8.369 \text{ and } q = 73.76.$$

The maximum deviation between the Beta distribution function and the experimental distribution function in Fig. 10 is $D = 0.076$, meaning that this probability distribution is also acceptable.

Figure 10
Probability distribution for American hunting rates for Greater Snow Geese



Each spring, while it stages in the St. Lawrence estuary, the Greater Snow Goose population is censused using aerial photography. This photograph shows a flock of some 5000 Greater Snow Geese near Isle-Verte, Quebec, on 3 May 1985.

Photo: P. Dupuis

Results

1. Simulation and scenarios

Formula [7] yields a stochastic model for simulating population growth when juvenile percentages $R(k)$ and hunting rates $S(k)$ and $T(k)$ are considered random variables distributed in accordance with the probability distributions estimated from the data. To generate those variables, different random numbers are produced simultaneously over the interval [0, 1], from which $R(k)$, $S(k)$ and $T(k)$ are calculated by applying the inverse function of each of the corresponding probability distributions. The model is available in the form of a program for IBM PC microcomputers equipped with a graphics card and colour monitor. Figures 11–21 illustrate the results of a number of experiments conducted with the program to show the relative influence of the survival parameter and random variables on population growth.

Figure 11 shows the plots of 40 simulations for 20 years starting in 1984 with the estimated natural survival rate $m = 0.895$ (10.5% natural mortality); population growth is unpredictable and chaotic. The mean values and range of standard deviations shown in Fig. 12 indicate a tendency toward positive population growth. This is to be expected, because the probability functions were derived from data for a period when the population exhibited strong growth.

Replacing the natural survival rate with a lower value $m = 0.82$ (18% natural mortality) results in a tendency toward negative population growth (Fig. 13). This adds to the credibility of the higher rate estimated from the data.

Figure 11
Predicted Greater Snow Goose population growth, 40 simulations with $m = 0.895$

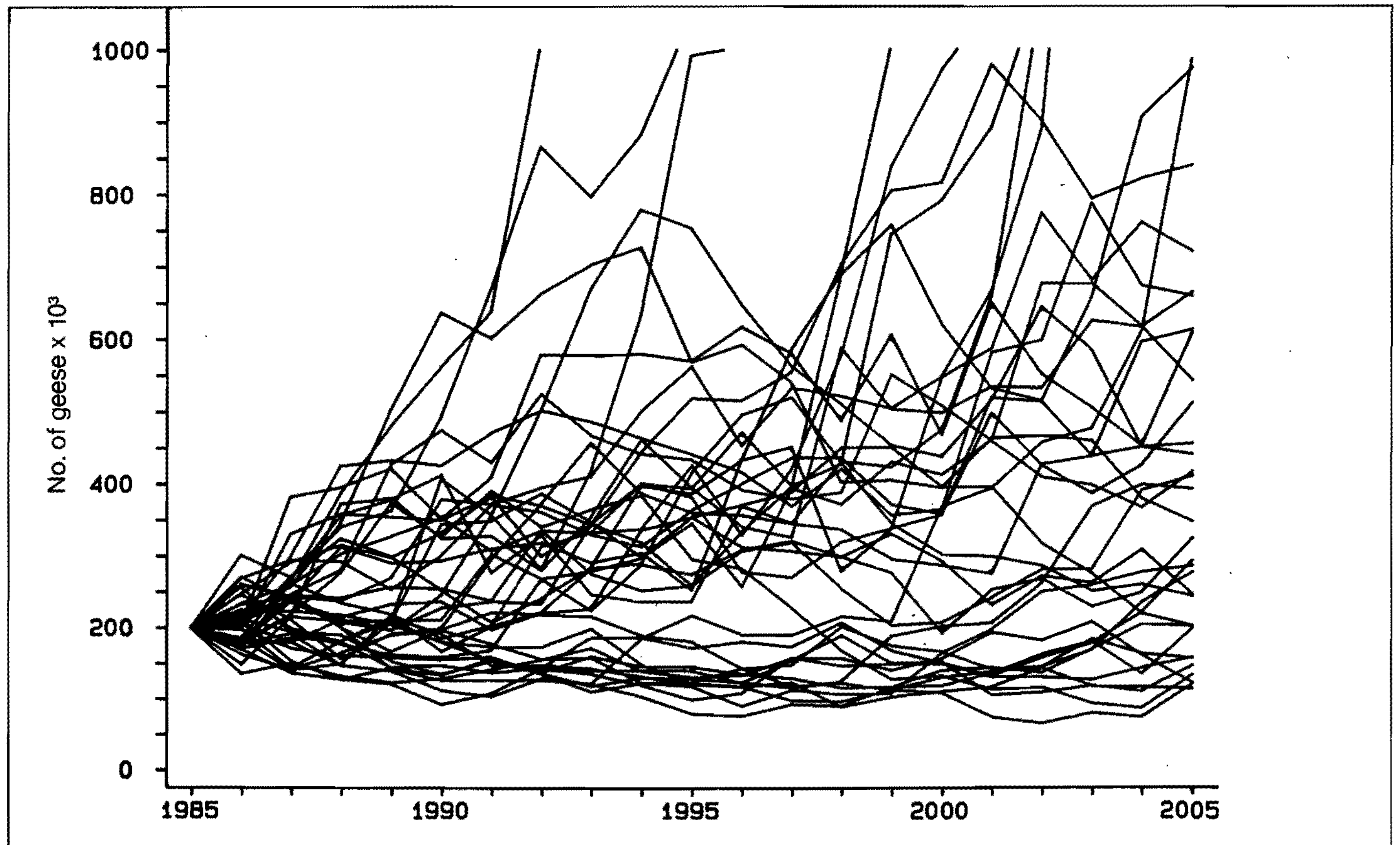


Figure 12
Predicted Greater Snow Goose population growth, mean and standard deviations for 40 simulations, $m = 0.895$

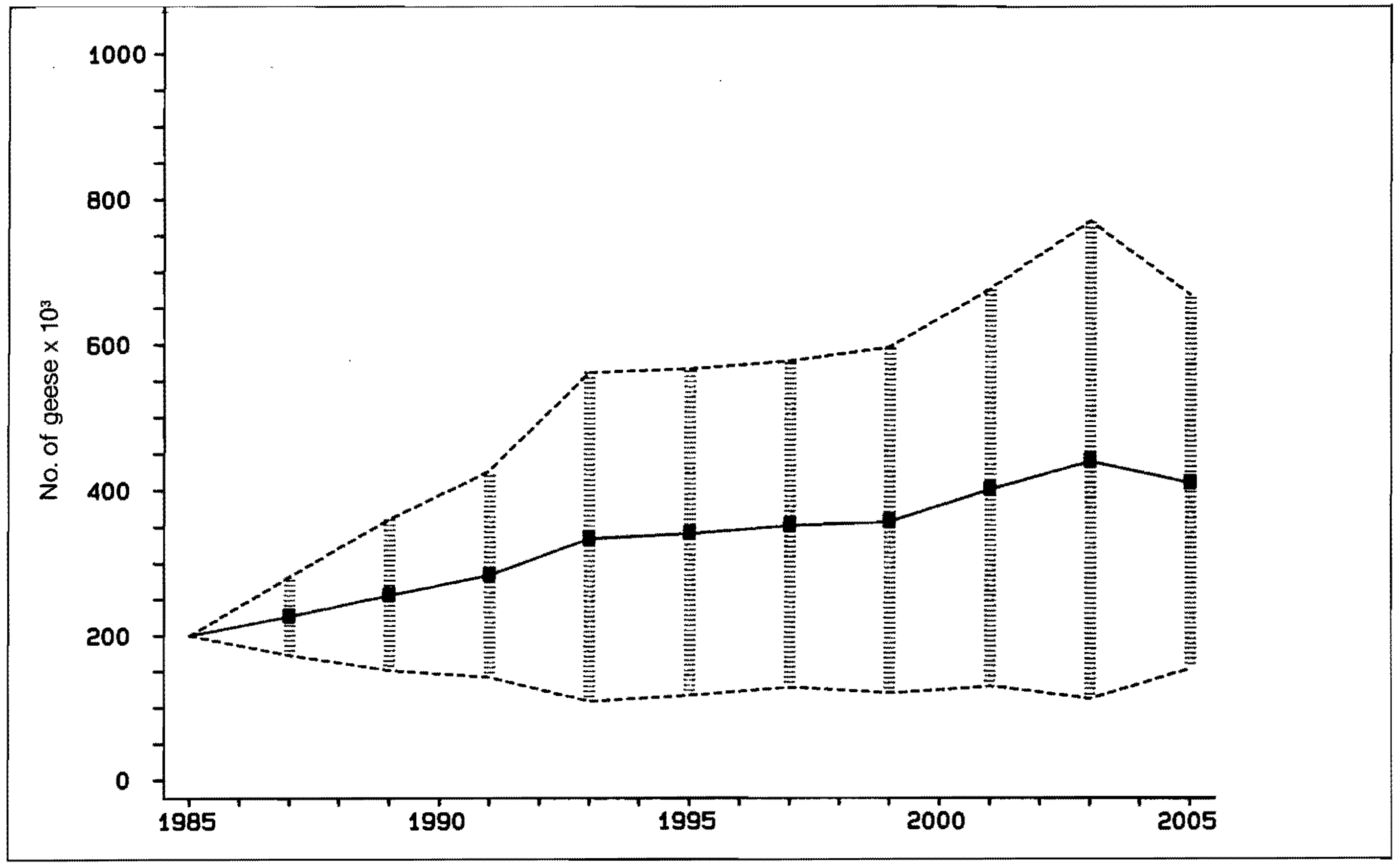


Figure 13
Predicted Greater Snow Goose population growth, mean and standard deviations for 40 simulations, with reduced natural survival ($m = 0.82$)

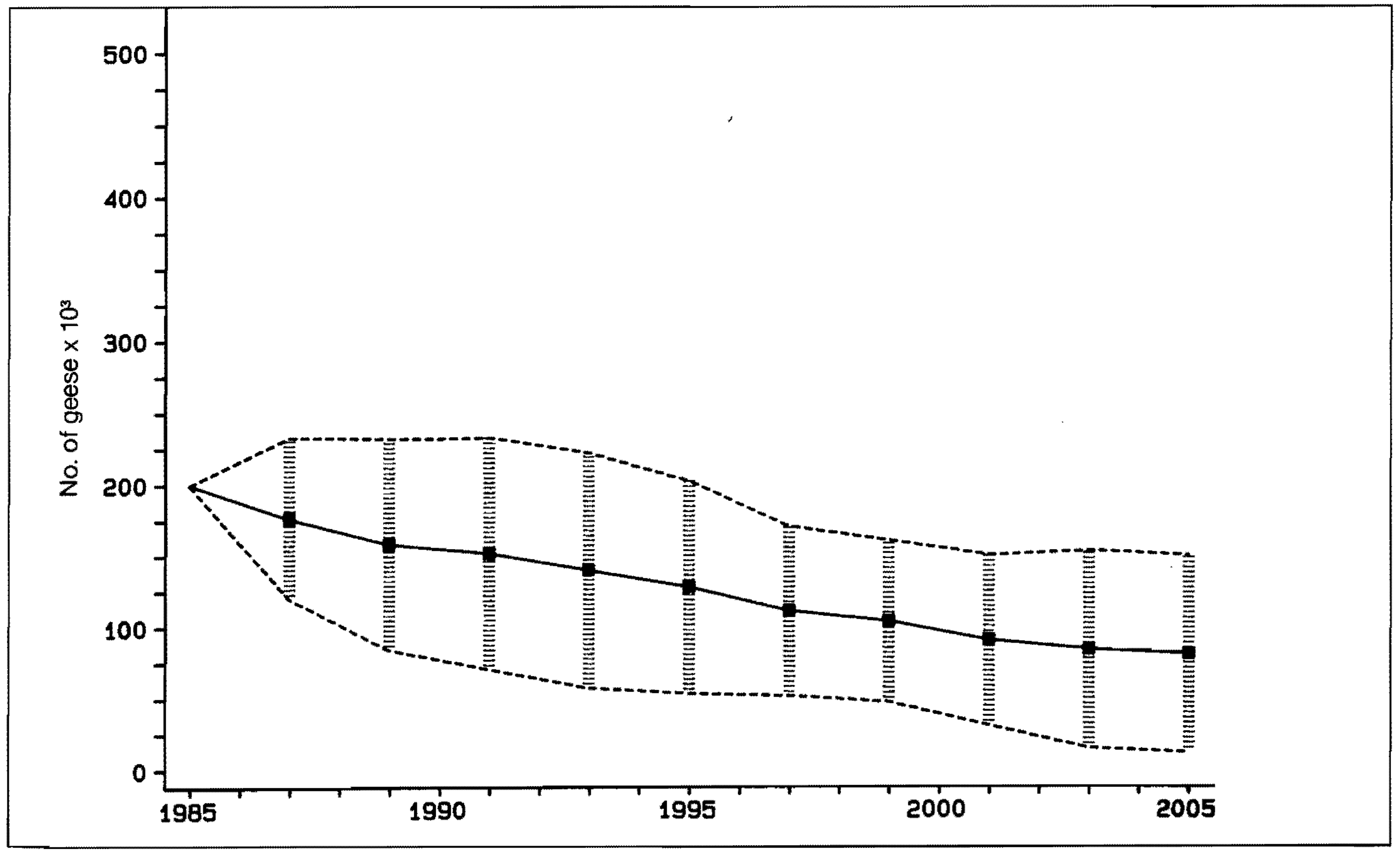


Figure 14
Predicted Greater Snow Goose population growth, mean and standard deviations for 40 simulations, with reduced reproductive success (juv. % × 0.75)

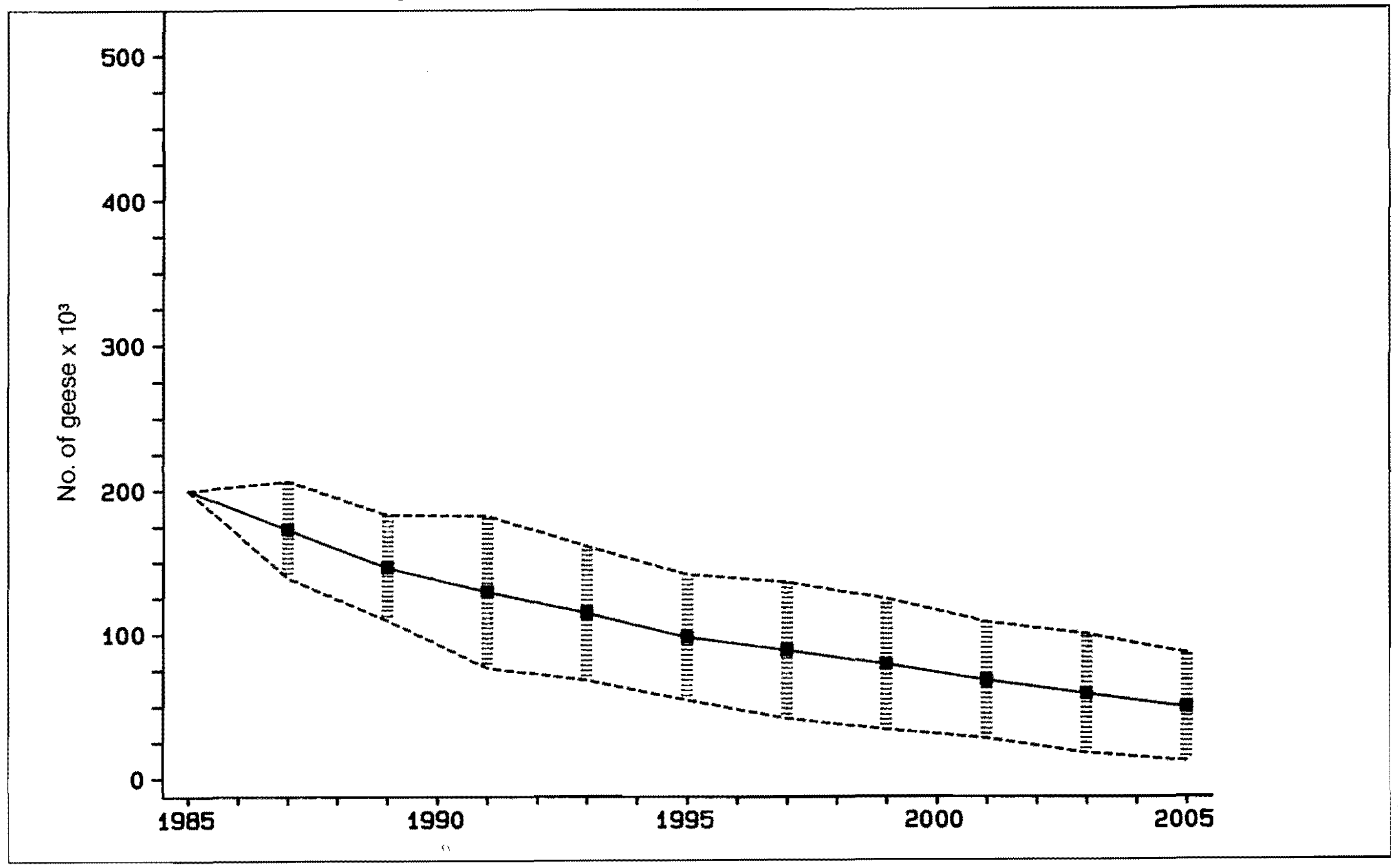


Figure 15
Predicted Greater Snow Goose population growth, mean and standard deviations for 40 simulations, with increased reproductive success (juv % × 1.25)

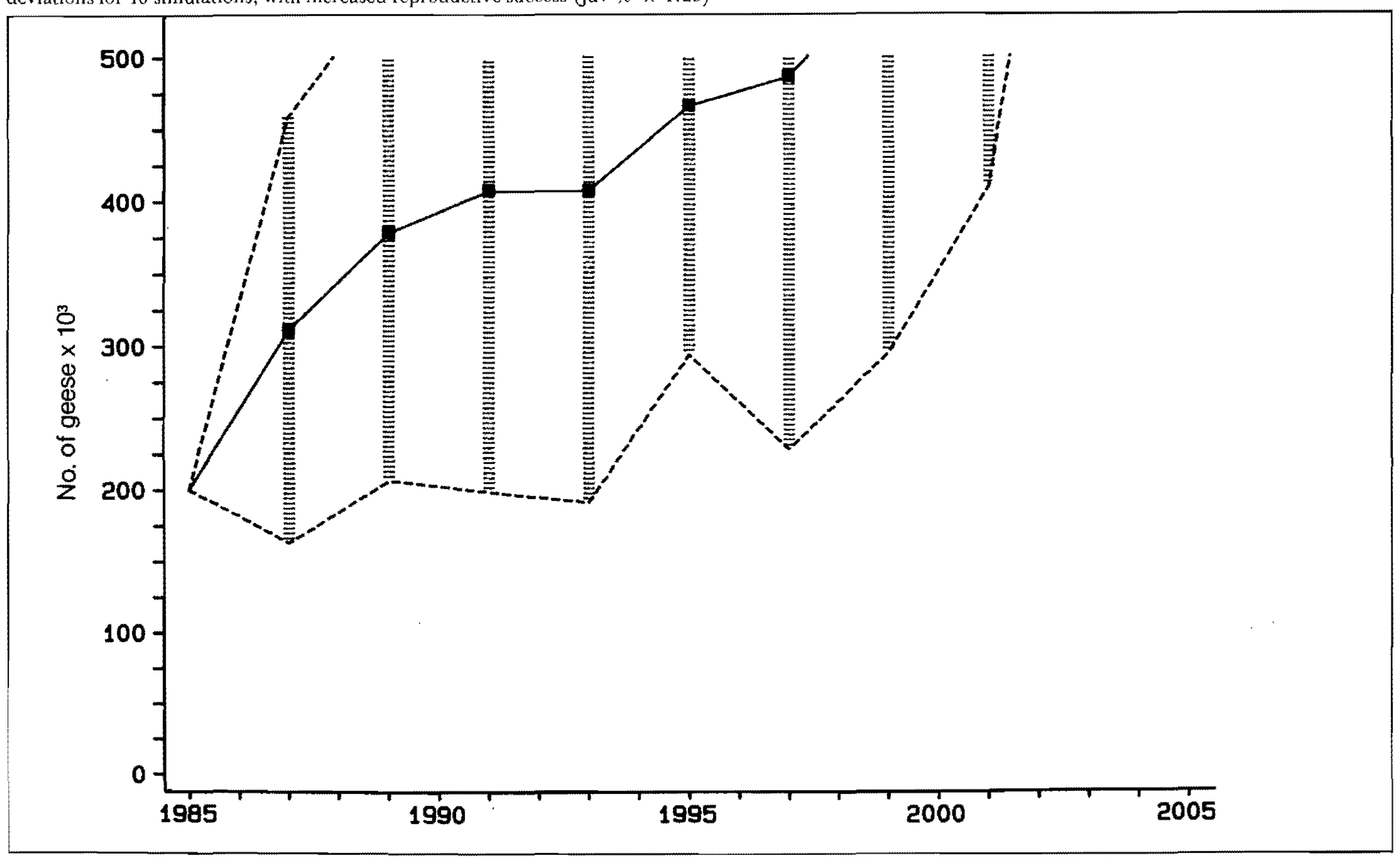


Figure 14 indicates that consistently reducing the generated juvenile percentages by one-quarter leads to rapid population decline. On the other hand, increasing the juvenile percentages by one-quarter produces an incredible population explosion (Fig. 15). This demonstrates the very high sensitivity of the population (or the model) to fluctuations in juvenile percentages.

Reducing the generated hunting rates by one-quarter yields a strong population increase (Fig. 16), suggesting that hunting kill is slowing down population increase. Raising hunting rates by one-quarter results in a slow decline (Fig. 17).

Five successive years of poor reproductive success (juvenile percentage = 10%) would cause the population to drop quickly to its 1965 level (Fig. 18); the success rate is then allowed to return to normal, and the population slowly starts to grow again. A constant juvenile percentage of 31.4% keeps the population stable at its 1985 level (Fig. 19). Figure 20 suggests that without the American hunt the population might have exhibited even more rapid growth since 1975.

Figure 21 shows the mean values and range of standard deviations of 40 simulations for 1964–84, as well as the observed population values. With the exception of one year the observed curve fell within the limits of the model's curve, which gives credibility to the model. On a more refined scale, however, the real population grew more rapidly from 1969 to 1974 than the average growth predicted by the model. From then on the two curves move in parallel. The dephasing of the two curves is the result of the chance occurrence of abnormally favourable combinations of low hunting kills and high juvenile percentages between 1968 and 1974.

Figure 16
Predicted Greater Snow Goose population growth, mean and standard deviations for 40 simulations, with reduced hunting rate (hunt % × 0.75)

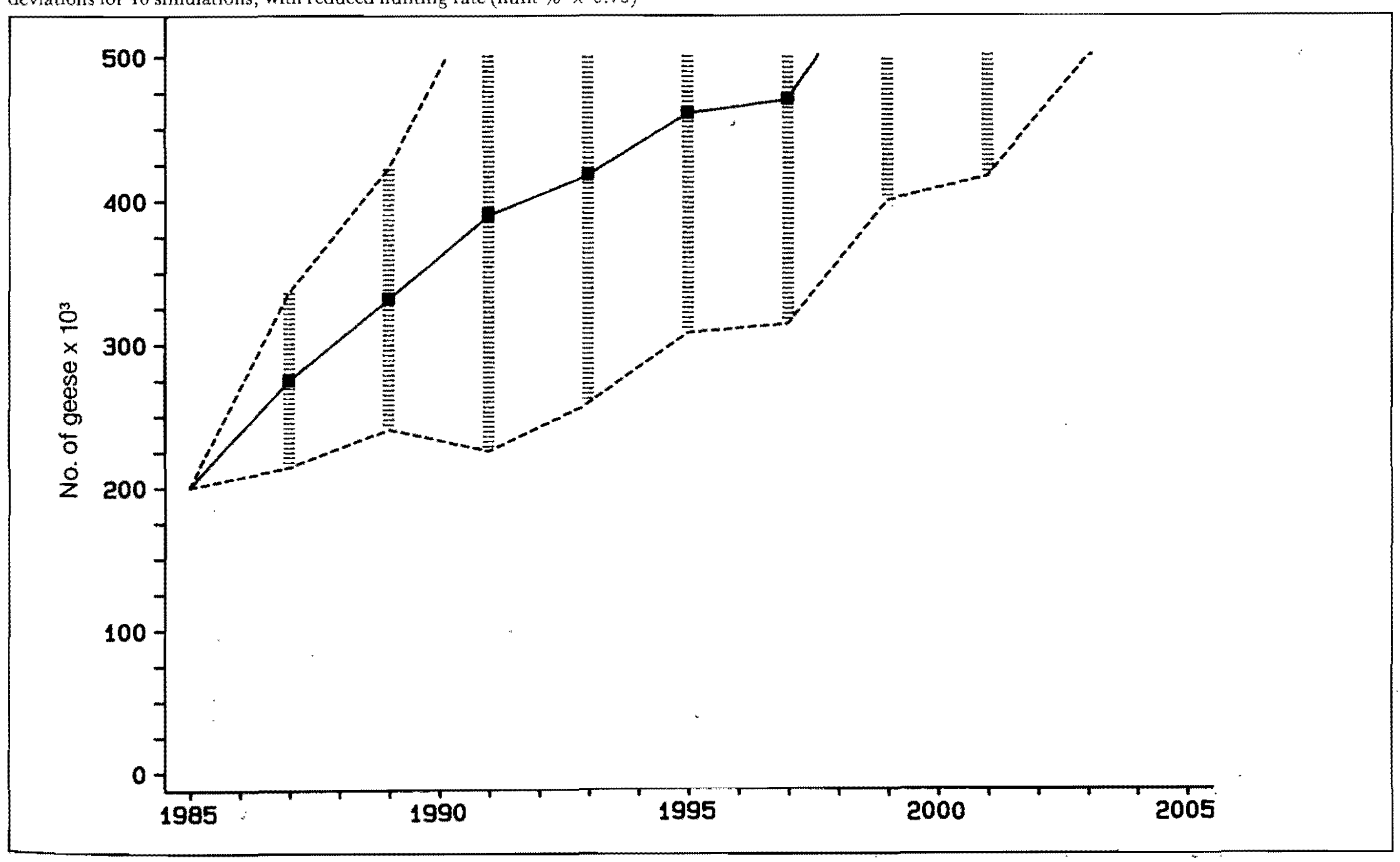


Figure 17
Predicted Greater Snow Goose population growth, mean and standard deviations for 40 simulations, with increased hunting rate (hunt % × 1.25)

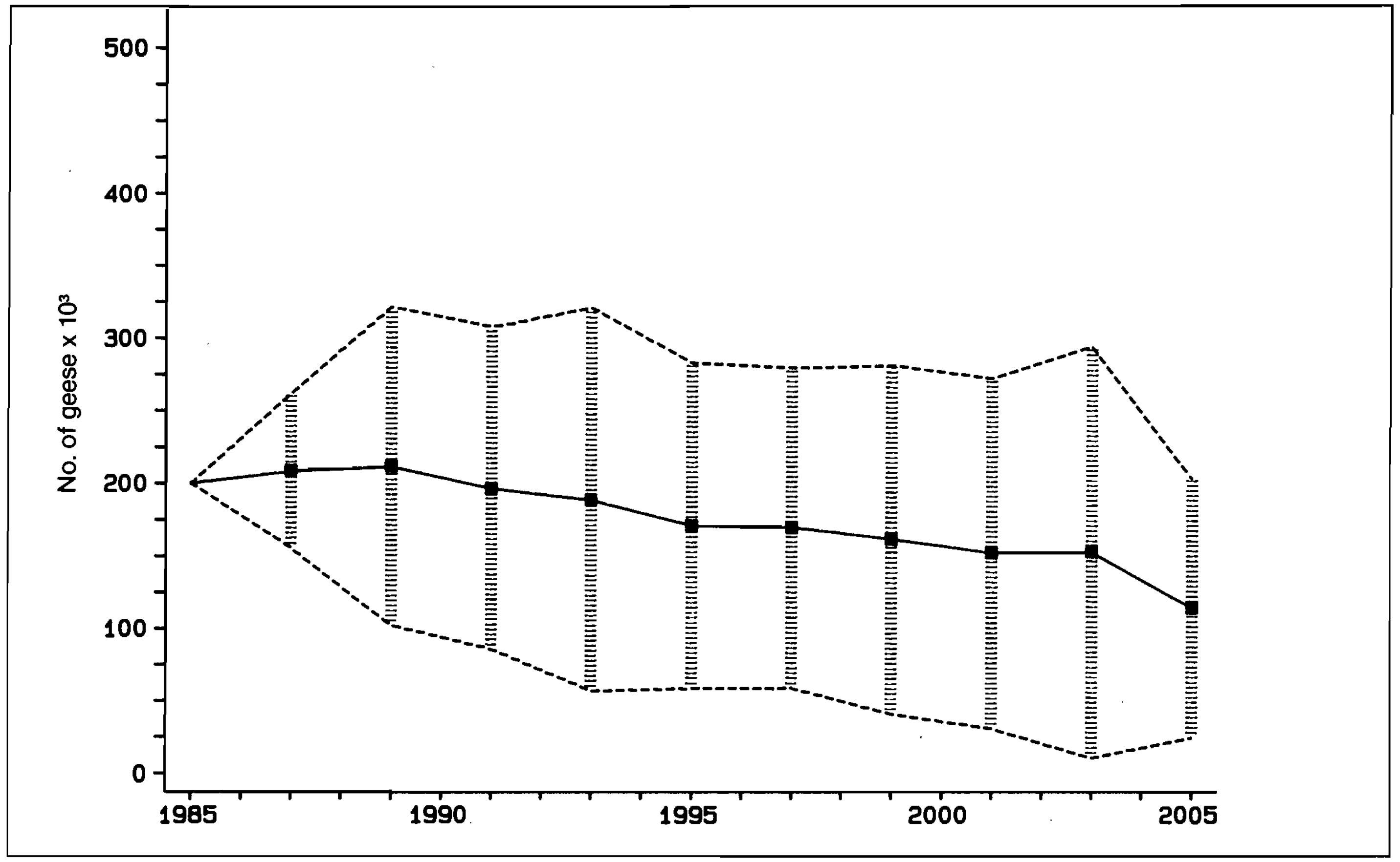


Figure 18
Predicted Greater Snow Goose population growth, mean and standard deviations for 40 simulations, with low (10%) reproductive success over the first 5 years

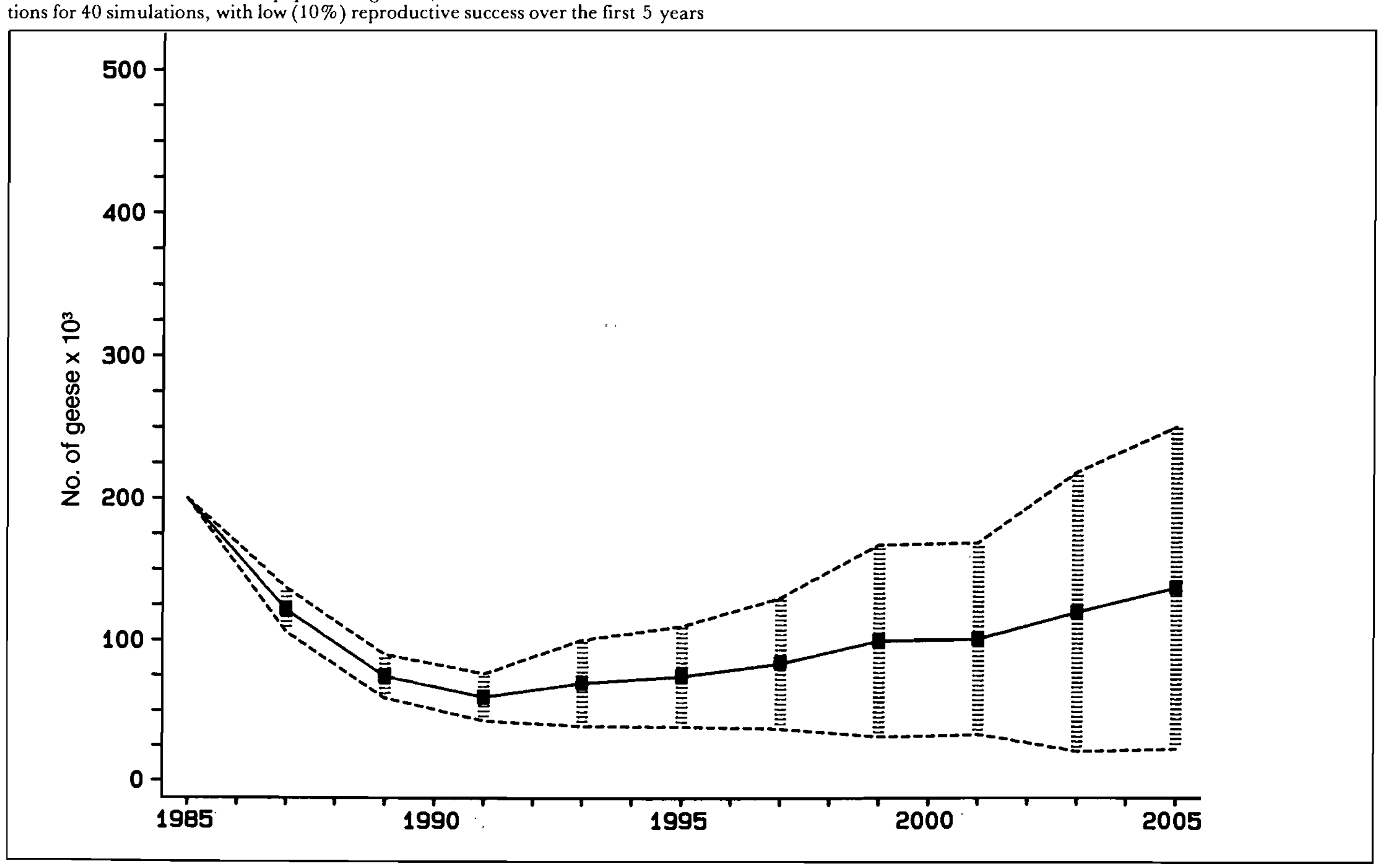


Figure 19
Predicted Greater Snow Goose population growth, mean and standard deviations for 40 simulations, with fixed annual reproductive rate (juv % = 31.4)

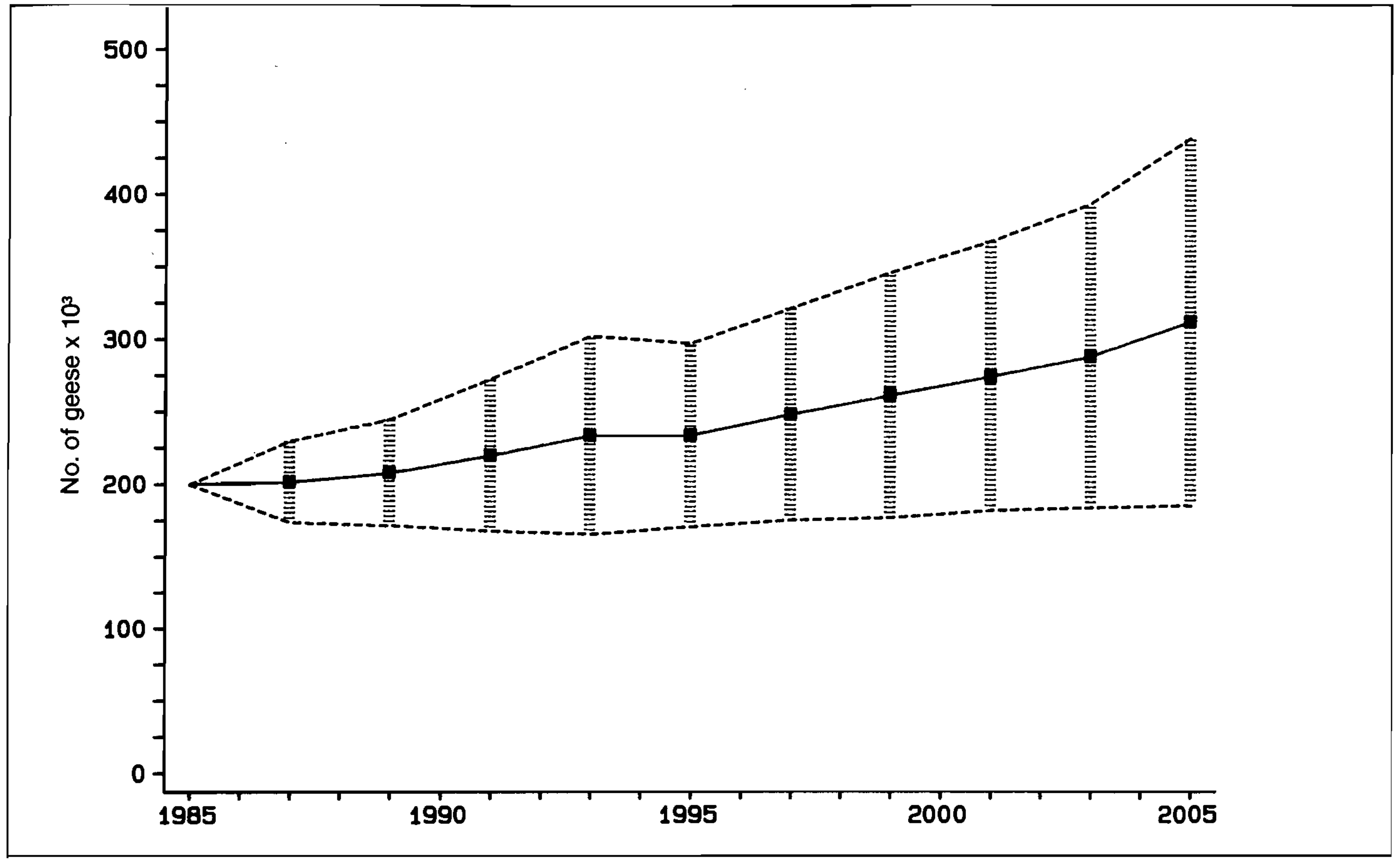


Figure 20
Predicted Greater Snow Goose population growth, with and without the American hunt

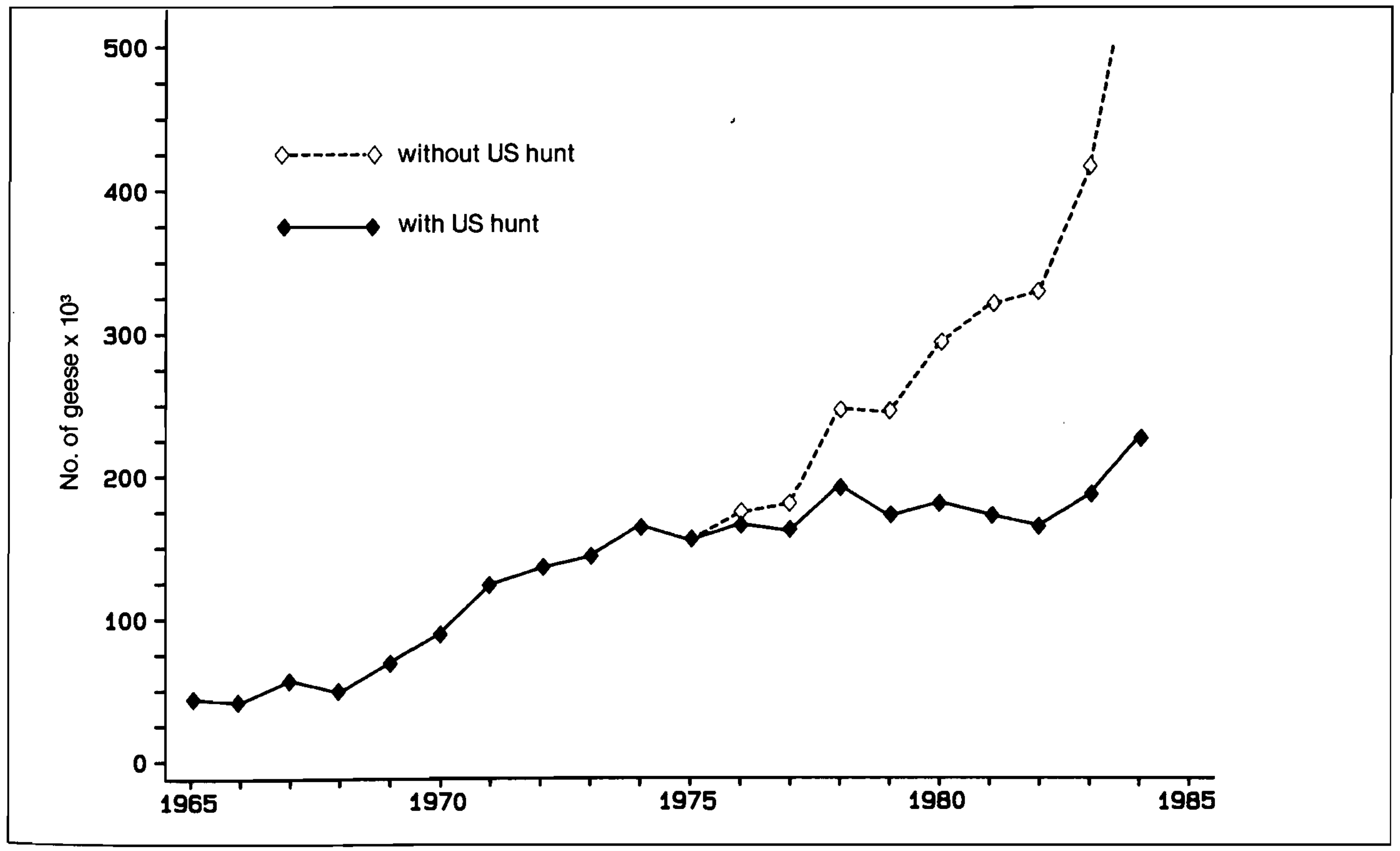
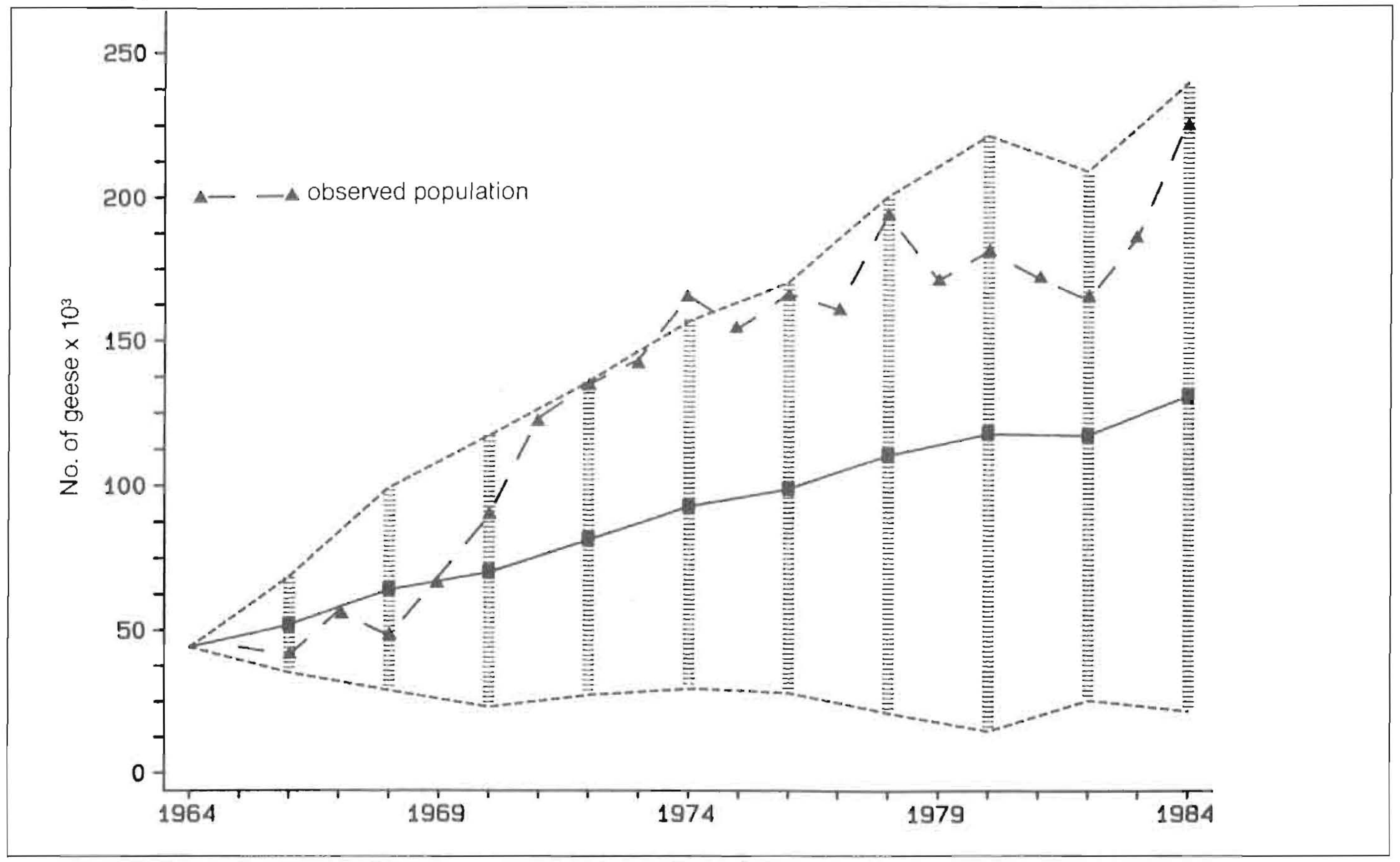


Figure 21
Comparison of 40 model simulations with the observed growth of the Greater Snow Goose population



During fall migration the juvenile geese, then about three months old, are easily distinguished by their grey plumage, which contrasts with the white plumage of the adult.

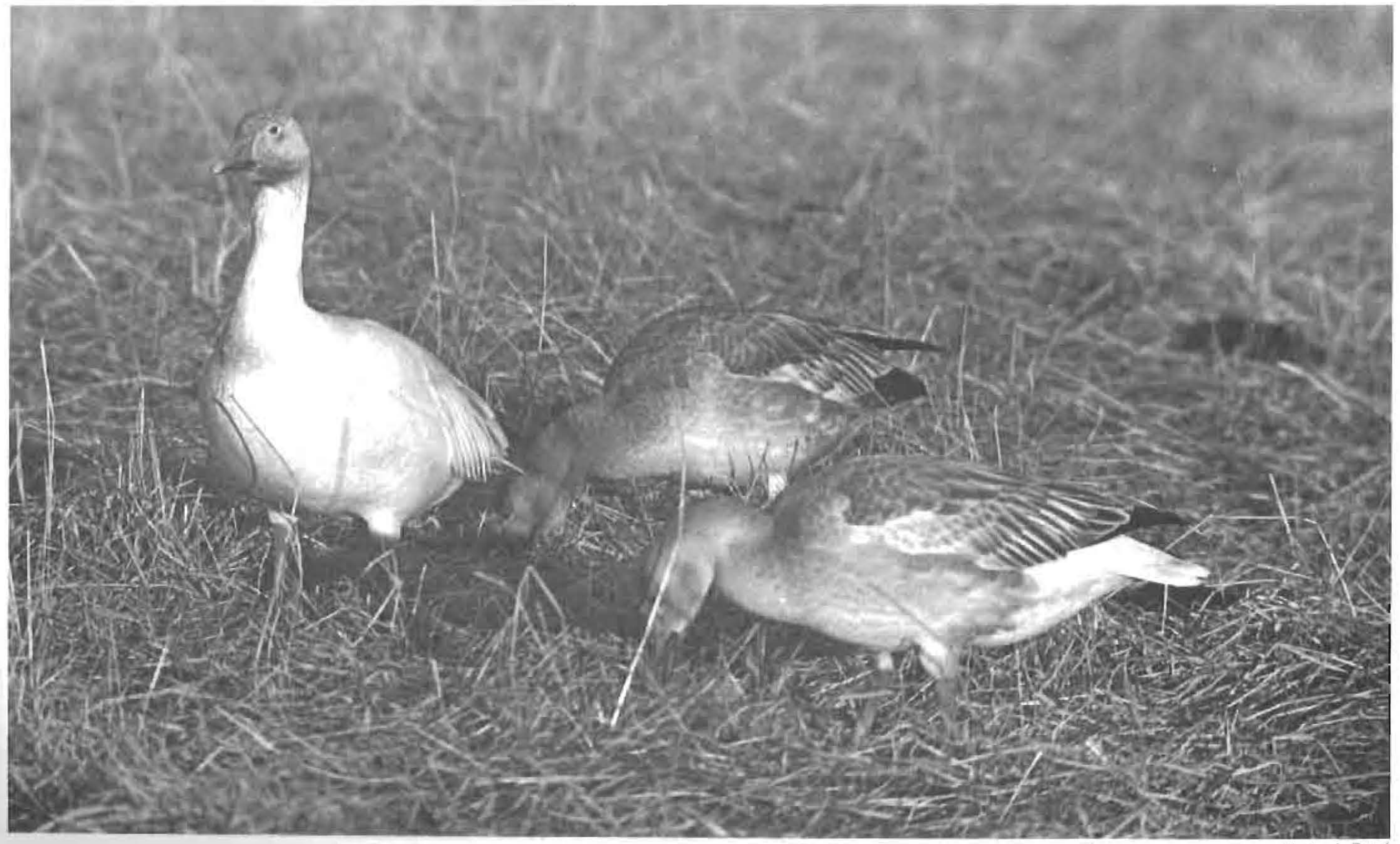


Photo: A. Reed

Conclusions

This paper describes a stochastic model capable of convincingly re-creating recent trends in the Greater Snow Goose population and permitting simulation of future population trends under various scenarios. In designing the model we assumed that the population figures measured in the spring were fairly accurate, that hunting kills had not been overestimated, and that juvenile percentages measured in the fall might have been generally underestimated. The model also assumes that hunting kills are random, an assumption that is clearly not totally accurate. This very basic model does not take into account the carrying capacity of the range or other ecological conditions. Moreover, the model assumes a uniform natural survival coefficient that does not account for annual variations in natural mortality caused by the age composition of the population, disease, or other factors.

A good knowledge of the spring population size, fall juvenile percentage, and hunting kills is indispensable for effective monitoring of population trends. Accurate juvenile percentages permit an accurate *a posteriori* calculation of hunting kills. We cannot stress too much the importance of good estimates of fall juvenile percentages based on larger samples than those available for certain past years (see Johnson *et al.* 1985 for further discussion on the importance of accuracy in modelling exploited waterfowl populations). Accurate measurements of fall and winter population size would appear not to be very important—the model can generate figures for these populations, which are difficult to survey.

Several factors warrant consideration in the design of models for the Greater Snow Goose population. One important inclusion would be a function to account for the carrying capacity of the range and other ecological conditions. There is also a need for a function relating hunting kill rates to population levels and juvenile percentages. Although kill rates contain a random component, they are undoubtedly linked to those parameters. At the same time, it would be desirable to include a relation quantifying hunting effort. Once these components have been added to the model, we will seek quantifiable objectives for which it should be possible to determine optimum hunting or management policies.

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Appendix

Appendix 1
Population and productivity surveys of Greater Snow Geese in Canada and the USA, 1950–84

	Population counts			Percentage of juveniles		
	St. Lawrence		United States	St. Lawrence		United States
Year	Spring	Fall	Fall/winter	Aerial photo	Visual, ground	Visual, ground
1950			41 800			
1951		30 000	43 900			
1952		41 000	55 800			
1953	30 100		51 400			
1954	50 800	35 700	46 200			
1955		48 200	45 000			
1956			34 800			33.8
1957		70 000	46 300			34.4
1958		47 500	37 500			3.1
1959			60 700			42.7
1960			67 100			34.1
1961			49 700			1.2
1962			64 900			28.4
1963			59 700			33.9 (2 728)*
1964			46 500			20.5 (8 179)
1965	25 400	48 500	43 400			2.8 (2 524)
1966	25 400	80 000	59 900			37.0 (5 516)
1967	40 900	75 000	50 500			12.4 (5 236)
1968	38 900	31 000	62 800			12.5 (3 613)
1969	68 800	79 600	29 500	30.0		24.3 (5 004)
1970	89 600	120 300	48 500	45.6		46.8 (6 930)
1971	123 300	145 400	81 100	29.7		11.3 (8 334)
1972	134 800	125 200	59 100			0.4 (3 214)
1973	143 000	172 600	95 300	46.6	40.6 (800)	41.1 (4 900)
1974	165 000	162 000	70 300		6.4 (7 282)	2.0 (6 148)
1975	153 800	202 700	117 000	32.7	31.2 (17 579)	37.3 (11 460)
1976	165 600	186 700	127 000	9.5 (120 755)	12.6 (20 847)	9.8 (34 892)
1977	160 000	186 000	74 000	21.6 (132 425)	23.9 (10 297)	23.8 (7 531)
1978	192 600	94 400	100 000	20.1 (205 419)	17.9 (9 679)	14.7 (16 159)
1979	170 100	110 600	107 000	22.5 (179 002)	28.2 (20 849)	23.2 (8 041)
1980	180 000	107 000	82 000	40.1 (164 453)	35.3 (12 120)	36.3 (12 140)
1981	170 800		100 000	16.8 (86 039)	16.3 (10 683)	17.0
1982	163 000		130 000	10.5 (65 436)	25.1 (9 577)	23.8
1983	185 000		176 000	41.6 (100 910)	47.4 (12 353)	48.9
1984	225 400		185 000	37.6 (103 000)	30.4 (39 781)	27.4

Source: *A Greater Snow Goose management plan* (1981) and unpublished CWS and USFWS data
*Values in parentheses are sample sizes

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