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Bell, M.C., Fox, A.D., Owen, M., Black, J.M. & Walsh, A.J. (1993)

*In: Lebreton, J-D. & North, P.M. (Eds.); Marked individuals in the Study of
Bird Populations. - Birkhauser Verlag, Basel, pp. 141-155.*

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Approaches to Estimation of Survival in Two Arctic-Nesting Goose Species.

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Summary. Survival rates are estimated in two populations of arctic-nesting geese: Svalbard-breeding Barnacle Geese *Branta leucopsis*, wintering on the Solway Firth, southwest Scotland; Greenland White-fronted Geese *Anser albifrons flavirostris*, wintering on the Wexford Slob, southeast Ireland. The Barnacle Goose population is discrete, with virtually no exchange with Greenland- and Russian-breeding populations. Annual survival rates are estimated from resightings of marked birds; the effects of sample size and resighting strategy are considered, and conclusions are drawn about the design of mark-resighting schemes. The Greenland White-fronted Goose population is neither discrete nor closed: there is significant exchange between population components. Annual survival rates are estimated from resightings and recoveries of marked birds, and also from census statistics.

1. Introduction

Eight species or sub-species of arctic-nesting geese have regular wintering grounds in Britain and Ireland. Most of these are legal quarry for hunters over at least part of their ranges. There is good information on the size of wintering goose populations, yet little is known of the processes by which numbers are regulated. This paper considers what is perhaps the most important population process, that of mortality. We examine methods for the estimation of survival in two arctic-nesting goose species, comparing estimates obtained from recoveries or resightings of marked birds with those obtained from population size and productivity data.

The population of Barnacle Geese *Branta leucopsis* (Bechstein) which winters on the Solway Firth in south-western Scotland and breeds in the Svalbard archipelago is probably the best studied goose population in the Western Palaearctic. The population has been studied on the wintering grounds and periodically on the breeding and staging grounds since 1973. During this time numbers of Barnacle Geese have risen from about 4,000 to 10-12,000. The population is virtually closed, with little or no interchange with Russian- and Greenland-breeding Barnacle Geese (Owen & Black, 1989a).

Over 6,000 Svalbard-Solway Barnacle Geese have been marked with plastic leg rings since 1973, and the resighting rate of birds alive and ringed has been estimated to be in excess of 95% (Owen & Black, 1989a). Owen (1982) calculated that only 0.14% of living birds were missed for more than one year. Owen (1982) and Owen & Black (1989a) estimated rates of mortality in cohorts of ringed Barnacle Geese under the simple assumption that a goose not seen in two successive seasons died soon after the date of its last resighting (see also Owen & Black, 1989b). In this paper we compare survival rates estimated using this *ad hoc* approach with

maximum-likelihood estimates obtained using a full Jolly-Seber approach in which both survival and resighting rates are estimated. We also address the question of how much marking and resighting data are required for the data-set to retain its essential information content with regard to annual variations in survival.

The Greenland White-fronted Goose *Anser albifrons flavirostris* Dalgety & Scott breeds in western Greenland, and winters in Britain and Ireland (Salomensen, 1950). This paper examines survival amongst geese wintering at the single most important site, the Wexford Slobs in southeast Ireland, where up to 37% of the world population is concentrated. Population size at the Slobs has risen from 6,000 geese in the early 1970's to over 8,000 after the introduction of protective legislation in Britain and Ireland. The population is neither discrete nor closed: about 15% of Wexford geese change wintering sites between years, most commonly being seen at the other major resort, Islay in western Scotland (Wilson *et al.*, 1991). We compare survival rates estimated from population census statistics with those estimated from a marking programme: both recoveries and resightings of marked birds are considered.

2. Methods

2.1. Barnacle Geese

2.1.1. Marking of birds

Captures are by rounding up of flightless birds during the post-breeding moult (July and August) on the breeding grounds on Svalbard and by cannon-netting of birds on the wintering grounds at the Caerlaverock wildfowl refuge on the Solway Firth. Worn or lost rings are replaced on recaptured birds. Geese are resighted by regular observers throughout the wintering period, October to March. Leg rings are individually identifiable by three-character codes, which can be read at distances of up to 250m with the aid of a telescope. See Owen (1982) and Owen & Black (1989a,b) for an overview of the Barnacle Goose population study.

2.1.2. Estimation of survival

Annual survival rates were estimated firstly by the *ad hoc* method, assuming that a bird not seen in two successive seasons did not live to return to its wintering grounds after the date of its last resighting, and secondly from Jolly-Seber models of survival and resighting probabilities. In both cases the survival year was between winters, nominally October to October, but the effective resighting period differed between methods. In the *ad hoc* approach, resightings at any time of the year were considered as evidence of a bird being alive. In the Jolly-Seber approach the resighting period was limited to October to March, in order to reduce sampling time as against time between samples; entry of summer-ringed birds into the resighting matrix was conditional on survival to October - surviving birds were included with the following winter's cohort.

We considered 15 years of ringing from winter 1973/74, involving 4640 ringed birds. Ringing totals varied from 0 to 1634 birds per year. Maximum-likelihood estimates were obtained using program SURGE4 (Clobert *et al.*, 1987; Pradel *et al.*, 1990). A complete hierarchy of time-dependent models from $S_{,,P}$ to S,P was

estimated (model notation after Kanyamibwa *et al.* (1990) and Peach *et al.* (1991) - S denotes survival probabilities, P denotes resighting probabilities, t indicates time-dependence in each case). For the sake of simplicity, survival and resighting probabilities were assumed not to be age-dependent (although it might be biologically more realistic to consider survival of first-years and adults separately, as with the Greenland White-fronted Geese below). Logistic constraints were applied to the estimated parameters ($\text{logit}(\theta)$, where θ is a parameter value), so that estimated survival and resighting probabilities were constrained in the range 0 to 1. Standard errors and confidence intervals around estimates were based on logit^{-1} transformation of the transformed values (Pradel *et al.*, 1990), thus confidence intervals are asymmetric. Models were compared through likelihood-ratio tests, by which were selected the most parsimonious and biologically meaningful models adequately to describe the data. Annual survival probabilities estimated under these models were compared with *ad hoc* survivorship estimates averaged over cohorts for any one year.

The effects of reducing ringing effort were explored through random selection (without replacement) of birds from the ringing totals for each year, i.e. random selection of capture-resighting histories. Ringing totals were reduced either to a fixed percentage of their original values, or to a fixed number of new rings in each year. We also considered the effects of restricting the resighting period. Models were estimated for resighting matrices constructed using resightings restricted to single months, October to March. In each case estimates were compared with those obtained for the full data set.

2.2. Greenland White-fronted Geese

2.2.1. Census statistics

Monthly counts were made of the Wexford Slobs each winter, 1970/71 to 1989/90. We used the peak mid-winter count to define the overall wintering population size after the end of the shooting season. Adult survival rates were calculated from estimates of population size and productivity by the method of difference (Owen, 1982; Ebbinge *et al.*, 1991): percentage survival (S) between winters $i-1$ and i is given by

$$S_{i-1 \rightarrow i} = 100 \times (N_i - N_i P_i) / N_{i-1}$$

where N_i and P_i are total population size and proportion of first year birds in winter i respectively.

2.2.2. Marking of birds

Between October 1983 and March 1990 706 geese have been captured at Wexford using cannon-nets. Birds were marked with a white plastic leg ring bearing three characters and an orange plastic neck collar bearing the same code in black. Collar codes may be read with the aid of a telescope at distances of up to 800m (Warren *et al.*, 1991). There is a regular resighting programme at the Wexford Slobs, and systematic checking of geese for rings and collars at the other major wintering site, Islay in western Scotland.

2.2.3. Recoveries of marked birds

Maximum-likelihood estimates of survival rates were obtained from recoveries of collared geese using the model framework of Brownie *et al.* (1985). It is known that survival is lower among juveniles than adults (Kampp *et al.*, 1988) and so a hierarchy of two-age-class models in the BROWNE-set was used: H1 - time-dependence in both survival and recovery rates; H02 - time-dependent recovery rates, constant survival in each age-class; H01 - constant annual rates of survival and recovery in each age-class. Model comparisons were through likelihood-ratio tests by which was selected the most parsimonious model. Goodness-of-fit χ^2 tests were applied to models, with expected values from the recovery matrix, and pooling within cohorts (rows) to give expected values >2 . All calculations were performed using program MULT (Conroy *et al.*, 1988).

In two years of the study (1985/86 and 1989/90) regulated shooting was permitted on the Wexford Slobs, coinciding with the period of marking and resighting. However, because marked geese were resighted frequently throughout the winter it was possible to construct a post-hunting-season recovery matrix, based on a January to January survival year. We removed from the banding vector any bird never seen again after December 31st in its winter of banding; similarly, birds recovered before December 31st in their winter of banding were removed from the banding vector and recovery matrix. Adjusted banding totals ranged from 28 to 100 adults and from 33 to 75 first-years. Geese collared in 1983/84 were excluded from the analysis because their low recovery rate precluded estimation of the full hierarchy of models.

2.2.3. Resightings of marked birds

Survival rates of adult and first-years were also estimated from resightings of collared birds. Data were restricted to birds marked and resighted in County Wexford. Maximum-likelihood estimates of survival and resighting probabilities were obtained using program SURGE4. Resighting matrices for birds collared as first-years and birds collared as adults were entered separately into the program, with equality constraints between data sets on the parameters fitted, as appropriate for each model. A starting model was adopted in which both survival and resighting rates were time- and age-dependent, with age-dependence limited to the distinction between first-year and adult birds. Estimates were obtained for a full hierarchy of models in the set S_{a2^*}, P_{a2^*} , to S,P ($a2$ indicates age-dependence of parameters limited to two age-classes - first-years and adults). Goodness-of-fit χ^2 tests were applied to final models, with expected values pooled according to time of last resighting in each cohort (Clobert & Lebreton, 1985; Lebreton & Clobert, 1986). In age-dependent models expected values were pooled separately for adults and first-year birds for the first year of each cohort, otherwise pooling was across data sets.

Resighting matrices were constructed in a similar fashion to the recovery matrix, in order to avoid coincidence of shooting with sampling: geese never resighted after December 31st in their winter of ringing were removed from the banding vector; only resightings occurring after December 31st in each winter were considered. The survival year is thus January to January, in line with both recovery and census analyses. Adjusted banding totals ranged from 15 to 99 adults and from 29 to 78 first-years.

3. Results

3.1. Barnacle Geese

3.1.1. Comparison of methods

Maximum-likelihood estimates of survival rates correspond quite closely to those estimated by the *ad hoc* method (Figure 1). However, estimates from the latter method tend to be slightly lower, indicating that the assumption of 100% resighting probability over two years is not entirely justified. These estimates differ from maximum-likelihood estimates by an average of 1.5%, which is not large in relation to annual survival in the order of 90%, but may cause significant bias in the corresponding mortality estimates. Mean resighting rate estimated by maximum-likelihood is 70.7%, which is much lower than expected, even considering the more restricted resighting period (October to March) compared with the *ad hoc* method (all year).

3.1.2. Ringing effort

The yearly pattern of survival rates estimated by the maximum-likelihood method is largely retained, even at greatly reduced ringing effort (Figure 1), but increased parameter variance means that estimates from different years cannot be statistically distinguished. As would be expected, the mean estimates for each year from repeated (five) random selections of capture histories did not differ markedly from those using the full resighting matrix, but the coefficient of variation between estimates increased from about 2% at 75% of the full ringing effort, to about 20% at 5% effort.

Reduction of ringing effort also has implications for model selection. Considering fixed ringing totals for a five year subset of the data, hypotheses of constancy of survival and/or resighting rates are firmly rejected at and above the threshold of 30 new rings per year (likelihood-ratio tests, $P < 0.001$). Presumably, rather larger ringing totals would be required to detect age-dependence in addition to time-dependence.

Figure 1. Annual survival rates of Barnacle Geese estimated from resightings. *Ad hoc* estimates: —. Maximum-likelihood estimates from model $S_{11}P_1$: □ all rings; + 20% ringing effort; ◇ 5% ringing effort. Vertical lines represent 95% confidence limits. See text for explanation.

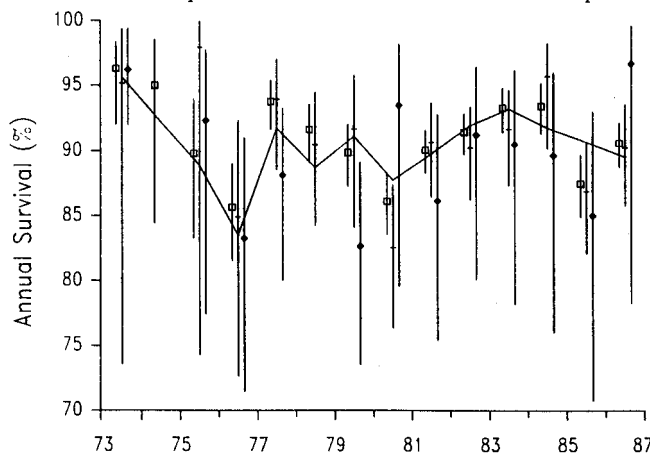


Figure 2. Distribution through the winter season of resightings of Barnacle Geese on the wintering grounds: mean and standard error of percentage of birds first resighted in each month.

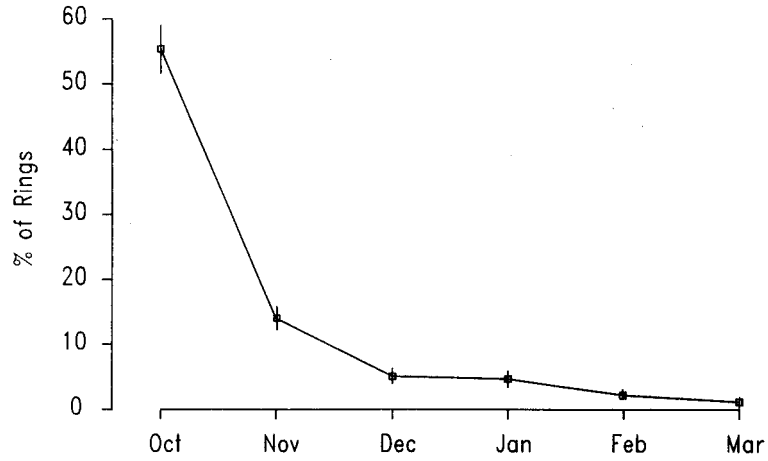


Figure 3. Maximum-likelihood estimates of annual survival rates of Barnacle Geese from model S₁P₁; comparison between estimates based on an October to March resighting period (—) and estimates based on single month resighting periods. □ October; + November; ◊ December; △ January; × February; ▽ March. See text for explanation.

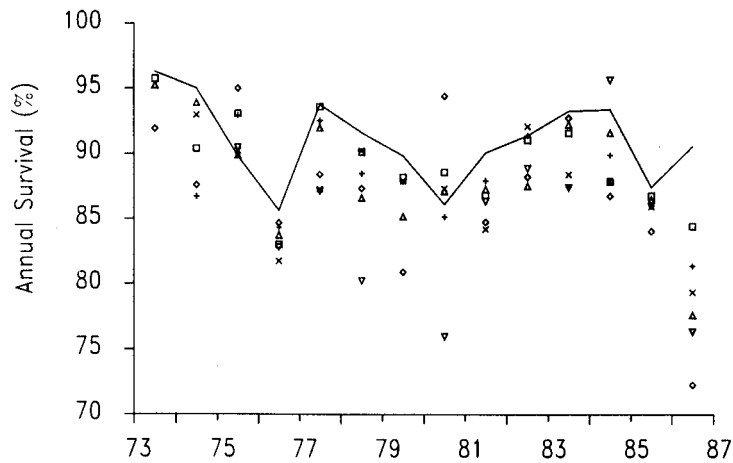


Table 1. Mean between-winter survival and resighting rates for Barnacle Geese, estimated from model $S_{t,P}$; comparisons between different sampling periods. Comparisons limited to 11 years for which survival and resighting rates were separately identifiable for all sampling periods.

Sampling Period	Survival Rate		Resighting Rate	
	Mean	S.E.	Mean	S.E.
October-March	0.9029	0.0086	0.7342	0.0263
October	0.8882	0.0103	0.6292	0.0473
November	0.8796	0.0108	0.5209	0.0556
December	0.8716	0.0188	0.3611	0.0550
January	0.8748	0.0127	0.4311	0.0671
February	0.8681	0.0114	0.3987	0.0654
March	0.8525	0.0180	0.2687	0.0559

3.1.3. Timing of resighting effort

The between-winter survival year dealt with so far is based on an October to March resighting period, which clearly violates the model assumption of negligible duration of sampling as against time between samples. On average, over half of all rings to be resighted in any one winter are seen by the end of October (Figure 2); this offers the possibility of a much shorter resighting period, such as the month of October or a similarly short period.

The yearly pattern of estimated survival differs considerably depending on which month is chosen for marking/resighting (Figure 3), which may be due in part to variations in within-winter survival. However, mean survival rates estimated using each single month, October to March, as the mark-resighting period are also different (Table 1), although not significantly so ($F_{5,50}=1.80$, $P=0.130$). Mean estimates of survival and resighting rates appear to be correlated between sampling periods (Pearson $r=0.950$, $d.f.=4$, $P=0.004$), the reasons for which are unclear, but it may result from heterogeneity of resighting and/or survival probabilities. The October results most closely resemble those for the full resighting period. Clearly, however, the time chosen for sampling strongly influences the modelling of survival, so that it is vital to define the survival year very clearly.

3.2. Greenland White-fronted Geese

3.2.1. Census statistics

Figure 4 shows annual survival rates of adult Greenland White-fronted Geese estimated by the method of difference. These ranged from 68.4% to 97.7% for the period 1970/71 to 1989/90, mean 84.4%.

3.2.2. Recoveries of marked birds

A BROWNIE format recovery matrix for birds collared as adults and first-years is shown in Table 2. Recovery rates were low so that the information content of the recovery matrix is correspondingly low. The null hypothesis of constant annual

Figure 4. Annual survival rates of Greenland White-fronted Geese wintering at Wexford, estimated from census statistics.

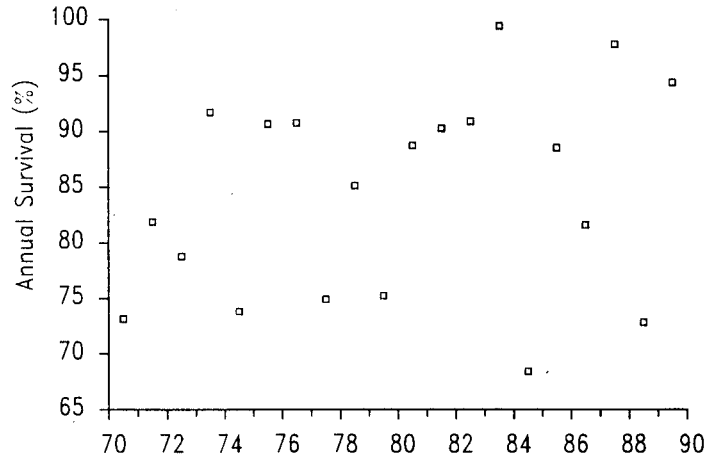


Table 2. Recovery matrix for Greenland White-fronted Geese marked with neck collars as adults and first-years at Wexford 1984 to 1989, adjusted for a January to January survival year.

Year Marked	Number Marked	Year of Recovery						
		1985	1986	1987	1988	1989	1990	
Geese marked and released as adults								
1984	100	9	1	2	5	2		
1985	53		1	1	1	1	3	
1986	30			3				
1987	28				2	1		
1988	69					6	1	
1989	33							1
Geese marked and released as first-years								
1984	61	7	2		2	2		
1985	75		4	4	3			
1986	60			4	2	3	1	
1987	62				2	1	1	
1988	38					4		
1989	33							1

Table 3. Annual survival and recovery probabilities for Greenland White-fronted Geese estimated under BROWNE-set model H01 from recoveries of geese neck banded at Wexford, 1984 to 1989. See text for explanation.

Parameter	Estimate	S.E.	95% C.L.	
First-Year Survival	0.5964	0.1521	0.2983	0.8945
First-Year Recovery	0.0699	0.0141	0.0424	0.0975
Adult Survival	0.7244	0.0723	0.5827	0.8661
Adult Recovery	0.0542	0.0723	0.5827	0.0742

survival rates within age-classes was not rejected (H1 vs H02, $X^2=3.51$, d.f.=8, $P=0.898$), nor was that of constant annual recovery rates (H01 vs H02, $X^2=14.8$, d.f.=10, $P=0.138$). The final model, H01 constant annual survival and recovery rates within each age-class, was a good fit to the data ($\chi^2=20.2$, d.f.=20, $P=0.447$). Parameter estimates from this model are shown in Table 3.

3.2.3. Resightings of marked birds

Comparisons of models in the hierarchy S_{a2^n}, P_{a2^n} to S,P are shown in Table 4. Null hypotheses of no age- or time-dependence of resighting probability were accepted, but it was not possible to simplify survival probabilities beyond age- and time-dependence. Estimates of survival and resighting probabilities under the final model S_{a2^n}, P are given in Table 5. This model fits the data very well ($\chi^2=11.1$, d.f.=27, $P=0.997$). Very low survival was estimated among the last cohort of first-years (20%). Inspection of the raw resighting data reveals that this was due to two groups of closely related collared juveniles which failed to return to Wexford after their first winter. The most likely fate of these birds is that they were shot as family groups on migration, probably in Iceland. Clearly, the fundamental assumption of independence in the behaviour of marked individuals is violated.

Table 4. Comparisons between models for survival rates of Greenland White-fronted Geese estimated from resightings of collared birds. n.p.: number of identifiable parameters; d.f.: degrees of freedom. See text for explanation.

Model	n.p.	Deviance	Likelihood-ratio test	d.f.	Outcome
Modelling resighting rate					
(1) S_{a2^n}, P_{a2^n}	26	2792.89	—	—	—
(2) S_{a2^n}, P	19	2795.42	(2)-(1)=2.53	7	(2) accepted, $P=0.925$
(3) S_{a2^n}, P	15	2800.45	(3)-(2)=5.03	4	(3) accepted, $P=0.284$
Modelling survival rate					
(4) S,P	8	2845.07	(4)-(3)=44.6	7	(4) rejected, $P<0.001$
(5) S_{a2^n}, P	3	2850.83	(5)-(3)=50.4	12	(5) rejected, $P<0.001$

Table 5. Annual survival and resighting probabilities for Greenland White-fronted Geese estimated under model S_{22^*}, P from resightings of collared birds. See text for explanation.

Parameter	Estimate	S.E.	95% C.L.	
Survival of first-years:				
1983-1984	0.7769	0.0888	0.5607	0.9047
1984-1985	0.6803	0.0651	0.5421	0.7927
1985-1986	0.7653	0.0569	0.6368	0.8585
1986-1987	0.6947	0.0633	0.5590	0.8033
1987-1988	0.8309	0.0573	0.6885	0.9161
1988-1989	0.5175	0.0880	0.3497	0.6815
1989-1990	0.1990	0.0817	0.0834	0.4042
Survival of adults:				
1983-1984	0.5722	0.1379	0.3072	0.8013
1984-1985	0.7159	0.0439	0.6227	0.7937
1985-1986	0.8604	0.0352	0.7762	0.9163
1986-1987	0.6659	0.0345	0.5953	0.7297
1987-1988	0.8332	0.0299	0.7663	0.8839
1988-1989	0.7456	0.0310	0.6802	0.8016
1989-1990	0.7716	0.0405	0.6828	0.8413
Resighting:				
	0.7852	0.0142	0.7561	0.8117

3.2.4. Comparison between estimates

Survival rates of adult Greenland White-fronted Geese were estimated to be higher from census statistics than from resightings or recoveries of marked birds. Mean annual survival of adults was estimated at 84% by the method of difference, whilst resighting and recovery analyses gave mean estimates in the range 72-74% (for slightly differing periods). Presumably the lower estimates from at least the resighting scheme result from the compounding of mortality with emigration of marked birds, estimated by Wilson *et al.* (1991) to be about 15% per year. However, in a geographically open population, conclusions about annual survival rates drawn even from census statistics depend strongly on the assumption of no net emigration; in practice it is difficult to distinguish between patterns of survival and site-fidelity.

Both resighting and recovery analyses estimated lower mean annual survival amongst first-years than adults, although the difference was not consistent across all years from the resighting analyses (see Table 5). Recovery analyses failed to pick up time-dependence of survival, presumably owing to the very low information content of the recovery matrix (Table 2). Estimates from BROWNIE-set model H1 are nonsensical, with confidence limits encompassing survival probabilities of 0 and 1. Estimates from resightings bear little relation to equivalent estimates from the method of difference (Pearson correlation coefficient, $r=0.013$), which may result from

variation in the annual rate of emigration of marked birds, as well as from over- or under-estimates of population size and/or productivity.

4. Discussion

4.1. Methods of survival estimation

In essence, the two approaches used in this paper to the estimation of Barnacle Goose survival rates from resightings of ringed birds are the same. The *ad hoc* method is a Jolly-Seber method, but with resighting rate assumed to be 100% over two years. Confidence intervals around estimates could have been constructed using binomial probabilities. In the light of the relatively low annual resighting probabilities estimated by maximum-likelihood, albeit for a shorter resighting period, the assumption of 100% resighting probability over two years needs in future to be more closely examined.

The more rigorous statistical framework of the maximum-likelihood approach is clearly preferable, particularly considering the availability of software such as SURGE4 providing flexible and efficient estimation of models and testing of hypotheses. Nevertheless, considering the use made of the *ad hoc* method in drawing conclusions about patterns of mortality (Owen, 1982; Owen & Black, 1989a), it is encouraging that the two approaches give comparable results. Owen (1982) provided evidence for the reliability of the *ad hoc* method through comparison of annual mortality estimates derived by this method with those obtained from population size and productivity data: correspondence between the estimates was good, but estimates from census data were considerably more variable. Owen concluded that small errors in counts or age-ratio assessments make a large difference in apparent mortality, but that such errors are largely self-compensating over time so that the mean over a number of years is reliable. Ebbinge *et al.* (1991) came to similar conclusions regarding estimation of survival of Russian Barnacle Geese from census statistics. Greater reliance may thus be placed on individual annual estimates derived from resightings.

Despite problems of non-independence of resighting histories (discussed below), the final model from Jolly-Seber analysis of resightings of Greenland White-fronted Geese is the most biologically sensible, or at least that which would be intuitively expected given our knowledge of the population - resighting probability constant between years, survival probabilities differing between years and between adult and first-year birds. Resighting effort at the Wexford Slobs is so high that resighting probability is effectively constant - most geese that are seen at all are seen repeatedly during the winter season. We already know that survival of first-years tends to be lower than that of adults (Kampp *et al.*, 1988), and it is suspected that winter shooting mortality, which is very variable between years, is a significant addition to natural mortality. In a forthcoming publication (Bell *et al.*, in prep.) the effects on annual survival of winter shooting mortality and hunter-induced emigration are examined through the incorporation of external variables into Jolly-Seber type models. However, despite this plausible modelling of survival, the survival rate estimates themselves are very different from those derived from census statistics. This must partly be because the resighting approach suffers from the compounding of emigration with mortality - the magnitude of the difference in estimates between methods appears to be accounted for by what we know about exchange of birds

between sites. Also, as has been noted above, the estimation of survival from census statistics depends on their being no net immigration or emigration, a probably unrealistic assumption for a geographically open population. It would be possible to include emigration probability as a third element in resighting models, but the proliferation of parameters to be estimated is likely to place unreasonable demands on the amount and quality of data collected. A preferable alternative for species such as Greenland White-fronted Geese concentrated at a few major sites, would be to consider data from several sites in the same analysis, examining exchange of birds between sites. This will soon be possible for the Greenland White-fronted Geese since, in addition to the Wexford marking scheme, wintering birds are now being marked with neck collars on Islay, the second most important winter resort.

Dead recoveries of marked birds appears to offer an advantage over resightings in that there is no confusion of emigration with mortality. However, data from recoveries tend to be sparse for two reasons: (1) recovery rates tend to be low, and not all recovered birds are reported; (2) each marked bird contributes information only once over the study period, in being recovered or not recovered, in contrast to a resighting scheme where a bird contributes data on each sampling occasion. In the case of the Greenland White-fronted Geese the information content of the recovery matrix was clearly insufficient to draw conclusions about temporal patterns of survival. It is probable that in future both recoveries and resightings of birds will be incorporated into a unified modelling approach for marked birds, but at present it is clearly preferable to deal with resightings than recoveries. The major practical drawback is the investment of time and resources involved in a resighting programme, but there are great advantages in terms of more controlled collection of information on the fate of marked birds.

4.2. Sample size for mark-resighting

The information content of the resighting matrix appears to be preserved at even quite low ringing totals. Time-dependence of survival and resighting probabilities over a five year period were detected at ringing totals as low as 30 per year, although at this level of effort, confidence intervals around estimates were so wide as to make interpretation hazardous. Clearly, it would be unreasonable to suggest that 30 new rings per year is an adequate ringing effort to allow survival estimation from a resighting programme, but it is still encouraging that pattern could be detected at this level. Ringing totals for Greenland White-fronted Geese at Wexford are in the region of 30-100 new rings per year each of adults and first years; this level of effort is fairly typical of other goose marking schemes in the British Isles, e.g. 50-100 Greylag Geese *Anser anser anser* per year on North Uist, up to 300 Pink-footed Geese *Anser brachyrhynchus* per year at Martin Mere in Lancashire (C. Mitchell, pers. comm.), although resighting effort is usually not so high as for the Greenland White-fronted Geese.

4.3. Sources of bias

In one respect at least, the comparison of randomly selected resighting histories with a complete resighting matrix of a similar size is not valid. Random selection results in a group of birds which are more-or-less independent of one another in their resighting histories. Captures of Greenland White-fronted Geese on their wintering grounds tend to have a higher proportion of first-years than the population as a whole

(Wilson *et al.*, 1991), owing to the dominance of family groups over single birds and pairs without young in the competition for feeding resources (Boyd, 1953). Some implications of this are clearly seen in the 1989/90 cohort of first-year birds, 27 out of 30 of which were not resighted in the following winter. Inspection of the ringing records reveals that these were a few groups of siblings, the fates of which were, presumably, not independent. There is evidence that Greenland White-fronted Geese remain associated with parents and siblings in extended family parties, even after their first year (Warren *et al.*, 1992), so that the implications of non-independence of related individuals are not confined to first-year birds. The survival estimates are not, of course, statistically biased in relation to the population of marked individuals, but parameter variances will be underestimated. A computer-intensive method, such as resampling of capture histories, could be used to indicate the true size of confidence intervals.

In order to draw conclusions about patterns of mortality from resightings of marked birds it is necessary to assume that the marked sample is representative of the population at large, and that the method of marking has no effect on the subsequent fate of marked individuals. As has been noted above, at least among Greenland White-fronted Geese, and possibly among wildfowl in general, the luring of birds to bait results in the capture of a biased sample of the study population, owing to competition for food resources. In an analysis designed to test whether neck collars had an adverse effect on breeding in Greenland White-fronted Geese, Warren *et al.* (1991) found that collared birds were more successful than uncollared birds owing to the biased nature of the captured sample. A further study of the effects of collars on Greenland White-fronted Geese is now underway, in which some captured first-year birds are marked with leg rings only, which are assumed to have no effect on survival or breeding success. In future, it should be possible to test for differences in survival between collared and uncollared birds. At present, one should be cautious about extending conclusions drawn about mortality among collared geese to the population at large.

Other potential sources of bias in the estimation of survival and resighting parameters and their variances from mark-resighting schemes include mark loss and misreading of mark codes. The effects of the latter are difficult to quantify. Ebbinge *et al.* (1991) discussed the problems of observer variability in some detail; these authors estimated that for Russian Barnacle Geese wintering in the Netherlands and northwestern Germany the annual probability of an undetected misreading of coloured plastic leg rings was 0.2%. In the case of the Svalbard-Solway Barnacle Geese and the Wexford Greenland White-fronted Geese misreading of ring and collar codes is thought not to be a great problem. In these two populations most geese which are seen at all during a winter season are seen repeatedly. Many errors are detected and removed from the database: the reporting of non-existent codes, the reporting of codes of birds known to be dead, or single isolated reports of birds which have not been seen for many years and are assumed to be dead. The extent of misreading is unknown, but it is probable that if all birds seen only once during a winter season were excluded from analysis then the problem could be almost entirely eliminated.

Loss of marks is potentially a more serious source of bias, leading to underestimation of survival rates. Owen (1982) estimated a ring loss rate of 0.14% per year in the Svalbard-Solway Barnacle Geese. The loss of collars in the Wexford Greenland White-fronted Geese has been found to be higher in years with winter-shooting, owing to the fracturing of collars by lead shot (Wilson *et al.*, 1991); overall, the annual rate of collar loss has been estimated at up to 9.4% (Wilson *et al.*, 1991).

However, the marking of these geese with both leg rings and neck collars, coupled with the high resighting effort, ensures that collar loss does not contribute much to apparent mortality. Only one instance is known of a collared bird losing a leg ring (Wilson *et al.*, 1991). Collar loss could introduce heterogeneity of resighting probabilities owing to the much lower visibility and legibility of leg rings, but in practice this is probably offset by the high resighting effort at Wexford.

A drawback to the marking of geese on the wintering grounds is that this generally coincides with the winter shooting season. In the drawing up of recommendations for the management of goose populations it is very often the effects of this shooting in which we are most interested. An obvious solution to this problem, that we regularly catch and mark geese on their arctic breeding grounds is too often precluded through expense and practical difficulties. In this paper we have attempted to avoid the problem by adjusting the resighting or recovery matrix for a post-hunting-season sampling period, but this is far from a satisfactory solution, and could potentially introduce biases.

4.4. Approaches to survival estimation

It is clear that none of the approaches considered here yields estimates of survival rates that are uninfluenced by other population processes or biases introduced by the application of the methods themselves. What we have estimated is *apparent* survival, the meaning of which changes according to the approach adopted. In order to draw reliable inferences about patterns of survival in wintering goose populations information from both marking and population census schemes are required. At present, improvement in survival estimation for arctic-nesting geese lies not with the development of new modelling techniques, but with the design and execution of marking and census schemes. In particular, there needs to be reliable estimates of the rates of other population processes and the extent of potential biases, and collection of adequate data on other sources of mortality.

Acknowledgements. We are indebted to the many observers who have assisted with ringing or provided observations of marked geese, and to all who have helped with the Greenland White-fronted Goose and Barnacle Goose projects. In particular we thank Dave Norriss, Paddy O'Sullivan, Paul Shimmings, Stephanie Warren and John Wilson. The paper was improved after the comments of Dr John Tautin and an anonymous referee.

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