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Shotgun pellet loads and infliction rates in pink-footed geese *Anser brachyrhynchus*

Henning Noer & Jesper Madsen

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Pink-footed geese *Anser brachyrhynchus* caught in western Denmark during March-April 1990-1992 were X-rayed to detect shotgun pellets. Among first-year and older geese, pellets were detected in 25% (N = 69) and 36% (N = 286), respectively. A simple theoretical model is proposed, relating frequencies of pellet carriers in different age classes, adult survival and the annual rate at which pellets are inflicted upon geese. This model resulted in estimates of pellets being inflicted upon 1,000 first-year and 800 older geese annually. However, annual bag is ca 1,000 first-year and 2,000 older geese, and thus, expectedly, pellets should be inflicted upon approximately two older geese for each first-year. From this it is concluded that the model leads to unrealistic estimates because the observed frequencies of first-year and older pellet carriers are inconsistent; if 25% of the geese carry pellets after their first hunting season, more than the observed 36% of the older geese should be carriers. One explanation of this could be statistical uncertainty of the observed frequency of first-year carriers. A frequency of 15% pellet carriers (lower 95% c.l.) after the first hunting season could account for the inconsistency. As an alternative explanation, lower survival of pellet carriers is proposed. A more general model including differential mortality predicts that survival rates of 87% and 78% for non-carriers and carriers, respectively, could explain the observed carrier frequencies. Use of lower 95% c.l. leads to estimates of pellets being inflicted upon a minimum of ca 0.5 goose per bagged one. If differential survival exists, this ratio will be somewhat higher.

Keywords: pink-footed geese, shotgun pellets, X-ray analysis, hunting

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Amongst hunted goose species, X-ray investigations have demonstrated frequencies of adult individuals carrying shotgun pellets ranging between 28% and 62% (Elder 1955a,b, Grieb 1970, Ankney 1975, Jönsson et al. 1985). For pink-footed geese *Anser brachyrhynchus*, Elder (1955a) found 39% adult pellet carriers among individuals belonging to the Iceland/Greenland population, caught on wintering grounds in the British Isles.

Though these frequencies appear high, they are not ne-

cessarily evidence that pellets are inflicted upon large numbers of geese within any single hunting season. Geese are long-lived, and relatively small annual rates of infliction could thus eventually lead to high frequencies of pellet carriers. Therefore, assessment of the number of individuals hit by shot and surviving as pellet carriers each year is essential for a proper interpretation of the frequencies measured by X-ray photography. Moreover, if these rates can be assessed and reliable data on bag statistics

and population sizes are available, the rate at which pellets are inflicted can be compared to harvest rates, in order to assess the ratio of wounded to killed birds. Because this ratio would provide a measure of hunters' performance, it should be of interest to both scientists, wildlife administrators and hunters.

In order to obtain data for the Svalbard population of pink-footed geese, one of us (JM) initiated X-ray recordings in 1990. After an initial period of data compilation, a simple theoretical model was developed in order to assess the 'annual rate of infliction' - defined as the fraction of the population that is hit by shot and survive as pellet carriers each year. However, application of this model led to the realisation that the observed frequencies of juvenile and older carriers observed by X-ray photography did not correspond. Accordingly, the purposes of this paper are: 1) to present the results of X-ray investigations of the Svalbard population of pink-footed geese, 2) to present a simple model intended for assessment of annual infliction rates, 3) to compare the results to the bag statistics for the Svalbard population of pink-footed geese, thereby demonstrating that the observed frequencies of first-year and older pellet carriers are inconsistent in relation to the age distribution of the bag, and 4) to discuss the possible causes of this inconsistency.

Material and methods

Data collection

Geese were caught by cannon-net at Vest Stadil Fjord (56°12'N, 08°08'E), Western Jutland, Denmark, 27 March 1990, 3 April 1991 and 25-26 March 1992. An additional sample consisting of 11 geese collected during a test catch in 1988 was included. Ageing and sexing was based on plumage characteristics and cloacal examination. Pink-footed geese moult into 'adult' plumage during their second summer, which means that two age classes can be discriminated in early spring catches, viz. 'first-year' and 'older'.

The geese belong to the Svalbard breeding population. Autumn migration is via the Norwegian mainland and Western Jutland, from whence they leave for wintering grounds in the Netherlands and Belgium during November. Depending on weather conditions, geese may return to Western Jutland from mid-December onwards. The species is protected in Germany, the Netherlands and Belgium, while open seasons exist in Norway (including Svalbard) and Denmark. The Danish season extends from 1 September to 31 December (Madsen 1987). Since 1994 hunting has also been permitted 1-15 January, but exclusively on the sea territory where very few pink-footed geese are bagged (Madsen et al. 1996). Thus, sampling was done 2.5-3 months after the hunting season closed.

The population size (November census counts 1993/1994) is 34,000 individuals, of which 4,500 are first-years (Madsen & Mitchell 1994). The annual bag is ca 3,000 individuals, of which ca 2,000 are taken in Denmark, the rest in Norway (Madsen et al. 1996). Wing surveys show that first-years make up one third of the Danish bag (Clausager 1990, 1991, 1992, 1993, 1994). We therefore assumed total bag composition to be ca 2,000 adults and 1,000 juveniles. Approximately half of the Danish bag is taken after the return of the geese from the Netherlands (i.e. after the November counts), and we subtracted 50% of the Danish bag size from the results of the November census in order to estimate numbers of pellet carriers from percentages observed in April. The resulting figures were ca 4,000 first-years and 29,000 older geese.

X-ray photography

X-raying of geese was done during capture sessions, using commercial portable equipment. Geese were masked and wrapped in cloth in order to restrain them during exposure. Picture frame size was 45 × 30 cm, and when present, pellets were easily identifiable in the photographs. Two cases where pellets may have resided in the gizzard, i.e. have been ingested and not inflicted, were excluded.

Infliction rates

If the exact age of captured geese could be determined, estimation of infliction rates could be done by subtraction of carrier frequencies of successive cohorts. However, only two age groups can be discriminated, 'first-years' and 'older'. First-year individuals X-rayed in March-April have experienced only one hunting season, and for these the infliction rate equals the percentage of pellet carriers. For older individuals, the relationship between infliction rate, adult survival and frequency of carriers can be derived under certain simplifying assumptions.

Assume that the population is stable, and that annual survival ϕ is constant after the first year of life. Thus, survival is identical for carriers and non-carriers. Assume further that the probability of pellets being inflicted upon a goose is constant over years and individuals, but differs between the two age classes. This means that within each hunting season, pellets are inflicted upon all individuals older than one year with equal probability π . This definition ignores the possibility that pellets may be inflicted upon some geese more than once within a single season, but since it is likely that very few geese will experience - and even fewer survive - this treatment, the above simplification is considered a good approximation.

Under these assumptions, the proportion of 'recruits' (i.e. individuals in their second year) in the 'older' seg-

ment of the population will be $1 - \phi$. At the time of recruitment (summer moult), this cohort still has experienced only one hunting season, and after that some proportion θ_j was carriers. At the time of X-raying in the following spring, these individuals will have survived their second hunting season, and if their survival rate was identical to that of older geese they will still make up a proportion $1 - \phi$ of the geese aged as 'more than one year'. If a proportion θ_j carried pellets after the first hunting season, the probability of an individual not being a carrier after two seasons will be

$$P\{\text{\#Pellets} = 0\} = (1 - \theta_j)(1 - \pi).$$

For each following age class, the probability of an individual not carrying pellets at the time of X-raying should therefore be

$$P\{\text{\#Pellets} = 0 \mid \text{Age} = i\} = (1 - \theta_j)(1 - \pi)^{i-1}, (i=1,2,\dots).$$

From this relationship, the expected proportion of non-carriers in the 'older' part of the population (geese aged more than one year) can be calculated by averaging over the age distribution

$$1 - \theta_a = (1 - \phi)(1 - \theta_j) \sum_{h=1}^{\infty} (1 - \pi)^h \phi^{h-1}$$

where h denotes 'adult' age (i.e. full age minus one) and θ_a the proportion of pellet carriers in the 'older' segment of the population. The sum of this series is convergent and readily calculated as

$$1 - \theta_a = \frac{(1 - \theta_j)(1 - \phi)(1 - \pi)}{1 - \phi(1 - \pi)} \quad (1)$$

Jönsson et al. (1985) used a similar approach to predict percentage of pellet carriers. However, their calculations were based on the assumption that infliction rates are age-independent and thus can be estimated directly by θ_j for all age classes. Since first-year individuals are overrepresented in the bag amongst virtually all waterfowl species, this assumption is unlikely to be supported by actual data.

According to formula 1, the frequency of adult carriers can be explained in terms of frequency of first-year carriers, annual adult survival and the probability that pellets are inflicted upon an adult goose during any one hunting season. In reality, information on θ_j , θ_a and ϕ is available, while π is unknown. By rearrangement, however, the expression can be solved with respect to π :

$$\pi = 1 - \frac{(1 - \theta_a)}{(1 - \theta_j)(1 - \phi) + (1 - \theta_a)\phi} \quad (2)$$

In the present case, estimates of θ_j and θ_a were obtained simultaneously, but other cases could be envisioned where first-year and older geese were caught on separate

occasions. Information on survival was obtained from subsequent resightings of released neck-banded geese (Madsen & Noer 1996). Hence, π is not an estimate derived from Maximum-Likelihood theory in the well-known statistical sense, but rather a combination of three different estimates obtained from three different sets of data. The variance of π can be assessed either by means of Bootstrapping (i.e. Monte-Carlo simulation of large numbers of data sets having the observed values as 'means'), or by means of Taylor-expansion of formula 2 above, the so-called delta method (Efron 1979, Seber 1982).

The sampling distribution of π was found empirically, by generation of data sets with N_j and N_a individuals, using the observed values of θ_j and θ_a as the probabilities that X-rayed individuals carry pellets. Thus, the distribution of π was simulated by 'Bootstrapping' frequencies of first-year and older carriers from binomial distributions with parameters $(N_j; \theta_j)$ and $(N_a; \theta_a)$ and values of ϕ from a normal distribution with expectation and variance estimated from capture-recapture analysis (Madsen & Noer 1996). By use of Taylor expansion, an approximate explicit expression for the variance of π is

$$V[\pi] \approx \left(\frac{\partial \pi}{\partial \theta_j}\right)^2 V[\theta_j] + \left(\frac{\partial \pi}{\partial \theta_a}\right)^2 V[\theta_a] + \left(\frac{\partial \pi}{\partial \phi}\right)^2 V[\phi] \quad (3)$$

where

$$\frac{\partial \pi}{\partial \theta_j} = \frac{(1 - \theta_a)(1 - \phi)}{[(1 - \theta_j)(1 - \phi) + (1 - \theta_a)\phi]^2}$$

$$\frac{\partial \pi}{\partial \theta_a} = \frac{(1 - \theta_j)(1 - \phi)}{[(1 - \theta_j)(1 - \phi) + (1 - \theta_a)\phi]^2}$$

and

$$\frac{\partial \pi}{\partial \phi} = \frac{(\theta_a - \theta_j)(1 - \theta_a)}{[(1 - \theta_j)(1 - \phi) + (1 - \theta_a)\phi]^2}$$

Formula 3 ignores second-order partial derivatives, particularly the covariance terms between θ_j , θ_a and ϕ . Since the three parameters are estimated from different data sets and so should have zero sampling covariances this assumption was considered justified. In particular, identical survival rates of carriers and non-carriers would mean that the covariance between ϕ and θ_j and θ_a , respectively, should be zero.

Moreover, the calculation of π by means of formula 2 could potentially be biased, i.e. the expectation of the resulting value differs from the true one. Bias was assessed from Taylor-expansion, too, by means of the formula

$$b \approx \frac{1}{2} \frac{\partial^2 \pi}{\partial \theta_j^2} \text{VAR}(\theta_j) + \frac{1}{2} \frac{\partial^2 \pi}{\partial \theta_a^2} \text{VAR}(\theta_a) + \frac{1}{2} \frac{\partial^2 \pi}{\partial \phi^2} \text{VAR}(\phi) \quad (4)$$

where

$$\frac{\partial^2 \pi}{\partial \theta_j^2} = 2 \frac{(1-\theta_a)(1-\phi)^2}{[(1-\theta_j)(1-\phi) + (1-\theta_a)\phi]^2}$$

$$\frac{\partial^2 \pi}{\partial \theta_a^2} = 2 \frac{(1-\theta_j)(1-\phi)\phi}{[(1-\theta_j)(1-\phi) + (1-\theta_a)\phi]^2}$$

and

$$\frac{\partial^2 \pi}{\partial \phi^2} = 2 \frac{(\theta_a - \theta_j)^2 (1-\theta_a)}{[(1-\theta_j)(1-\phi) + (1-\theta_a)\phi]^2}$$

Testing of the null hypothesis $H_0: \pi = 0$ was done by comparing θ_j and θ_a , which can be done for example by a 2×2 χ^2 -test. Since the alternative hypothesis, to be accepted if H_0 is rejected, would be $H_1: \pi > 0$ (i.e. $\theta_a > \theta_j$), the test should be one-sided. This could be done by accepting H_0 if $\theta_a < \theta_j$ and using the 90% quantile - i.e. a significance level $1-\alpha$ of 0.05 - as limit of significance for all other results. For a χ^2 -distribution with $df = 1$, this would correspond to a significance limit of 2.71. If the two frequencies are not significantly different, π is not significantly larger than 0.

Results

Frequencies of pellet carriers

Including the 11 specimens collected in 1988, a total of 355 pink-footed geese were X-rayed (Table 1). Frequencies of carriers in each of the three sampling years (excluding 1988) were very similar (see Table 1, first-years $\chi^2 = 0.40$, $df = 2$, $P > 0.70$, older geese $\chi^2 = 0.06$, $df = 2$, $P = 0.82$). Hence, data were pooled over years.

Of 69 first-years, 17 carried pellets ($\theta_j = 0.246$, see Ta-

Table 1. Numbers of pink-footed geese in the two age classes with and without shotgun pellets, detected by X-ray photography of 355 geese caught using cannon-net at Vest Stadil Fjord, West Jutland, Denmark, during March-April 1988-1992.

Year	First-year		Older		Total
	+ Pellets	- Pellets	+ Pellets	- Pellets	
1988	2	2	4	3	11
1990	1	4	22	41	68
1991	8	22	47	87	164
1992	6	24	30	52	112
Total	17	52	103	183	355

ble 1). 'Exact' 95% confidence limits were calculated by interpolation between tabulated values (Anon. 1970) and were [0.151; 0.365]. For older geese, 103 out of 286 were carriers ($\theta_a = 0.360$, see Table 1). The 95% c.l. were [0.300; 0.407].

Test of the difference between carrier frequencies of juvenile and older geese resulted in a test statistic of $\chi^2 = 3.22$. Using the one-sided test outlined above, the difference was significant ($P = 0.04$), though it should be noted that if the test is interpreted to be two-sided, P would be ca 0.07 and H_0 accepted.

Mean and variance of number of pellets were 1.60 and 0.54 for first-year carriers and 2.45 and 3.74 for older carriers. The former carried up to three pellets, the latter up to 10. Adult males tended to carry more pellets than females (mean and variance were 2.62 and 4.95 for males, and 2.21 and 1.85 for females). The larger means for adults were caused by a few geese with high numbers of pellets, and variance increased with mean number of pellets, which complicated statistical comparisons. Assuming that the means were normally distributed, approximate test statistics can be calculated from the standard

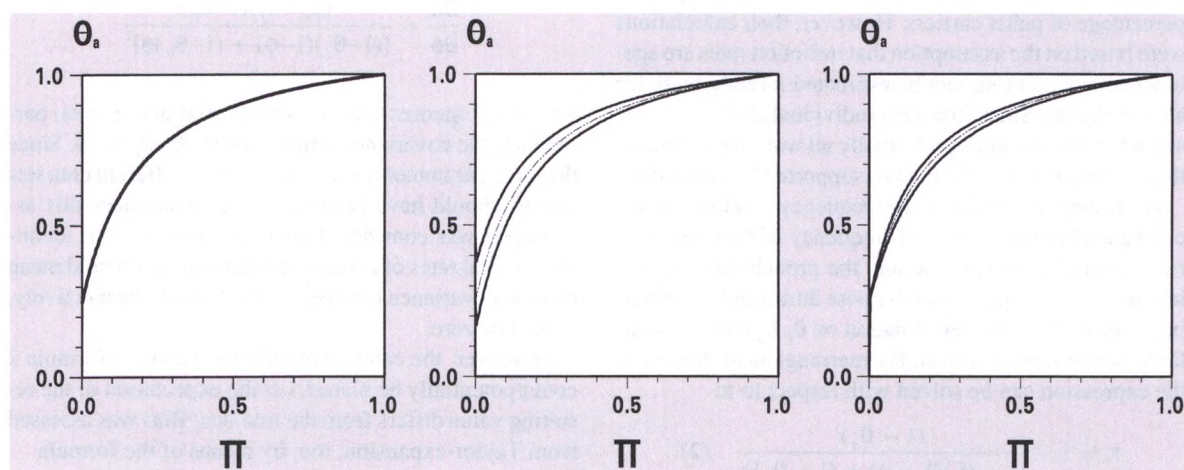


Figure 1. Predicted relationship between frequency of adult carriers (θ_a) and inflection rate (π), for an adult survival rate $\phi = 0.838$ and a frequency of first-year carriers θ_j of 0.246 (left diagram). Variation in the predicted function resulting from variation in θ_j (upper and lower 95% c.l.) is shown as solid lines in the diagram in the middle and variation in the predicted function resulting from variation in ϕ (upper and lower 95% c.l.) is shown as solid lines in the right diagram.

normal distribution, i.e. the distribution with mean 0 and variance 1. Using this, the difference between older males and females was not significant ($z = 1.14$, $P = 0.13$), but may be real since similar tendencies were found for other species by Elder (1955b). The difference between first-years and older geese, however, was significant ($z = 2.36$, $P = 0.01$). The latter test should be considered tentative since the 17 first-year carriers included in the mean make up a relatively sparse sample for the test.

Infliction rates

Infliction rate for first-year geese was estimated directly from $\theta_j = 0.246$. Based on evidence from resightings of neck-banded individuals, the estimated annual adult survival of pink-footed geese in the Svalbard population is $\phi = 0.838$, with 95% c.i. [0.815; 0.859] (Madsen & Noer 1996).

For the observed values of θ_j and ϕ , formula 1 predicts that θ_a increases sharply for small values of π . Annual infliction rates between 0.0 and 0.1 can account for adult carrier frequencies of up to ca 50% (Fig. 1). Thus, the high frequencies of pellet carriers found by X-raying of hunted geese may be explained by infliction of pellets upon only a few per cent of the population annually.

An initial sensitivity analysis was made by calculating the graphs resulting from the upper and lower 95% c.i. for θ_j and ϕ . This showed that uncertainty in θ_j has a considerable impact on the predicted relationship, while uncertainty in ϕ is less important. The uncertainty of ϕ has the largest implications for frequencies of adult carriers between 0.60 and 0.90 (see Fig. 1), but nearly all reported frequencies (studies cited above) lie below this range.

Therefore, uncertainty in the input survival rate is of less practical consequence.

Direct calculation by means of formula 2 leads to a predicted infliction rate of $\pi = 0.028$. The calculated variance of π (formula 3) was $V[\pi] = 0.239063^2 \cdot 0.002691 + 0.281567^2 \cdot 0.000806 + 0.167984^2 \cdot 0.000126 \approx 0.000150 + 0.000068 + 0.000004 = 0.000222$. Approximate 95% c.i. were obtained by multiplying the standard deviation by 1.96, which resulted in the values $\pi = 0.028 \pm 0.029$. From this 95% confidence interval is seen that the predicted π -value does not differ significantly from zero, which is consistent with the two-sided version of the χ^2 -comparison of frequencies of juvenile and adult carriers given above. By far the largest contribution to the variance of π derived from θ_j . Thus, in order to improve on the precision of the calculated π -value, particularly the sample size for estimation of θ_j should be increased.

Evaluation of bias by means of formula 4 showed that the second order partial derivative for θ_j included a factor of $(1-\phi)^2$, while the corresponding term for θ_a was $(1-\phi)\phi$. This means that for species with high adult survival, like the pink-footed goose, uncertainty in θ_a will make a much larger contribution to any bias, while, for example, for a species with an annual adult survival of 0.5 the two carrier percentages would contribute more equally. For the present data set, bias was calculated (using formula 4) to be $b \approx 0.5 \cdot [0.077409 \cdot 0.0002691 + 0.471963 \cdot 0.000805 + 0.038221 \cdot 0.000126] = 0.000297$. This shows that the estimated value of π is positively biased, i.e. π is overestimated, but if the number of X-rayed older geese is large, i.e. $\text{VAR}(\theta_a)$ is small, the calculated value of π is relatively unaffected.

The distribution of π was examined by Monte Carlo

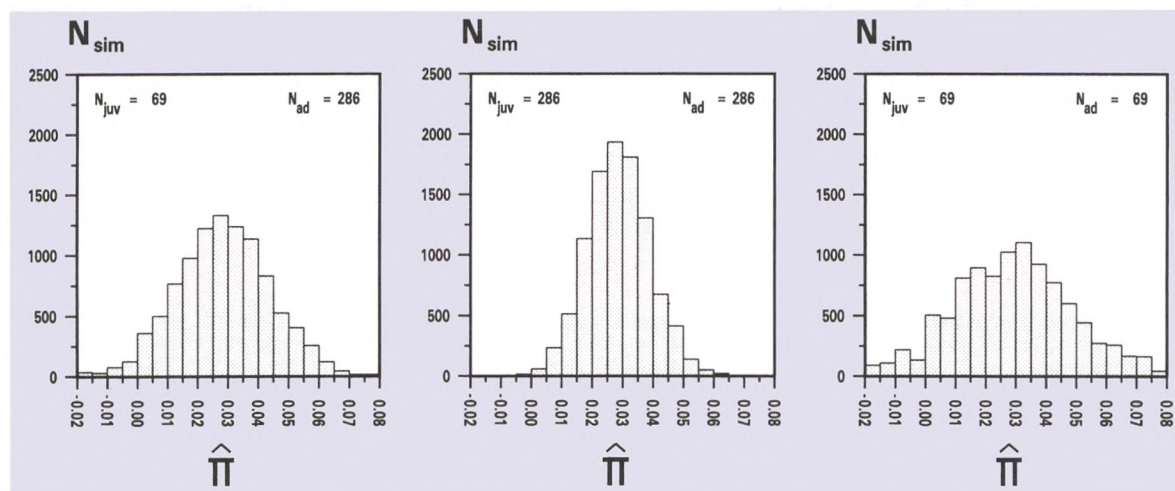


Figure 2. Distribution of π -values for 10,000 data sets generated by Monte-Carlo simulation, with samples sizes of 69 first-years and 286 older geese (left diagram). For the shown series, average observed frequencies were $\theta_j = 0.244$ and $\theta_a = 0.358$. The corresponding distributions resulting from increasing the sample size of first-years to 286 (middle diagram) or from decreasing the sample size of older geese to 69 (right diagram) are given.

simulations (Bootstrapping). For the observed sample sizes and carrier frequencies, the distribution of π is approximately normal (Fig. 2). The variance of the simulated distribution was $V(\pi) = 0.000221$, with 95% c.l. $\pi = 0.028 \pm 0.029$, in good agreement with the results of formula 3.

The gain in precision that could be obtained from increasing the sample size of first-year geese was evaluated by repeating the simulations for $N_j = 286$ (i.e. equal sample sizes of juveniles and adults). This would have resulted in a 50% reduction of the variance of π (to 0.000103), with corresponding 95% c.l. $\pi = 0.028 \pm 0.020$, i.e. a π -value roughly between one and five per cent.

Furthermore, the loss of precision in π with small sample sizes was evaluated by simulating data sets with $N_a = 69$, i.e. by small samples of both first-year and older geese. This resulted in considerable loss of precision (see Fig. 2). The average value of π was 0.029, close to the expected value of 0.028. The variance of this distribution, however, was $V(\pi) = 0.000409$, with 95% c.l. $\pi = 0.029 \pm 0.040$.

Discussion

Infliction rates and age of bagged geese

In addition to the statistical evaluation of the model presented above, the model's performance can be assessed by comparison of the predicted infliction rates for the two age classes. The bag sizes of 1,000 first-year and 2,000 older geese are relatively well documented. It is not known whether the ratio of inflicted to bagged geese depends on age, but a plausible first hypothesis would be that this is not the case. This hypothesis would imply that pellets are inflicted upon roughly two older geese for each first-year individual. Alternatively, if the ratio of inflicted to bagged individuals depends on age, older geese might be predicted to have the higher ratio because 1) they are larger and heavier (J. Madsen, unpubl. data) and so should be physically more robust to shot, and 2) they are

more wary (as evidenced by the age composition of the bag being biased towards first-years), which could mean that the average distance at which they are shot at is larger, increasing the probability that they are wounded instead of being killed. For these reasons, the model was *a priori* expected to predict infliction of pellets upon at least two older geese for each first-year.

From the observed values of θ_j (0.246) and θ_a (0.360), the value of π calculated from the model was 0.028. Assuming that sizes of the two age classes are 4,000 first-years and 29,000 older geese, these rates correspond to infliction of pellets upon ca 1,000 first-years and 800 older geese annually (Table 2, A), or to 0.8 older goose for each first-year. In our opinion, therefore, the model failed to predict what might be considered realistic infliction rates for the two age classes.

Uncertainty in π could not explain this inconsistency; if pellets are inflicted upon 1,000 first-years annually, pellets should be inflicted upon 2,000 older geese, or 6.9%, a rate that clearly cannot be accounted for by the observations (see Fig. 2). For $\pi = 0.069$, a frequency of adult carriers of ca 50% should be expected (see Fig. 1). Thus, the failure of the model to predict a realistic age distribution is apparently caused by a 'too small' difference between the observed frequencies: if 24.6% carry pellets after one hunting season, 36.0% older carriers is too low a figure, given the high survival of the species and the age-composition of the bag.

Evidence in support of this conclusion was obtained from an investigation of bean geese *Anser fabalis* in Sweden (Jönsson et al. 1985). For this species, 28% of the geese carried pellets after their first hunting season, while 62% of the older geese carried pellets. That difference was highly significant.

Two possible explanations for the inconsistency of the observed frequencies can be envisioned, viz. 1) the observed values of θ_j and θ_a are influenced by sampling variation, and hence their true values might differ from the observed values, and 2) the model is wrong. In the following, we discuss these possible explanations separately.

Table 2. Assessment of annual numbers of first-year (N_{juv}) and adult (N_{ad}) pink-footed geese inflicted with pellets and surviving (sexes pooled). Input values are frequency of adult (θ_a) and first-year (θ_j) pellet carriers as detected by X-ray photography, and adult survival rate ϕ . From these values, annual rates of infliction of adult individuals (π) are calculated. The details of the various calculations (A-E) are given in the text. Bag size is total bag for Denmark and Norway, and the age distribution is based on Danish wing surveys.

	θ_a	θ_j	ϕ	π	Bag size	N_{ad}	N_{juv}
A	0.360	0.246	0.838	0.028	2,000 ad. + 1,000 juv.	810	1,020
B	0.360	0.151	0.838	0.050	-	1,440	625
C	0.407	0.246	0.838	0.042	-	1,210	1,020
D	0.407	0.151	0.838	0.065	-	1,875	625
E	0.300	0.151	0.859	0.029	-	835	625

Sampling variation of carrier frequencies

The sample size of first-year individuals was small, and 95% c.l. correspondingly large. Use of the lower 95% c.l. for θ_j (0.151) led to an estimated value of π of 0.050, which would correspond to infliction of pellets upon 625 first-years and 1,440 older geese annually (see Table 2, B). This would be consistent with an age-independent ratio of inflicted to killed geese. Hence, the observed inconsistency could be explained by assuming that the true percentage of first-year carriers was close to the lower 95% confidence limit.

With respect to θ_a , the upper 95% c.l. (0.407) corresponded to infliction of pellets upon ca 1,000 first-year and 1,200 older geese annually (see Table 2, C). Thus, because of the larger sample sizes for older geese, variation in θ_a could not account convincingly for the inconsistency.

A combined overestimation of θ_a and underestimation of θ_j could more than explain the discrepancy. Three times as many adults as juveniles are predicted to be inflicted (see Table 2, D). Clearly, one way to account for the inconsistency was to assume that either one (first-year) or both observed carrier frequencies differed from the true values to an extent where they might be considered unrepresentative. In this case, the 'bootstrapped' distribution of π -values in Figure 2 would likewise be based on wrong assumptions. A more realistic distribution would then be obtained by shifting the shown distribution five intervals to the right.

Model assumptions

In assuming population stability, no senescence, constant rates of infliction over years and individuals, and identical survival rates of carriers and non-carriers, the model undoubtedly represents a simplified version of reality.

For a growing population, the proportion of recruits in the adult segment will be larger than assumed (i.e. $> 1 - \phi$). Since $\theta_j \leq \theta_a$, violation of this assumption will lead to underestimation of θ_a , and consequently to underestimation of π . However, the pink-footed goose population has been growing at an annual rate of only 1% during the investigated period (Madsen & Mitchell 1994). This rate is too low to affect the estimated π -value.

Effects of senescence were assessed by means of a truncated survivorship curve. For infliction rates of 0.246 and 0.069 (i.e. for age independent ratios of inflicted to bagged numbers), a maximum life-span of 9-10 years would be required to account for the observed 36% frequency of adult carriers. Ringing recoveries show that pink-footed geese reach considerably higher ages (e.g. 21 years, Cramp & Simmons 1977), hence this is clearly unrealistic.

The use of constant annual infliction rates was invoked

to represent an 'average' situation. Over the three years of this investigation, little variation in carrier frequencies was observed (see Table 1). Moreover, X-ray photography of 58 adult geese collected for physiological analysis (by rifle shooting) in Denmark and Norway, January-May 1996, revealed 21 pellet carriers, or 36.2% (J. Madsen, unpubl. data). This evidence clearly supported the assumptions of time constancy and representability of carrier frequencies in cannon-net catches. Hence, there is no evidence that the assumptions of constant annual infliction rates and carrier percentages are violated. The assumption that the probability of infliction was identical for all individuals admittedly could be violated, but if some subset of the geese had a higher probability of infliction they would undoubtedly also have a higher probability of being killed by hunters, and in this case a lower survival of pellet carriers might be expected.

The one untested assumption of the model thus appeared to be that survival of pellet carriers and non-carriers was identical. Obviously, violation of this assumption by higher mortality of carriers could cause systematic underrepresentation in X-ray sampling. To assess this possibility, the model was generalised to include differential survival of non-carriers (ϕ_n) and carriers (ϕ_c). In this case, mean adult mortality would be $1 - (1 - \theta_a)\phi_n - \theta_a\phi_c$, and for a stable adult population this would be the frequency of recruits. Mean survival of adults and frequency of recruits would thus depend on θ_a , and possibly on π . After the second hunting season (i.e. at the time of X-raying), the expected frequency of non-carriers amongst the newly recruited adults would be

$$1 - \theta_{a,1} = \frac{(1 - \theta_j)(1 - \pi)\phi_n}{(1 - \theta_j)(1 - \pi)\phi_n + (\theta_j + \pi(1 - \theta_j))\phi_c}$$

while the relative frequency of non-carriers in each following age class would be

$$1 - \theta_{a,i} = \frac{(1 - \theta_{a,i-1})(1 - \pi)\phi_n}{(1 - \theta_{a,i-1})(1 - \pi)\phi_n + (\theta_{a,i-1} + \pi(1 - \theta_{a,i-1}))\phi_c}$$

($i = 2, 3, \dots$).

Using the relative size of the first age class $(1 - (1 - \theta_a)\phi_n + \theta_a\phi_c)$ as a starting point, the size of each following age class can be calculated successively by

$$a_i = a_{i-1} [(1 - \theta_{a,i-1})(1 - \pi)\phi_n + (\theta_{a,i-1} + \pi(1 - \theta_{a,i-1}))\phi_c]$$

($i = 2, 3, \dots$). Note that in the case of identical survival rates of carriers and non-carriers, the expressions collapse into formula 1 given above.

Since overall survival was 0.838, ϕ_c and ϕ_n were further constrained to the relationship $0.838 = \theta_a\phi_c + (1 - \theta_a)\phi_n$, i.e. the equation $\phi_c = (0.838 - (1 - \theta_a)\phi_n)/\theta_a$ must be satisfied. Combining this and the formulas given above, the overall adult carrier frequency θ_a can be found as in for-

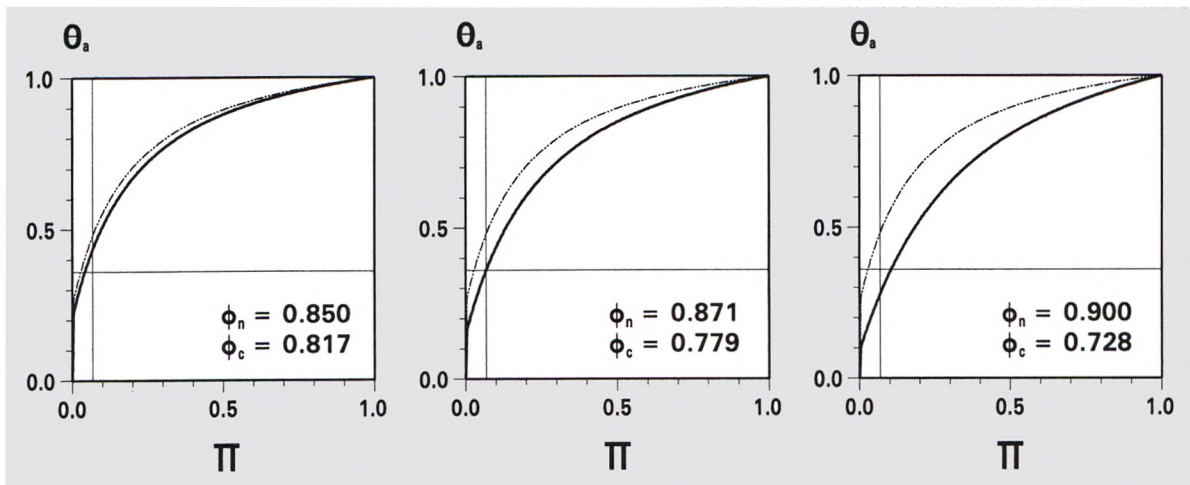


Figure 3. Predicted relationship between frequency of adult carriers (θ_a) and inflection rate (π) if survival differs for non-carriers (ϕ_n) and carriers (ϕ_c). The frequency of pellet carriers among recruits is $\theta_j = 0.246$, annual adult inflection rate is $\pi = 0.069$, and ϕ_n and ϕ_c are constrained to a mean population survival of 0.838. Survival rates of 0.850 and 0.817 predict over 40% adult carriers, i.e. a higher than observed value (left diagram). Conversely, survival rates of 0.900 and 0.728 predict less than 30% adult carriers (right diagram). To predict the correct frequency of 36.0% adult carriers, survival must be 0.871 for non-carriers and 0.779 for carriers (middle diagram). The graph for identical survival of carriers and non-carriers ($\phi_n = \phi_c$) is shown for comparison (thin dashed line, cp. Fig. 1), and π and θ_a are indicated by vertical and horizontal thin lines.

mula 1 above, by averaging over age classes. This was done numerically. The successive values of $\theta_{a,i}$ and a_i corresponding to ϕ_n were calculated, and the resulting value of θ_a was found by summation over cohorts. This process was then repeated iteratively, until the value of ϕ_n predicting the correct value of θ_a (0.36) had been determined.

Assuming that $\theta_j = 0.246$ and that the ratio of bagged to wounded geese is similar for first-year and older geese, i.e. that ca 2,000 older geese are inflicted annually ($\pi = 0.069$), the model predicts that if the inconsistency is explained by differential mortality between carriers and non-carriers, the values of ϕ_n and ϕ_c would have to be approximately 0.871 and 0.779 (Fig. 3). It should be noted that for this more general model the assumption of no sampling covariance between θ_a and ϕ would be invalidated, i.e. formulas 3 and 4 are not valid for the model with differential mortality.

Concluding remarks

The proposed model rests on rather strict assumptions with respect to population stability and constancy of annual survival and harvest rates. These assumptions may represent species with high annual survival rates - like the pink-footed goose - better than species with lower annual survival and presumably more fluctuating population sizes and harvest rates. Hence, the model should not be applied to data for species with fluctuating survival and harvest rates and population sizes unless sensitivity analysis can demonstrate that the conclusions are robust.

The results of the statistical analysis of the model's

properties, moreover, emphasised that this approach should only be used when numbers of X-rayed individuals are sufficient to ensure a fairly high precision of the estimated carrier frequencies. For the pink-footed geese, the major source of uncertainty undoubtedly is that only 69 first-year individuals were X-rayed, but in addition the estimated annual inflection rate π will be biased unless sample sizes of older birds are substantial.

Given these limitations, we found this model useful in the initial analyses of the pink-footed goose data. In the first step, the model showed that relatively small annual inflection rates - below ca 0.07 - could account for the observed frequency of adult pellet carriers; in the next step, the model helped us to realise that the predicted inflection rates were inconsistent with the age distribution of bagged geese, and that the observed frequencies of pellet carriers in the two age classes were mutually conflicting. The possibility of random variation affecting the observed frequencies could not be excluded, but in that case the true value of θ_j would have to be considerably lower than the observed one.

Assuming that the first of these explanations was true, estimates of minimum inflection rates were obtained by combining the lower 95% c.l. of carrier frequencies for both first-year and older geese with the upper 95% c.l. of survival. The resulting inflection rate was $\pi = 0.029$, corresponding to infliction of pellets to 625 first-year and 835 older geese annually (see Table 2, E). Though these minimum numbers tend to be inconsistent with the age distribution expected on the basis of bag composition, they cannot be directly refuted.

Compared to the overall bag size of ca 3,000 geese, the estimated minimum of pellets being inflicted upon 1,460 geese annually thus suggests that the ratio of inflicted to bagged geese is at least ca 0.5. To derive this minimum estimate, moreover, we used the most conservative assumptions of sampling variation in both θ_j , θ_a and ϕ , which together represent an unlikely combination.

In addition to the geese identified as carriers by X-ray examination, an unknown loss of crippled, non-retrieved individuals must be added, together with the geese which are wounded but survive without retaining pellets. Few data exist concerning the size of these proportions, but for North American mallards *Anas platyrhynchos* Bellrose (1953) presented data suggesting that they may add a further 0.5-1.0 individuals for each individual inflicted with pellets. Thus, the minimum ratio of wounded to bagged individuals is likely to be substantially higher than 0.5.

Alternatively, the discrepancy between the 24.6% first-years and the 36.0% older geese carrying pellets might be explained by lower survival of pellet carriers. In this case, the estimated annual infliction rates will be somewhat higher. The 'differential survival' hypothesis can be tested by analysis of resightings of neck-banded geese. This will be treated in a companion paper (Madsen & Noer 1996).

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