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of
Rehabilitated Guillemots

Authors

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SURVIVAL RATES OF REHABILITATED GUILLEMOTS

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SUMMARY

1 A recent analysis of ring recoveries of oiled and rehabilitated North American seabirds suggested that post-release survival is very low (Sharp 1996), leading to concerns about the conservation value of seabird rehabilitation programmes. Here we use BTO ring recoveries for Britain and Ireland to investigate post-release survival of rehabilitated (RH) guillemots. We compare post-release survival with natural survival rates from general ringing and assess whether improved rehabilitation techniques have increased post-release survival in recent years.

2 Most RH guillemots were released as fully-grown birds during the winter months (January-March), while most general ringing of non-rehabilitated (non-RH) guillemots involves nestlings and takes place at breeding colonies during June and July.

3 More than 70% of recoveries of RH guillemots occurred within 14 days of release. The median survival time of RH guillemots ringed since 1985 (n=77) was only 7 days and the median distance moved was only 8km. This compares with a median survival time of 599 days for non-RH fully-grown guillemots (n=113) and 227 days for non-RH nestlings (n=1784). The median distance moved by non-RH guillemots was 496km for birds ringed as fully-grown, and 638km for birds ringed as nestlings.

4 The survival times of RH guillemots released before 1985 (median 6.5 days) was very similar to that after 1985 (median 7 days). Hence, there is no evidence that improvements in cleaning and treatment techniques have increased the survival rates of RH guillemots.

5 Since 1985, the survival rates of RH guillemots have averaged 17% (95% c.l. 10-29%) per 30-days in the first 60 days after release and 86% (58-96%) thereafter (to the end of the first year), equating to an annual survival of 0.6% in the first year after release. Hence for every 100 RH guillemots released, we predict that 17 will survive the first month after release, 3 will survive the second month and 0.6 will be alive one year after release. The observed number of recoveries of RH guillemots more than one year after release was only 5-7% of the expected number based on our estimated survival rates for non-RH guillemots, confirming the low survival of RH birds.

6 Survival rates of non-RH guillemots (*i.e.* 'natural' survival) average 46% (95% c.l. 39-52%) during the first-year of life, 75% (67-81%) during the second year of life, and 88% (82-92%) for older birds. Annual survival rates of non-RH fully-grown birds (*i.e.* birds at least 1 year old) average 73% (65-79%). Hence, the survival rates of RH guillemots are only 0.7-1.3% of natural survival rates.

7 Most live recoveries of RH guillemots (92%) were 'unwell' at the time of recovery, and the median time between release and recovery was only 4 days. However, there is some limited evidence that small numbers of RH guillemots do survive and return to breeding colonies, and even successfully rear young.

8 It is unclear why so few RH guillemots survive after release. Some possible causes of post-release mortality are discussed and recommendations are made for improved data collection in future. These recommendations include:

(a) *Continued ringing of ALL rehabilitated birds* and establishment of a national ringing and recovery database.

(b) *Routine collection of information describing the condition and treatment of rehabilitated birds*, to allow the identification of the most successful methods of cleaning and rehabilitation. Information to be collected should include the condition of each bird at the time of capture, site of capture, details of cleaning and treatment procedures, the duration of captivity, condition at the time of release, and date and location of release.

(c) *Colour-ringing of rehabilitated birds* to increase detection rates at breeding colonies and allow monitoring of breeding performance. Professional and volunteer ornithologists should be encouraged to search for colour-ringed birds at colonies. Birds can only be considered to be fully rehabilitated if they can be shown to have re-entered the breeding population and are capable of rearing viable young to fledging.

1 INTRODUCTION

During February 1996, the *Sea Empress* oil tanker ran aground at the mouth of Milford Haven in Pembrokeshire, southwest Wales and discharged 72,000 tons of crude oil and 360 tons of heavy fuel oil into the sea. This incident resulted in almost 7,000 oiled bird casualties (28% of which were guillemots *Uria aalge*), of which half were rescued (Parr *et al.* 1997). A recent study which examined the post-release survival of oiled and cleaned North American seabirds, using ring recovery data from the Bird Banding Laboratory of the U.S. Fish and Wildlife Service (Sharp 1996), showed that the number of days between ringing and death (recovery) was very low. Oiled, cleaned guillemots had a post-release life expectancy of only 9.6 days and their long-term recovery rates (in year two and beyond) were only 10-20% of those of non-oiled birds.

These results have lead to considerable concern that seabird rehabilitation programmes are of low conservation value and may even prolong the suffering of the rescued birds. For this reason, the post-release survival of British seabirds after rehabilitation needs to be urgently assessed. The only available information is that from the National Ringing Scheme held at the BTO, and recoveries of guillemots constitute the most comprehensive data set (over 300 recoveries of rehabilitated (RH) guillemots and almost 6,000 recoveries of non-rehabilitated (non-RH) birds ringed during general ringing). Hence the current study aimed to (i) calculate the survival rates of oiled, cleaned and released guillemots, (ii) compare these with the natural survival rates of guillemots which have not been oiled, cleaned and released (hereafter referred to as non-RH birds), (iii) assess whether the survival of rehabilitated birds has increased in recent years as cleaning techniques have improved, and (iv) critically examine the quality of the available data and make recommendations for future improvements.

2 METHODS

Because of the probable loss and abrasion of the older-style, monel guillemot rings (Mead 1974, Harris 1980), most of the analyses in the present study used only data from birds ringed with 'guillemot specials' made of stronger incoloy, which were introduced in the early 1980s. The ringing database holds details of 133,472 guillemots ringed with 'guillemot specials', of which 2834 were held for more than 24 hours before release (*ie.* RH birds). Before 1983, less than 25 birds were ringed with 'guillemot specials' each year, numbers increasing to 2272 in 1983 and 7955-11861 per year from 1984 to 1995. Before 1985, RH birds may not have been coded as such in the ringing data set (there are few such birds in the data set prior to 1985). Therefore, the analyses focused on comparison of survival rates from 1985 onwards, although recoveries of RH birds before and after 1985 were compared (Section 2.1).

The recoveries database holds details of 309 guillemots which were rehabilitated, ringed and released between 1918 and 1995, 132 before 1985 and 177 from 1985 onwards. It was necessary to exclude a number of cases from this data to allow appropriate survival analyses to be carried out (Table 1). In particular, 57 recoveries for which the finding date is inaccurate had to be excluded since birds not freshly dead on recovery or cases where only the ring, or the ring and leg bone are found (the majority of cases in this type of exclusion) may have been dead for some time before recovery, so that the time elapsed between ringing and recovery does not accurately reflect true survival time. A total of 5734 recoveries of non-RH guillemots from general ringing between 1918 and 1995 were available, of which 2728 were ringed from 1985 onwards and were used for estimating natural survival rates with which to compare those of RH birds ringed since 1985 (Section 2.3). These recoveries were treated in exactly the same manner as those of RH guillemots, and 504 cases with inaccurate finding date were excluded (Table 1).

Rehabilitated guillemots are not coded specifically as oil victims within the main recovery database but rather as birds held for more than 24 hours before release. After checking the original recovery records for birds ringed from 1985 onwards, 77 of these birds were found to have oiling mentioned in the text field and 33 did not. The ringing months, finding months, survival time and distance moved between ringing and recovery of these two groups were compared and all but distance were found to differ significantly. Hence the 33 recoveries of probable non-oiled RH birds were excluded from subsequent analyses. Similarly for the period prior to 1985, only recoveries of guillemots known to be *oiled* and rehabilitated were analyzed. Although live recoveries were not generally appropriate for use in the main survival analyses for either non-RH or oiled and rehabilitated birds (but see Section 2.2), such recoveries of rehabilitated birds were nevertheless documented in the results.

2.1 Simple comparisons of RH and non-RH recoveries

From the ringing data, 99% of non-RH guillemots were ringed at breeding colonies in June and July, while 81% of RH birds were ringed in the winter months (January-March inclusive)(Figure 1a); this difference in month of ringing was significant (Kolmogorov-Smirnov 2-Sample Test: KSa=47.98, P=0.0001, n=120809 non-RH & 2912 RH). Most non-RH guillemots were ringed as nestlings (87%) while, in contrast, 96% of RH birds were ringed as fully-grown birds (Figure 1b) (Yates' corrected χ^2=17031.5, df=1, P=0.001, n=120739 non-RH & 2877 RH). Due to these significant differences in ringing month and age at ringing, we compared the number of days between ringing and recovery, and the distance moved, of RH birds ringed from 1985 onwards (n=77) both with non-RH birds ringed when fully-grown (*ie.* of similar coded age classes as the RH birds, n=113) and with non-RH birds ringed as nestlings (n=1784) for a number of reasons:-

(i) Perhaps 50% of RH guillemots are released into the sea close to the rehabilitation centres, rather than back at the point of initial capture (T.Thomas, pers. comm.), and these centres may be closer to areas of dense human population than the ranging areas of non-RH birds. Hence the reporting rates of RH birds may be higher than those of non-RH birds of a similar age. Comparison of RH birds with non-RH birds ringed as nestlings, rather than as fully-grown birds, may therefore be preferable because younger birds range further from breeding colonies (Birkhead 1974, Mead 1974, Baillie *et al.* 1994), into sea areas closer to denser human populations and may, therefore, have a higher reporting rate than fully-grown non-RH birds (demonstrated in Section 3.3).

(ii) The non-RH fully-grown birds used in the present analyses were ringed almost exclusively at breeding colonies and therefore probably comprise largely breeding adults (aged 6+ years) together with some immature birds (M.P.Harris, pers. comm.). The immatures are probably largely birds aged 4-5 years, as 1-year old birds rarely return to colonies, and 2- and 3-year old birds attend for only short periods (Halley 1992, Halley & Harris 1993). In contrast, many RH birds (ringed as fully-grown) may be one and two years old (T.Thomas, pers. comm.), and might be expected to have lower survival rates than the generally older fully-grown non-RH birds.

(iii) Many RH birds are released close to rehabilitation centres, rather than at capture points. Hence they may need to 'familiarise' themselves with a new area in order to forage successfully within the first few days after release, or they may attempt to return to their original feeding range; there is no information available on the behaviour of RH guillemots soon after release at present (T.Thomas, pers. comm.). In this respect, the survival of RH birds might be more appropriately compared to that of guillemots ringed as 'naive' nestlings, which range more widely than adults of breeding age. Similarly, the released RH birds may experience a degree of competition with resident (older) guillemots more similar to that experienced by young birds, which disperse more widely away from their own natal colonies during the winter months.

The time elapsed and distance moved between ringing and recovery of the 64 dead recoveries of RH birds ringed before 1985 (all ringed with old-style rings) were compared with recoveries of RH birds ringed from 1985 onwards (n=77), in order to assess whether improved treatment techniques have increased the survival chances of RH birds in recent years. The use of old-style, monel rings on the pre-1985 sample was unlikely to bias the results because most RH guillemots were recovered within a few months after release (during the winter) before returning to breeding colonies, where ring abrasion can occur.

All analyses were carried out using SAS (SAS 1990). Comparisons between groups of time elapsed and distance moved between ringing and recovery were made using non-parametric two-sample tests (Mann-Whitney) based on ranks because the data were highly skewed, and medians should be used for these formal comparisons (although means and standard errors are included in tables for completeness).

2.2 Formal survival and reporting rate of RH guillemots

Survival rates of RH guillemots were initially estimated from the sample of 77 dead recoveries of birds ringed between 1985 and 1995 (Table 1); of these, 10 birds ringed in 1996 and subsequently recovered had to be excluded because recoveries for the 1996/97 recovery year are not yet complete in the recoveries database. Of the 67 remaining recoveries, only 1 was recovered more than a year after release. Hence it was not appropriate to estimate annual survival rates from the data. Instead, all the ringing and recovery data were pooled, regardless of calendar year, and the ringing data were split into 4 monthly classes (January to April inclusive), which included 88% of all ringed RH individuals and 60 of the 67 recoveries (Table 2). The recoveries were then grouped into 30-day periods after the ringing date, allowing a formal analysis of 30-day survival rates using a one-age class modelling approach (after Brownie *et al.* 1985) in the MARK software (White & Burnham 1997). These groupings resulted in 215-871 RH guillemots ringed in each month and 60 recoveries in 13 30-day periods from the date of ringing (the longest survivor was recovered after 381 days) (Table 2). This approach allowed us to test whether survival rates increased with time elapsed after release using an 'age-structured' approach. In order to produce identifiable models using this approach, it was necessary to assume that the reporting rate of RH guillemots was independent of time since release (as for the family of models developed by Freeman & Morgan 1992). Model selection was carried out using likelihood ratio tests (Brownie *et al.* 1985). Aikaike's Information Criterion (AIC, Akaike 1973, 1981, and the adjusted qAIC from program MARK) was used as a further check of model selection (Burnham & Anderson 1992). The formal approach also resulted in estimation of the reporting rate for RH birds, which is time-independent with the parameterisation of survival (S) and reporting rate (λ) used in our models, allowing comparison with the reporting rates of non-RH guillemots (Section 2.3).

Analysis of the live recoveries of RH guillemots ringed since 1985 (Section 3.1) showed that the majority of these birds were in poor condition when they were recaptured (some were returned to rehabilitation centres). Comparison of the 20 'unwell' live recoveries (Table 6) and the 77 dead recoveries (Table 5) of RH birds ringed since 1985 showed that the time elapsed between ringing and recovery was significantly shorter for birds recovered alive (medians 4 days for live recoveries and 7 days for dead recoveries, Mann-Whitney test: Z=-2.71, P=0.0067). The formal survival analysis was repeated, including 17 of these live recoveries (Table 2); the remaining 3 live recoveries were excluded because two were ringed in 1996 and one was ringed in October. This second analysis assumed that the live recoveries which were recaptured in poor condition were rehabilitation failures, and so should be included in estimation of post-release survival.

2.3 Formal survival and reporting rates of non-RH guillemots

Dead recoveries of non-RH guillemots ringed in June and July only (>99% of the ringing data) between 1985 and 1993 were used in the analysis; those ringed from 1994 onwards were excluded because no non-RH birds ringed when fully grown in 1994 were recovered. Only birds ringed in June and July were used to keep the ringing period short compared to the length of the recovery period (one year) and the recovery year extended to 30 June in each following year. This made available 82,584 nestlings ringed between 1985 and 1993 (7087-10,090 per year), producing 1575 recoveries, and 11,844 fully-grown birds ringed (916-1840 per year), producing 98 recoveries (Table 3). Two age class models (after Brownie *et al.* 1985) were used to formally estimate annual survival and reporting rates from the data using programs SURVIV (White 1983) and MARK (White & Burnham 1997). Model selection was carried out using likelihood ratio tests and confirmed using AIC (Section 2.2). More complex models, with more than two age classes for survival estimation were fitted using program MARK (White & Burnham 1997).

3 RESULTS

3.1 Simple comparisons of RH and non-RH recoveries

A comparison of RH guillemots ringed from 1985 onwards which were known to have been cleaned after oiling with RH birds for which oiling was not specified showed that non-oiled birds were ringed significantly earlier in the winter than oiled birds (Kolmogorov-Smirnov 2-sample Test: KSa=1.37, P=0.0460) and were also recovered earlier in the year than oiled birds (KSa=1.39, P=0.0410) (Figure 2). The time elapsed between ringing and recovery was significantly shorter for non-oiled guillemots than for oiled birds (Mann-Whitney Test: Z=-1.93, P=0.0379) but distance moved between ringing and recovery did not differ between the two groups (Z=0.44, P=0.6569) (Table 4). The significant differences between oiled and non-oiled birds, particularly the shorter period between ringing and recovery of non-oiled birds, made the exclusion of non-oiled birds from subsequent analyses appropriate.

Non-RH guillemots ringed as fully-grown birds survived significantly longer between ringing and recovery than those ringed as nestlings (median 599 days *c.f.* 227 days, Mann-Whitney Test: Z=6.34, P=0.0001)(Table 5). Guillemots ringed as nestlings moved further between ringing and recovery than those ringed when fully-grown (median 637.5 km *c.f.* 496 km, Z=-4.44, P=0.0001) (Table 5). From 1985 onwards, oiled and rehabilitated guillemots survived a significantly shorter time and moved a significantly shorter distance between ringing and recovery than non-RH birds, regardless of the age at ringing of the latter (Table 5). The median survival time between ringing and recovery of RH guillemots was much less than the median of non-RH birds ringed as nestlings (7 days *c.f.* 227 days, Mann-Whitney Test: Z=-13.81, P=0.0001) or the median of non-RH birds ringed when fully-grown (7 days *c.f.* 599 days, Z=-10.55, P=0.0001). Similarly, the median distance moved between ringing and recovery by RH guillemots was significantly less than that for non-RH birds ringed as nestlings (8 km *c.f.* 637.5 km, Z=-13.52, P=0.0001). The median for RH birds was also significantly less than the median for non-RH birds ringed as fully-grown birds (8 km *c.f.* 496 km, Z=-8.27, P=0.0001)(Table 5).

Rehabilitated guillemots ringed from 1985 onwards did not survive significantly longer between ringing and recovery than those ringed before 1985 (median 7 days *c.f.* 6.5 days, Mann-Whitney Test: Z=-0.68, P=0.4935). Median times elapsed between ringing and recovery for blocks of years also gave no indication of a temporal increase in number of days survived by RH guillemots (Figure 3); on the contrary, the number of days survived was higher before 1970 than in subsequent years (Kruskal-Wallis χ^2=14.6, df=5, P=0.0121). Those RH birds ringed from 1985 onwards moved significantly shorter distances between ringing and recovery than those ringed before 1985 (median of 8 km *c.f.* 21.5 km, Z=2.60, P=0.0093)(Table 5).

The time elapsed and days survived between ringing and recovery for live recoveries of oiled and RH guillemots, which were excluded from the main survival analyses (above and Sections 3.2 and 3.3), are summarised in Table 6. All of the RH birds ringed before 1985 and the majority of those ringed from 1985 onwards were in poor condition when recaptured alive; the time elapsed and distance moved between ringing and recovery of these birds were similar to those of RH birds recovered dead during the same years (Table 5). Of note were the two RH guillemots ringed in 1985 in Devon which were 'healthy' when recaptured in 1994 in Cornwall; both had survived more than 9 years after rehabilitation and were subsequently re-released.

3.2 Formal 30-day survival rates and reporting rate of RH guillemots

Most dead recoveries (95%) of oiled and rehabilitated guillemots occurred within the first 60 days after ringing (Table 2), the longest survivor being recovered after 381 days (in recovery period 13). The survival of RH guillemots was estimated as 30.6 (95% confidence limits: 21.7-41.4%) per 30-day period using the model with survival and reporting rate held constant (Table 7a). Likelihood ratio tests between this and more complex models provided evidence for variation in survival with time elapsed after release (Table 7a). The model in which survival during the first 30 days after release differed from that in subsequent 30-day periods, model $\{S_{1,2+}\ \lambda\}$, provided a significantly better description of the data than the model with survival held constant, and the model with separate survival estimates for the first, second and subsequent 30-day periods was preferred over the model with only two 30-day survival classes (Table 7a). Further separation of later 30-day periods was not required, however (likelihood ratio test between $\{S_{1,2,3+}\ \lambda\}$ and $\{S_{1,2,3,4+}\ \lambda\}$: P=0.3600) (Table 7a). The model with three survival periods with time elapsed after release, $\{S_{1,2,3+}\ \lambda\}$, was not preferable to a model in which survival rates in the first two 30-day periods were constrained to be equal but were different from survival rates in subsequent periods, (defined as $\{S_{1+2,3+}\ \lambda\}$); the likelihood ratio test statistic had a significance level of P=0.0800 (Table 7a). The AIC values of models $\{S_{1,2,3+}\ \lambda\}$ and $\{S_{1+2,3+}\ \lambda\}$ were very similar but the goodness-of-fit of the former model (P=0.9857) was far preferable to the latter (P<0.0001, Table 7a). The wide confidence limits of the estimates from model $\{S_{1,2,3+}\ \lambda\}$ suggested that convergence was poor (Table 7a) however, and this was supported by the sampling correlations between the survival estimates, which were very high (all > 0.8) for model $\{S_{1,2,3+}\ \lambda\}$ but much lower and acceptable (0.19) for model $\{S_{1+2,3+}\ \lambda\}$. The poor goodness-of-fit for the latter model is not really cause for concern given the small amount of data used in the analysis and the many cells with zero values; in such instances a more appropriate goodness-of-fit should be derived from Monte Carlo simulation (Catchpole 1995), which is outside the scope of the present study.

Hence $\{S_{1+2,3+}\ \lambda\}$ was the model from which the survival rates and reporting rate of RH guillemots were estimated (Table 7a), indicating that survival rates in the first and second 30-day periods were similar but differ significantly from survival after the 60th day. Using this model, survival was 17.0% (95% confidence limits: 9.5-28.6%) per 30-days in the first 60 days after release and 85.8% (57.5-96.4%) per 30-days from the 61st day onwards; the latter survival rate corresponds to an annual survival of 15.9% and overall only 0.6% of RH birds survived the first year after release. The estimated reporting rate of RH guillemots from model $\{S_{1+2,3+}\ \lambda\}$ was 2.4% (1.8-3.1).

The inclusion of 17 recoveries of RH birds which were 'unwell' at the time of recapture in the formal survival analysis had little effect on the overall results (Table 7b). There was clear evidence that survival in the first 30 days after release differed from that in the subsequent period (significant likelihood ratio test between models $\{S\ \lambda\}$ and $\{S_{1,2+}\ \lambda\}$, Table 7b) but the need for a separate survival estimate for the period 31-60 days after release was marginal (likelihood ratio test between models $\{S_{1,2+}\ \lambda\}$ and $\{S_{1,2,3+}\ \lambda\}$, P=0.0500, Table 7b). Model $\{S_{1+2,3+}\ \lambda\}$, which was the favoured model in the previous analysis using only dead recoveries, was clearly rejected (likelihood ratio test P=0.0200, Table 7b). The AIC marginally favoured model $\{S_{1,2,3+}\ \lambda\}$ over $\{S_{1,2+}\ \lambda\}$ (qAIC 777 *c.f.* 779) and the sampling correlations between the survival estimates from the former were marginally acceptable (0.35 or less) but considerably lower (<0.1) from the latter model. The 30-day survival rates from these two competing models are shown in Table 7b. The choice between the two models has little effect on the conclusions however; rates from model $\{S_{1,2,3+}\ \lambda\}$ correspond to an overall survival for RH birds of 1.1% in the first year after release and those from model $\{S_{1,2+}\ \lambda\}$ to only 0.2% survival in the first year after release, compared to an estimate of 0.6% survival in the first year after release from the modelling excluding the live recoveries. The reporting rate from the models incorporating 'unwell' live recoveries was 3.0% (2.4-3.8%), slightly higher than that from models without the live recoveries data (2.4%).

Knowledge of the time at which RH guillemots die after release may help in assessment of the potential cause(s) of such mortality; for example, mortality peaking almost immediately upon release may be due to attacks by predatory gulls *Larus* sp. rather than due to lowering of the immune system post-treatment, the latter resulting in delayed mortality (T.Thomas & A.Lindley, RSPCA, pers. comm.). Due to the small number of recoveries of RH guillemots available, the formal investigation of survival rates over periods shorter than 30 days was impracticable. A plot of the frequency of recoveries recorded on each day after release demonstrated that most mortality (>70%) occurs in the first 2 weeks, with the modal number of recoveries on day 6 after release (Figure 4).

3.3 Formal annual survival rates and reporting rates of non-RH guillemots

Comparison of a global model with both survival and reporting rates dependent on age and year, model $\{S_{at}\ \lambda_{at}\}$, with a series of constrained models using likelihood ratio tests and AIC values indicated, first, that the reporting rate did not show temporal variation (Table 8a: comparison of initial model (1) with $\{S_{at}\ \lambda_{a}\}$ P=0.8423). Comparison of this reduced model with further constrained models (Table 8a: initial model (2)) indicated that no further simplification could be made without significantly reducing model fit(Table 8a). Hence model

$\{S_{at}\ \lambda_a\}$ was selected, in the first instance, to estimate age- and year-dependent survival rates and age-dependent reporting rates for non-RH guillemots ringed between 1985 and 1993.

According to model $\{S_{at}\ \lambda_a\}$, the survival rates of first year and older guillemots were very similar; the only years in which the 95% confidence limits of the annual estimates for the two age classes did not overlap were 1985/86 and 1991/92 (Figure 5). On average, the survival of first year non-RH guillemots was 71.3% (95% confidence limits: 55.6-87.1%) and the survival of older birds was 64.4% (60.3-68.5%), using the estimates from model $\{S_a\ \lambda_a\}$. The survival rates of first years and older birds varied temporally in a similar manner, particularly showing lowest rates (*ca* 60%) in the late 1980s and early 1990s, followed by an increase to higher rates (>80%) from 1991/92 onwards (Figure 5). From the selected model $\{S_{at}\ \lambda_a\}$, the reporting rate of 5.0% (2.2-7.7%) for first year guillemots was greater than the rate of 1.0% (0.8-1.2%) for older birds by a factor of five.

The goodness-of-fit of the global model $\{S_{at}\ \lambda_{at}\}$, used to estimate the survival and reporting rates of non-RH guillemots, was poor however (Table 8a: P=0.0001), as was the fit of the selected model $\{S_{at}\ \lambda_a\}$ (Table 8a: P=0.0005); the models were, therefore, inadequate to model the heterogeneity within the data set. Part of the lack of fit may have been caused by the mixture of ages at ringing of the guillemots categorised as fully-grown (Section 2.1). Therefore, the global model used in the formal survival analysis (equivalent to 'Model H_1' of Brownie *et al.* 1985 but parameterised in terms of reporting rate (λ) rather than recovery rate (F)) was compared with Models H_2 and H_3 using the BROWNIE software (Brownie *et al.* 1985) and tests analogous to goodness-of-fit tests (Brownie & Robson 1976). In particular, comparison of models H_2 and H_3 provided a formal test of the need for more than one age class for fully-grown birds in the present analyses of non-RH guillemots. The test between H_2 and H_3 was significant (χ^2=45.6, df=7, P <0.0001) and Model H_3 had a satisfactory goodness-of-fit statistic (χ^2=15.5, df=12, P=0.2142). This indicated that the survival and/or the reporting rates of fully-grown guillemots in the present study differed between the first year after ringing and subsequent years, an effect that could result from the inclusion of a mixture of immatures and birds of breeding age in our fully-grown age class.

A further source of heterogeneity in the non-RH data resulted from the likely exclusion of some age classes of immature guillemots in the ringing data, probably because these immatures (largely birds in their first and second summers) only rarely visit breeding colonies and are not therefore available to be ringed (Halley 1992, Halley & Harris 1993, M.P.Harris pers. comm.). To address this potential source of bias in the survival estimates, the MARK software (White & Burnham 1997) was used to fit further elaborations of model $\{S_{at}\ \lambda_a\}$, in which guillemots ringed as nestlings did not acquire the survival rates of those ringed as fully-grown birds until two, three or four years after ringing (models $\{S_{a3t}\ \lambda_{a2}\}$,$\{S_{a4t}\ \lambda_{a2}\}$ and $\{S_{a5t}\ \lambda_{a2}\}$ respectively). In order to render the parameters in these models identifiable, reporting rates were assumed constant (and equal to those of first year birds) until the survival rates of fully-grown birds were acquired. Hence in model $\{S_{a3t}\ \lambda_{a2}\}$, annual survival rates differed between first year, second year and older birds (*ie.* S_{a3t}) but first and second years had equal year-independent reporting rates which differed from those of older birds (*ie.* λ_{a2}). Using this approach (Table 8b), the model with two pre-fully-grown age classes $\{S_{a3t}\ \lambda_{a2}\}$ was significantly better than the original two-age class model $\{S_{a2t}\ \lambda_{a2}\}$ (Table 8b: initial model 3) and the model with three pre-fully-grown age classes $\{S_{a4t}\ \lambda_a\}$ was a further improvement (Table 8b: initial model 4); an increase to four pre-fully-grown age classes using $\{S_{a5t}\ \lambda_a\}$ did not significantly improve model fit (Table 8b: initial model 5). Model $\{S_{a4t}\ \lambda_a\}$ could not be simplified, either by removing the year-dependence of survival using $\{S_{a4}\ \lambda_a\}$ or by constraining the reporting rate to be constant across both the pre-fully-grown and fully-grown age classes using $\{S_{a4t}\ \lambda\}$, without significantly reducing the fit of the model (Table 8b: initial model 4). The selection of model $\{S_{a4t}\ \lambda_{a2}\}$ was confirmed by its low qAIC value (White & Burnham 1997) and its favourable goodness of fit (P=0.0630) (Table 8b).

Year-specific survival estimates from the selected model $\{S_{a4t}\ \lambda_{a2}\}$ are shown in Figure 6. The temporal trend in survival was similar to that from the model selected previously $\{S_{a2t}\ \lambda_{a2}\}$ (Figure 5), being relatively lower in the late 1980s. First year birds showed generally lower, and larger between-year variation, in survival than the older age classes but birds defined as fully-grown birds appeared to have survival rates similar to those of second years and lower than those of third years. The average estimates for the four age classes (from model $\{S_{a4}\ \lambda_{a2}\}$) confirmed these differences: the survival rates were 45.7% (95% confidence limits: 39.2-52.3%) for first years, 74.5% (66.9-80.9%) for second years, 87.6% (81.8-91.8%) for third years and 72.7% (65.4-79.0%) for fully-grown birds. The estimated reporting rates from $\{S_{a4t}\ \lambda_{a2}\}$ were 3.4% (2.9-4.0%) for guillemots aged 1-3 years and 1.3% (1.0-1.8%) for fully-grown birds.

Using the average survival for non-RH guillemots from model $\{S_{a4}\ \lambda_{a2}\}$ and the reporting rates from the selected model $\{S_{a4t}\ \lambda_{a2}\}$, the expected number of recoveries of oiled and rehabilitated guillemots could be calculated based on the number ringed and released, assuming that their survival rates were the same as those of non-RH birds (Table 9). Depending on the age class of non-RH guillemot rates used, the observed number of 62 recoveries of RH guillemots in the first year after release (from a total of 2699 ringed, Table 2) was higher than the expected number by a factor of 1.2-6.4. The most realistic comparison might be that using the survival rates of 'naive' first year non-RH birds (Section 2.1) and the observed reporting rate of RH guillemots (Table 9: scenario e), producing an observed number of recoveries higher than the expected number by a factor of 1.4. The expected number of recoveries more than one year after release was also calculated, based on the expected number of birds surviving the first year after release, and taking on the survival and reporting rates of the consecutive older age classes under the five scenarios. This calculation took account of the fact that RH guillemots released in 1985 had more years in which they could be recovered than those ringed more recently. The expected number of recoveries more than one year after release for the years 1986-1996 varied from 13.6 to 18.1, depending on the scenario (Table 9), whereas the actual number recovered was only one.

4 DISCUSSION

4.1 Survival of rehabilitated British guillemots

On average, guillemots which were oiled, cleaned and released from 1985 onwards survived only 7 days between release and (dead) recovery and were recovered, on average, only 8 km from the release site (Table 5). The number of days survived by RH guillemots ringed after 1985 was not an improvement on that of those rehabilitated before 1985, which on average survived for 6.5 days (Table 5). Live recoveries of RH guillemots generally supported the poor survival times of those recovered dead because most were recovered in poor condition and/or taken back into care during a similar period after release to those recovered dead. Similarly, the median time elapsed between release and recovery ranged from 5-8 days in the recent study of North American oiled and rehabilitated guillemots (Sharp 1996). Formal survival modelling using dead recoveries of RH guillemots released from 1985 onwards gave survival rates of 17% in the first 60-days after release and 86% thereafter, amounting to an annual survival of only 0.6%. The inclusion of live but 'unwell' recoveries had little influence on the conclusions; the two competing best models estimated survival in the first year after release as 1.1% and 0.2% respectively (Table 10). In the analysis based on North American oiled and rehabilitated guillemots (Sharp 1996), the estimated survival rate was only 13% per 20-day period, amounting to negligible annual survival. The present study demonstrated that survival increased with time after release, which was not investigated in the North American study. The present study did not address the issue of how many guillemots actually survive the rehabilitation process; the mean percentage of oiled birds that survived treatment in North America was 35% (range 9-60%) (Sharp 1996) and, in Britain, around 30% of birds found on the beach (live and dead combined) may be released after treatment (T.Thomas, pers. comm.).

Other, less recent studies indicated that oiled and rehabilitated birds have low post-release survival. Auks released into the North Sea had a recovery rate of 11% in the first six months, compared to a rate for non-rehabilitated birds of 3% over their entire lifetime (J.P.Croxall in Swennen 1977). The survival of oiled and rehabilitated brown pelicans *Pelecanus occidentalis* monitored via radiotelemetry was one-third that of non-oiled controls during the first six months after release and one-sixth that of controls thereafter (D.Anderson cited in Sharp 1996). Rehabilitation was stated as being "of little use ... even in the best case" when released Magellanic penguins *Spheniscus magellanicus* were never seen again (D.Boersma cited in Sharp 1996). Only in jackass (African) penguins *Spheniscus demersus* has cleaning and treatment been shown to result in successful rehabilitation, with 37-84% of released birds later seen alive at breeding colonies, and 10-29% of these subsequently seen breeding, after oil spills at Dassen Island (1972) and St. Croix Island (1979) in South Africa (Morant *et al.* 1981), and a minimum of 45% of released birds resighted at breeding colonies after a further large oil spill near Dassen Island in 1994 (Underhill *et al.* 1996). In addition, one penguin was resighted incubating eggs, four holding territories and one returned to its young (which hatched before the parent was oiled) within a month of release (Underhill *et al.* 1996). In contrast to the present and previous studies of other species, all the available evidence suggests that there is no post-release mass mortality of rehabilitated jackass penguins

4.2 Comparison with natural survival rates

Rehabilitated guillemots survived a significantly shorter time between ringing and recovery than all ages of non-RH birds. Their median survival time between ringing and recovery (7 days) was 30x less than that of non-RH birds ringed as nestlings and 85x less than that of fully-grown non-RH birds (Table 5). Similarly, the median time elapsed between ringing and recovery for North American rehabilitated guillemots was 36x less than that of non-RH birds with all ages combined (Sharp 1996). Presumably RH guillemots moved a significantly shorter distance between ringing and recovery than non-RH birds (by a factor of 62-80x, Table 5) due to their reduced survival time, as did North American oiled and rehabilitated guillemots (Sharp 1996).

Our formal survival analyses estimated an annual survival rate for RH guillemots in the first year after release of only 0.2-1.1% compared with annual rates of 46-88% for non-RH birds, depending on their age class; hence the annual survival of RH birds was only 0.2-2.3% of that of non-RH birds (Table 10). The annual survival rate of first year non-RH birds in the present study (46%) was at the higher end of the range of those previous quoted for guillemots *Uria aalge* in the first four years of life of 16-41% (Birkhead & Hudson 1977, Hatchwell & Birkhead 1991). Our survival rates for second and third year birds (75% and 88% respectively) were considerably higher than previously suggested however (Table 10). Previous survival estimates from observations of colour-ringed breeding guillemots average 90-95%, with a range of 82% to almost 100% (Table 10) depending in some studies on sex, and on sub-colony because of variation in predation pressure (Southern *et al.* 1965, Birkhead

& Hudson 1977, Hatchwell & Birkhead 1991, Sydeman 1993, Harris & Wanless 1995). The survival rates of fully-grown birds estimated in the present study are not strictly comparable to these previous rates because our sample of birds ringed when fully grown was known to include both breeding birds and immatures of pre-breeding age, which were probably mostly birds of three or four years old with a few younger individuals (M.P.Harris, pers. comm.). The survival rate of third year guillemots in the present study (88%) did approach those previous estimates for breeding adults however. The survival rate of British guillemots between 1960 and 1972, calculated using ring recoveries (Birkhead 1974), was 88% but ring loss was believed to occur and a re-analysis using only 'middle-aged' birds increased the estimate to 94% (Mead 1974). Despite the relatively low 'adult' survival rates estimated in the present, it is appropriate to compare these with the survival estimates for RH guillemots. First, they are calculated over a very similar span of years to those of the RH birds and, second, most RH birds are probably immatures (T.Thomas pers. comm.), the non-RH survival rates for which have been successfully quantified in the present study. The exact age class of non-RH birds with which to compare the survival of RH guillemots remains unclear but this has little influence on the conclusions drawn; even if the RH birds are compared to first year non-RH birds with the lowest annual survival (Table 10), the RH birds still have substantially lower survival (only 0.4-2.4% of those of non-RH first years).

The reporting rate of RH birds during the initial period after release could potentially be higher than that of non-RH birds for several reasons. First, onshore winds may blow the birds back ashore and the increased publicity may mean that more people look for dead birds along the coast near to the release point. Second, most British RH guillemots are released closer to areas of dense human population (mostly in southern and south-west England) than the majority of non-RH birds (many of which are ringed in more remote Scottish colonies), so that the overall reporting rate of RH birds may be enhanced relative to that of non-RH birds. The present study showed that a formal estimate of the reporting rate of RH birds (2.4-3.0%) lay between the estimates for non-RH fully-grown birds (1.3%) and non-RH birds in their first three years of life (3.4%) however. This implied that the higher than expected number of recoveries of RH birds during the first year after release (higher by a factor of 1.2-6.4, Table 9) was due to the greater mortality rather than a higher reporting rate of RH birds. In further support of this, the number of recoveries of RH guillemots more than one year after release, when the reporting rates were unlikely to be inflated relative to non-RH birds, was only 5-7% of the expected number (Table 9); this could only result from the abnormally high mortality of RH birds during the first year after release, leaving few survivors to be recovered in year two. Similarly, in the North American study the long-term recovery rate (in years two and beyond) of rehabilitated guillemots was only 9.9-20.3% of that of non-RH birds (Sharp 1996).

In summary, using our survival rates estimated from dead recoveries of RH guillemots, for every 100 RH birds released 17 will survive the first month, 3 will survive the second month and only 1 (actually 0.6) will be alive at the end of the first year after release.

4.3 Reasons for the low survival of rehabilitated guillemots

The survival of RH guillemots was particularly low (only 17%) during the first two months after release, and most mortality of RH birds (>70%) occurred within the first two weeks (Figure 4). By the third month after release, their survival (86% per 30-days, equivalent to an annual survival of 16%) was still lower than that of first year non-RH birds (46%). The high mortality of RH birds in the first two weeks after release suggests that they may be adversely affected by oil in a way that is not reversed by current cleaning and treatment methods, so that they are unfit at the time of release. In support of this, RH birds held in large enclosures in captivity had an annual survival rate of only 63-65% compared to a rate of 93% for non-oiled birds held in enclosures (Swennen 1977). Oiled guillemots autopsied after cleaning and treatment had various internal physiological damage (*eg.* liver, kidney and intestinal disorders), which were likely to have affected post-release survival (Khan & Ryan 1991, Wood & Heaphy 1991).

Other putative causes of mortality shortly after release are not distinguishable based on our present knowledge. Rehabilitated birds may succumb to infections, either contracted whilst in captivity, or once released due to suppression of the immune system. They may also suffer waterlogging and consequent hypothermia because their plumage has not sufficiently regained condition after cleaning. For a species which spends the entire winter at sea, the condition of the plumage at the time of release is likely to play a crucial role in the survival of rehabilitated guillemots. Whether or not a bird moults into fresh plumage in captivity could have a large influence on post-release survival (Morant *et al.* 1981). Unfortunately information on moult has not been routinely collected in the past but deserves further investigation (Section 4.4). Birds in poor condition or suffering from disease may be susceptible to attacks by marine predators, such as gulls *Larus* sp.. The stress of oiling and subsequent handling could itself contribute to the observed high mortality after release.

Although the release of rehabilitated birds into the normal wintering range of the sub-population is always attempted (T.Thomas, pers. comm.), birds may still be released into an unfamiliar area away from their original wintering range, where they must learn to forage successfully or return to their local area. They may also suffer foraging competition from the local resident population. These pressures may be more problematic if the birds are in sub-optimal internal or external condition. First year non-RH birds probably constitute the most appropriate age class with which to compare the survival rates of RH guillemots because they range most widely away from the natal colony and must learn to forage for themselves. However, RH birds may be even more disadvantaged than 'naive' first year non-RH birds because many are released in unfamiliar surroundings without other guillemots to aid in location of prey (T.Thomas, pers. comm.); nestlings leaving the colony for the first time at least have older guillemots around them from which to learn where to forage successfully and are invariably accompanied by their male parent for up to four months after fledging (M.Tasker, pers. comm.). In recent years, attempts have been made to release some RH guillemots in areas where non-oiled birds are known to be feeding, based on observations from boats (T.Thomas, pers. comm.). Oiled and rehabilitated guillemots are also normally released during the winter months, when environmental conditions are most unfavourable and natural mortality rates are highest (Figure 7). Clearly much further research into the behaviour of RH birds shortly after release is urgently required in order to determine the causes of post-release mortality and measures which can be taken to improve the survival of these birds. Such research is currently being planned by the RSPCA (A.Lindley & T.Thomas, pers. comm.).

While this and previous studies of auks have shown that the survival of oiled and rehabilitated birds is low (J.P.Croxall in Swennen 1977, Sharp 1996), the rehabilitation of penguins appears to be much more successful (Morant *et al.* 1981, Underhill *et al.* 1996). As the internal physiology of penguins and auks and the effects of ingested oil are unlikely to differ significantly because of their similar lifestyles and prey, some other factors may be responsible for the apparent differences in rehabilitation success. The lack of flight feathers in penguins makes it possible to use more vigorous cleaning methods than those used on auks (Morant *et al.* 1981) and this, together with a rapid response to oiling, may mean that penguins ingest less oil. It is also possible that the general composition of the oils involved differs between South Africa and Britain/North America; the majority of oiling incidents to which penguins have been subjected in South Africa may have involved 'light' fuel oils rather than 'heavy' crudes, and these light oils may be more effectively removed by current cleaning techniques (P.Whittington, pers. comm.). Similarly, birds oiled by chronic sources, from which the very toxic, light hydrocarbons have evaporated, may have higher chances of survival than those oiled during a major spill (Partridge 1997). Variation in the success of rehabilitation efforts may also result from differences in the quality of treatment available and the experience of handlers. As well as removal of the oil, South African penguins are held long enough for the development of plumage waterproofing and undergo specific waterproofing tests to ensure they are fit for discharge (Morant *et al.* 1981, Moldan & Westphal 1994).

The experience of the rehabilitator may play a crucial role in the quality of the rehabilitation treatment (Frink & Miller 1996-97, T.Thomas, pers. comm.) and the inability to train all volunteers needed to deal with oiling incidents prior to the events may explain the lack of improvement in the survival of rehabilitated guillemots in recent years, despite improved cleaning and treatment regimes. Equally, variation in the condition of birds at the time of initial capture, the type and quality of the treatment given, the length of time for which the birds are held in captivity, the condition of individuals at the time of release, the prevailing environmental conditions and the site of release may all play a part in determining post-release survival. Birds which are held in captivity for longer periods may have increased survival chances (Sharp 1996) because they have more time to gain condition or even to moult into fresh, undamaged plumage. A favourable combination of the above factors could be responsible for the few long-term survivors of rehabilitation efforts. In the present study, two guillemots were recaptured alive and subsequently re-released more than 9 years after rehabilitation (Table 6). Based on our formal 30-day survival rates (Section 3.2), and even assuming that RH guillemots acquired survival rates of breeding adults (say 90%) at the end of their first year after release, from a total of 170 RH birds released in 1985, less than one would have been expected to be alive nine years later. Hence the recovery of two RH birds more than nine years after release was a truly extraordinary event. The two survivors were both released after rehabilitation in Dorset in the winter of 1985 and were apparently trapped together in boulders on a beach in Cornwall in 1994. The chances of this event occurring were so low that doubt was cast on the records. For this reason, we attempted to re-contact the finder to confirm his recovery information but found no record of the person in the town in the address, and that the address was actually fictitious. A further long-term survivor, which was recovered dead after 8.6 years, was known to be held in captivity for several months while it underwent delayed moult. Similarly, there is some evidence that a small number of oiled and rehabilitated guillemots do manage to return to breeding colonies: three birds found in the breeding colony on the Isle of May, east Scotland were released after cleaning in the Netherlands and Germany, and a further individual, with a non-British ring, was in an unusual stage of moult, also suggesting recent release from care (Harris & Wanless 1997). Of these four birds, three were seen more than a year after release, one was assumed to have bred and one definitely reared young during two breeding seasons. A single kittiwake *Rissa tridactyla* was also seen at a breeding colony after rehabilitation from oiling (Clark 1978). More such survivors might be found were it not for the difficulties of surveying many colonies for marked birds (J.P.Croxall pers. comm. in Morant *et al.* 1981).

4.4 Data quality and recommendations for the future

Although the present study has demonstrated that the post-release survival of British RH guillemots is low, insufficient data have been collected to allow us to assess why this should be the case. The survival of RH birds could clearly be influenced by their condition at initial capture (including the type of oil affecting the bird), the cleaning and treatment regimes used during rehabilitation, the experience of the rehabilitators, the time for which the birds are held in captivity, their condition at the time of release, environmental conditions at the time of release and the release site relative to the site of initial capture. If some or all of these possible influences can be documented in the future, a more 'experimental' approach to the analysis of the survival of RH birds could be adopted and the suite of conditions resulting in the highest success rates might be determined. In the study of North American rehabilitated birds (Sharp 1996), the relationships between survival time and several potential influencing variables (degree of oiling, the number of days in captivity, body mass at the time of capture and release, and blood chemistry shortly before release) were investigated but sample sizes were generally small. Obviously the time required to collect such explanatory data must not itself be allowed to influence the future survival chances of the birds by increasing handling times and associated stress, so that the number of variables collected may have to depend on the number of birds arriving at rehabilitation centres in relation to the availability of carers. However, a series of target variables could be formulated, and assigned an order of priority to be followed depending on available time at the rehabilitation centre. Even if all such seemingly appropriate explanatory variables were collected, sample sizes may be insufficient to allow all possible analyses but it should be possible to look at the effects on future survival of broad categories of bird condition and treatment received. Such work should be carried out concurrent with research on the behaviour of RH birds in the period immediately after release (Section 4.3), in order to maximise the chances of detecting the causes of current post-release mortality and hence reducing this in the future. If we wish to improve our knowledge of the survival of rehabilitated birds in the future, we recommend that:-

1) All RH birds should be ringed with BTO rings before release. The establishment of a database of RH birds, indexed by ring number and containing all the treatment/condition variables suggested below, would be extremely useful.

2) It would be worthwhile to ring all RH guillemots with coloured and numbered DARVIC rings, so that birds could be identified at breeding colonies. This would be essential in order to determine whether survivors of rehabilitation are able to recruit/reenter the breeding population and to allow monitoring of breeding performance (information which is very limited at present). It would also be important to publicise the scheme properly, encouraging ringers, members of the public and professional ornithologists to check for colour-ringed birds at breeding colonies. A specific coloured ring for rehabilitated birds could be designed, in order to minimise loss of colour combinations on rehabilitated birds.

3) As many of the following variables as possible should be collected during the rehabilitation process (the priority order needs to be discussed and agreed between interested parties):-

(a) Initial condition variables: site of capture, body mass and body size (to calculate body condition), type and degree of oiling, time elapsed between capture and treatment

(b) Treatment variables: cleaning and treatment regimes, experience of rehabilitator, length of time held, whether moulting occurs

(c) Release variables: body mass (to calculate body condition), stage of moult and plumage condition (resistance to water), blood chemistry variables, environmental conditions at the time of release (weather, sea conditions, release site (and location relative to the oiling incident)

4) It would also be useful to collect more information on the age distribution of RH (and non-RH) birds, so that their survival could be compared with that of non-RH birds of the same age with more certainty. This may be difficult, however, as little is known about the pattern of moult in immature guillemots because they do not return to land during the winter months, and

because the timing of body moult in adults may vary by several months depending on geographical area (Harris & Wanless 1990, M.P.Harris, pers. comm.). Camphuysen (1995) gives a recent review of ageing techniques which may be used in the hand, allowing guillemots to be subdivided into juveniles, young immatures, old immatures (sub-adults) and sexually mature adults; these may be difficult for those inexperienced at ageing to apply however (T.Thomas pers. comm.). It would be useful to produce a summary of this recent review of ageing to make it easier to use in rehabilitation centres. The ages of dead birds aged by these methods could be confirmed using bone sections, although further work in this area is required to validate the technique for guillemots (Klomp & Furness 1992).

Whilst less than 2% of rehabilitated guillemots survive the first year after release, there is evidence that a small number of rehabilitated guillemots survive for long periods and return to breeding colonies (Harris & Wanless 1997 and the present study). In the long-term, much effort must be directed into reducing the occurrence of oil spills (Morant *et al.* 1981, Sharp 1996) but oil spills will continue to occur so long as oil is transported by sea, no matter what safeguards are put in place (Partridge 1997). Hence efforts to clean and release oiled seabirds will be required but it is essential that more appropriate data are collected, in order to monitor the success of the rehabilitation effort more satisfactorily and to identify specific techniques and conditions which result in improved post-release survival. In this way, the effort of the rehabilitators and the resources required may be more efficiently employed in the future. Continued ringing and monitoring of rehabilitated birds in the future is therefore essential.

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TABLES & FIGURES

Table 1 **Breakdown of the available data and the necessary exclusions.**

Data set	Total available recoveries	Unusual ringing circumstances[1]	Inaccurate finding date[2]	Total suitable recoveries (no-mention of oiling)[3] Dead	Live
Rehabilitated guillemots (pre-1985)	132	1	21	64 (4)	42
Rehabilitated guillemots (1985 onwards)	177	0	36	77 (33)	22 (9)
non-RH guillemots (1985 onwards)	2728	0	504	1897[4]	321

Notes

1 A single bird which was hand-reared
2 Ring, or ring and leg only found, bird not freshly dead on recovery, finding date not accurate to within ± 50 days, or finding date = reporting date
3 Samples in parentheses comprise cases with no mention of oiling in the ringing information, which were presumably rehabilitated for other reasons. These were excluded from the main survival analyses (see Sections 2 & 3.1)
4 Six birds of unknown age class at ringing (*i.e.* which could not be categorised as either nestlings or fully-grown birds) were excluded

Table 2 Recoveries matrix used to estimate the 30-day survival rates and reporting rate of oiled and rehabilitated guillemots. Rehabilitated birds ringed from 1985 onwards were grouped by month of ringing, regardless of calendar year. Alterations to sample sizes after the addition of 17 live recoveries which were 'unwell' at the time of recapture are shown in parenthese.

Ringing month	Number ringed	30-day period after ringing												
		1st	2nd	3rd	4th	5th	6th	7th	8th	9th	10th	11th	12th	13th
January	594 (597)	9 (12)	0	0	0	0	0	0	0	0	0	0	0	0
February	871 (877)	11	2	0	0	0	1	0	0	0	0	0	0	0
		(16)		(1)										
March	831 (839)	21 (29)	2	0	0	1	0	0	0	0	0	1	0	0
April	215	10	1	0	0	0	0	0	0	0	0	0	0	1

Table 3 Recovery matrices used to estimate the annual survival rates and reporting rates of non-RH guillemots.

Ringed when fully grown

Ringing year	Number ringed	Recovery year 1985-1986	1986-1987	1987-1988	1988-1989	1989-1990	1990-1991	1991-1992	1992-1993	1993-1994
1985	1565	3	3	1	2	2	3	1	0	1
1986	1840		1	3	3	5	0	3	1	3
1987	1341			7	2	3	3	0	2	0
1988	1057				5	3	3	1	0	0
1989	1919					15	2	1	0	2
1990	916						4	1	0	0
1991	1174							2	0	3
1992	994								2	1
1993	1038									1

Ringed as nestlings

Ringing year	Number ringed	Recovery year 1985-1986	1986-1987	1987-1988	1988-1989	1989-1990	1990-1991	1991-1992	1992-1993	1993-1994
1985	7087	170	11	2	10	9	0	0	2	0
1986	8333		48	37	17	22	8	2	2	4
1987	9422			188	36	11	8	2	6	4
1988	10090				210	43	15	4	2	2
1989	9592					207	30	1	2	4
1990	9607						137	15	4	14
1991	9564							23	28	20
1992	9783								101	24
1993	9106									90

Table 4 **Comparison of time elapsed and distance moved between ringing and recovery (as a dead bird) of rehabilitated guillemots ringed from 1985 onwards with oiling mentioned in the recoveries text field and rehabilitated birds with no mention of oiling.**

		'Oiled'	'Non-oiled'
Time elapsed (days)	Mean	28.7	18.3
	s.e.	7.9	9.7
	Median	7	4
	(n)	(77)	(33)
Distance moved (km)	Mean	45.1	66.9
	s.e.	16.5	35.0
	Median	8	8
	(n)	(77)	(33)

Table 5 **Comparison of time elapsed and distance moved between ringing and recovery (as a dead bird) of oiled and rehabilitated guillemots (ringed when fully-grown) and non-RH birds ringed from 1985 onwards. The non-RH guillemots were ringed as either nestlings or fully-grown birds. Oiled and rehabilitated guillemots ringed prior to 1985 are included for comparison with those ringed from 1985 onwards.**

		Non-RH (nestlings) 1985 onwards	Non-RH (fully-grown) 1985 onwards	Rehabilitated Oiled 1985 onwards	Rehabilitated Oiled Pre-1985
Time elapsed (days)	Mean	405.7	875.9	28.7	104.3
	s.e.	11.4	79.7	7.9	60.2
	Median	227	599	7	6.5
	Range	10-3762	3-3795	1-381	0-3130
	(n)	(1784)	(113)	(77)	(64)
Distance moved (km)	Mean	617.3	465.1	45.1	83.0
	s.e.	8.1	39.2	16.5	10.4
	Median	637.5	496	8	21.5
	Range	0-1866	0-1527	0-1134	0-474
	(n)	(1784)	(113)	(77)	(64)

Table 6 **Live recoveries of oiled and rehabilitated guillemots ringed before and after 1985, which were excluded from the main survival analyses. All except 3 of those ringed before 1985 were known to be 'unwell' at the time of recovery (3 of which were taken back into captivity), the others being of unknown condition.**

		Rehabilitated Pre-1985	Rehabilitated 1985 onwards 'Unwell'	Rehabilitated 1985 onwards Healthy
Time elapsed (days)	Mean	8.2	10.9	3612.5
	s.e.	1.9	6.2	3.5
	Median	3	4	-
	Range	0-62	0-127	3609-3616
	(n)	(42)	(20)	(2)
Distance moved (km)	Mean	29.4	70.9	167.0
	s.e.	7.6	30.3	0
	Median	10.5	6.5	-
	Range	0-224	0-475	-
	(n)	(42)	(20)	(2)

Table 7a Model selection and survival rates (S) and reporting rate (λ) estimated using dead recoveries of oiled and rehabilitated guillemots ringed from 1985 onwards. Maximum likelihood estimates from program MARK are presented with 95% confidence limits in parentheses. Ringing data were grouped into 4 month classes, regardless of calendar year, and survival rates were estimated per 30-day period after release (see Table 2). The model with constant survival and reporting rate was compared to models in which survival rates varied with time after release. In the model definitions, C=constant with time after release. The reporting rate was held constant throughout. For S, figures refer to dependence on periods after release (*e.g.* 1,2,3+ indicates three separate estimates of S; one for the first 30 days, one for the second 30 days, and one for the period after 60 days). Arrows indicate S estimates which span more than one 30-day recovery class. NI= non-identifiable due to sparse data (giving boundary estimates). The favoured model is shown in bold.

Model S	S1	S2	S3	S4+	λ	Goodness-of-fit	qAIC	Likelihood ratio test χ^2	df	P
C	30.6 (21.7-41.4)	→	→	→	2.4 (1.8-3.0)	<0.0001	668			
1,2+	13.7 (7.0-25.0)	70.3 (48.5-85.6)	→	→	2.4 (1.8-3.0)	<0.0001	644	25.9	1	<0.0001
1,2,3+	16.8 (3.5-52.6)	51.3 (3.7-96.6)	93.6 (10.3-99.9)	→	2.4 (1.7-3.5)	0.9857	640	6.3	1	0.0100
1,2,3,4+	14.9 (6.5-30.6)	43.9 (10.5-83.9)	NI	88.3 (27.5-99.3)	2.4 (1.8-3.1)	0.9558	641	0.8	1	0.3600
1+2,3+	**17.0 (9.5-28.6)**	→	**85.8 (57.5-96.4)**	→	**2.4 (1.8-3.0)**	**<0.0001**	**641**	{Test against model S1,2,3+λ} 3.2	1	0.0800

Table 7b **Model selection and survival rates (S) and reporting rate (λ) estimated using dead *and 'unwell' live* recoveries of oiled and rehabilitated guillemots ringed from 1985 onwards. Maximum likelihood estimates from program MARK arepresented with 95% confidence limits in parentheses. Ringing data were grouped into 4 month classes, regardless of calendar year, and survival rates were estimated per 30-day period after release (see Table 2). The model with constant survival and reporting rate was compared to models in which survival rates varied with timeafter release. In the model definitions, C=constant with time after release. The reporting rate was held constant throughout. For S, figures refer to dependence on periods after release (*e.g.* 1,2,3+ indicates three separate estimates of S; one for the first 30 days, onefor the second 30 days, and one for the period after 60 days). Arrows indicate S estimates which span more than one 30-day recoveryclass. NI= non-identifiable due to sparse data (giving boundary estimates). The favoured models are shown in bold (see Section 3.2).**

Model S	S1	S2	S3	S4+	λ	Goodness-of-fit	qAIC	Likelihood ratio test χ^2	df	P
C	26.9 (19.3-36.2)	→	→	→	3.0 (2.4-3.7)	<0.0001	808			
1,2+	**11.9 (6.3-21.3)**	**68.7 (48.1-83.8)**	→	→	**3.0 (2.4-3.8)**	**<0.0001**	**779**	30.8	1	<0.0001
1,2,3+	**12.5 (6.4-22.9)**	**47.5 (18.2-78.7)**	**84.4 (44.6-97.3)**	→	**3.0 (2.4-3.8)**	**0.8673**	**777**	3.7	1	0.0500
1,2,3,4+	12.9 (5.9-25.8)	49.5 (15.9-83.6)	79.6 (22.9-98.1)	88.3 (27.5-99.3)	3.0 (2.4-3.8)	0.9601	779	0.2	1	0.6600
1+2,3+	15.5 (9.2-25.0)	→	80.5 (54.3-93.5)	→	3.0 (2.4-3.8)	<0.0001	780	Test against model {S1,2,3+ λ}		
								5.5	1	0.0200

Table 8a **Modelling the annual survival (S) and reporting rates (λ) of non-RH guillemots ringed between 1985 and 1993 using program SURVIV. Two age classes were discriminated at the time of ringing: nestlings and fully-grown birds. Subscript 'a' in the model definition is used to denote dependence on age (first year of life and after first year of life) and 't' to denote dependence on time (calendar year). The favoured model is shown in bold.**

Initial model	np	G-O-F (P)	AIC	Constrained model	np	G-O-F (P)	AIC	Likelihood ratio test χ^2	df	P
1) S_{at} λ_{at}	34	0.0001	473	**S_{at} λ_a**	**20**	**0.0005**	**454**	**8.8**	**14**	**0.8423 ***
				S_{at} λ_t	25	<0.0001	509	53.9	9	<0.0001
				S_a λ_{at}	20	<0.0001	474	28.7	14	0.0114
				S_t λ_{at}	25	<0.0001	908	452.5	9	<0.0001
2) S_{at} λ_a	**20**	**0.0005**	**454**	S_{at} λ	19	<0.0001	521	68.9	1	<0.0001
				S_a λ_a	4	<0.0001	865	443.1	16	<0.0001
				S_t λ_a	11	<0.0001	481	45.1	9	<0.0001

Table 8b **Further elaboration of the model from which to estimate the survival (S) and reporting rates (λ) of non-RH guillemots ringed between 1985 and 1993 using program MARK. Two age classes (nestlings and fully grown) were discriminated at the time of ringing. Subscript 'a' in the model definition denotes dependence on age, and 't' denotes dependence on time (year-specific estimates). The numbers in the subscripts denote the number of age classes discriminated in the analysis (see Section 3.3 for full details). The favoured model is shown in bold.**

Initial model	np	G-O-F (P)	qAIC	Constrained model	np	G-O-F (P)	qAIC	Likelihood ratio test χ^2	df	P
3) $S_{a3t}\ \lambda_{a2}$	28	0.0269	19250	$S_{a2}\ \lambda_{a2t}$	20	0.0005	19280	46.5	8	<0.0001
4) $S_{a4t}\ \lambda_{a2}$	**35**	**0.0630**	**19251**	$S_{a3t}\ \lambda_{a2}$	28	0.0269	19250	13.0	7	0.0700
				$S_{a4}\ \lambda_{a2}$	6	<0.0001	19669	476.6	29	<0.0001
				$S_{a4t}\ \lambda$	34	0.0553	19261	11.96	1	<0.0001
5) $S_{a5t}\ \lambda_{a2}$	41	0.0525	19258	**$S_{a4t}\ \lambda_{a2}$**	**35**	**0.0630**	**19251**	**4.4**	**6**	**0.6300**

Table 9 Comparison of the observed number of recoveries of oiled and rehabilitated guillemots ringed between 1985 and 1995 with the expected number based on the survival rates (S) of control guillemots and the reporting rate (λ) of control and rehabilitated guillemots estimated in the present study. S and λ for controls are from model $\{S_{a4t}\ \lambda_{a2}\}$ and for rehabilitated birds from model $\{S_{1,2,3+}\ \lambda\}$, inlcluding live but 'unwell''recoveries of rehabilitated birds. The observed number of recoveries of rehabilitated birds in the first year after release are compared with an expected number under five scenarios:-

(a) Based on the survival and reporting rates of first year non-RH birds.
(b) Based on the survival and reporting rates of second year non-RH birds.
(c) Based on the survival and reporting rates of third year non-RH birds.
(d) Based on the survival and reporting rates of fully grown non-RH birds.
(e) Based on the 'worst case' survival of non-RH birds (first years) and the reporting rate of rehabilitated birds.

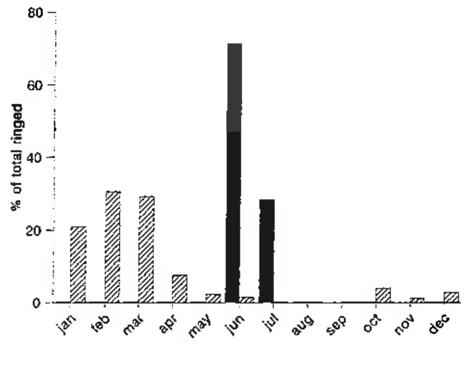
		(a) 1st year rates	(b) 2nd year rates	(c) 3rd year rates	(d) F-G rates	(e) 'Worst case' non-RH S & rehabilitated λ
(1)	n at start of year 1 (n rehabilitated birds ringed)	2699	2699	2699	2699	2699
(2)	Survival rate	45.7%	74.5%	87.6%	72.7%	45.7%
(3)	n surviving year 1 (1) x (2)	1233	2011	2364	1962	1233
(4)	n dying in year 1 (1) - (3)	1466	688	335	737	1466
(5)	Reporting rate	3.4%	3.4%	3.4%	1.3%	3.0%
(6)	Expected n recoveries in year 1 (4) x (5)	50.4	23.7	11.5	9.7	44.0
(7)	Observed n recoveries of rehabilitated guillemots	62	62	62	62	62
(8)	Factor increase in recoveries in year 1 n rehabilitated recoveries (7) / Expected n recoveries (6)	1.2	2.6	5.4	6.4	1.4
(9)	**Expected n in year 2+ (where observed n=1)**	**14.9**	**16.7**	**16.4**	**13.6**	**18.1**

Table 10 Comparison of the survival rates of rehabilitated and non-RH guillemots estimated in the present study with previous published estimates.

	Annual survival rate	Method	Years	Location	Source
Rehabilitated guillemots					
Age unknown	0.2-1.1%[1]	Metal ring recoveries	1985-1996	All British recoveries	PRESENT STUDY
	Negligible	Metal ring recoveries	1969-1994	North American recoveries	Sharp (1996)
Natural survival					
First year	46%	Metal ring recoveries	1985-1994	All British recoveries	PRESENT STUDY
Second year	75%	"	"	"	"
Third year	88%	"	"	"	"
'Fully grown'	73%	"	"	"	"
Natural survival					
Aged 1-5 years	16-20%	Colour-ringed immatures in clubs	1972-1977	Skomer Island, Wales	Birkhead & Hudson (1977)
	27-41%	Metal ring recoveries	Various	Various (Britain, Canada, Norway)	Birkhead & Hudson (1977)
	41%	Population modelling	1985-1989	Skomer Island, Wales	Hatchwell & Birkhead (1991)
Breeding adults	86-88%	Colour-ringing	1951-1953	Whinnyfold, northeast Scotland	Southern *et al.* (1965)
	91.5%	Colour-ringing	1973-1975	Skomer Island, Wales	Birkhead & Hudson (1977)
	94%	Colour-ringing	1986-1989	Skomer Island, Wales	Hatchwell & Birkhead (1991)
	82-100%	Colour-ringing	1986-1991	Southeast Farallon Island, California	Sydeman (1993)
	92-99%	Colour-ringing	1982-1992	Isle of May, Scotland	Harris & Wanless (1995)
All ages	88%	Metal ring recoveries	1960-1972	All British recoveries	Birkhead (1974)
	93%[2]	Metal ring recoveries	1960-1972	All British recoveries[2]	Mead (1974)
	87%	Metal ring recoveries	1933-1943	Helgoland recoveries	Mead (1974)

Notes 1 0.6% with dead recoveries only, 0.2%/1.1% including live but 'unwell' recoveries and depending on model selected.
2 Using 'middle-aged' recoveries only.

(A)



(B)

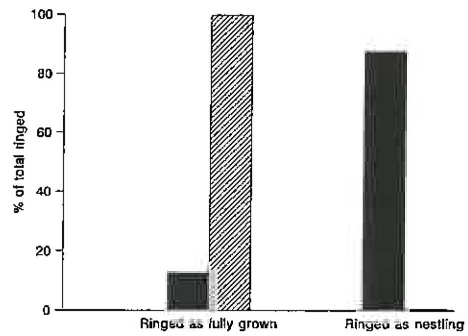


Figure 1 **Differences in (A) month of ringing and (B) age at ringing between rehabilitated guillemots (striped bars) and non-RH birds (solid bars).**
Sample sizes: (A) 2912 rehabilitated & 120,809 controls
(B) 2877 rehabilitated & 120,739 controls

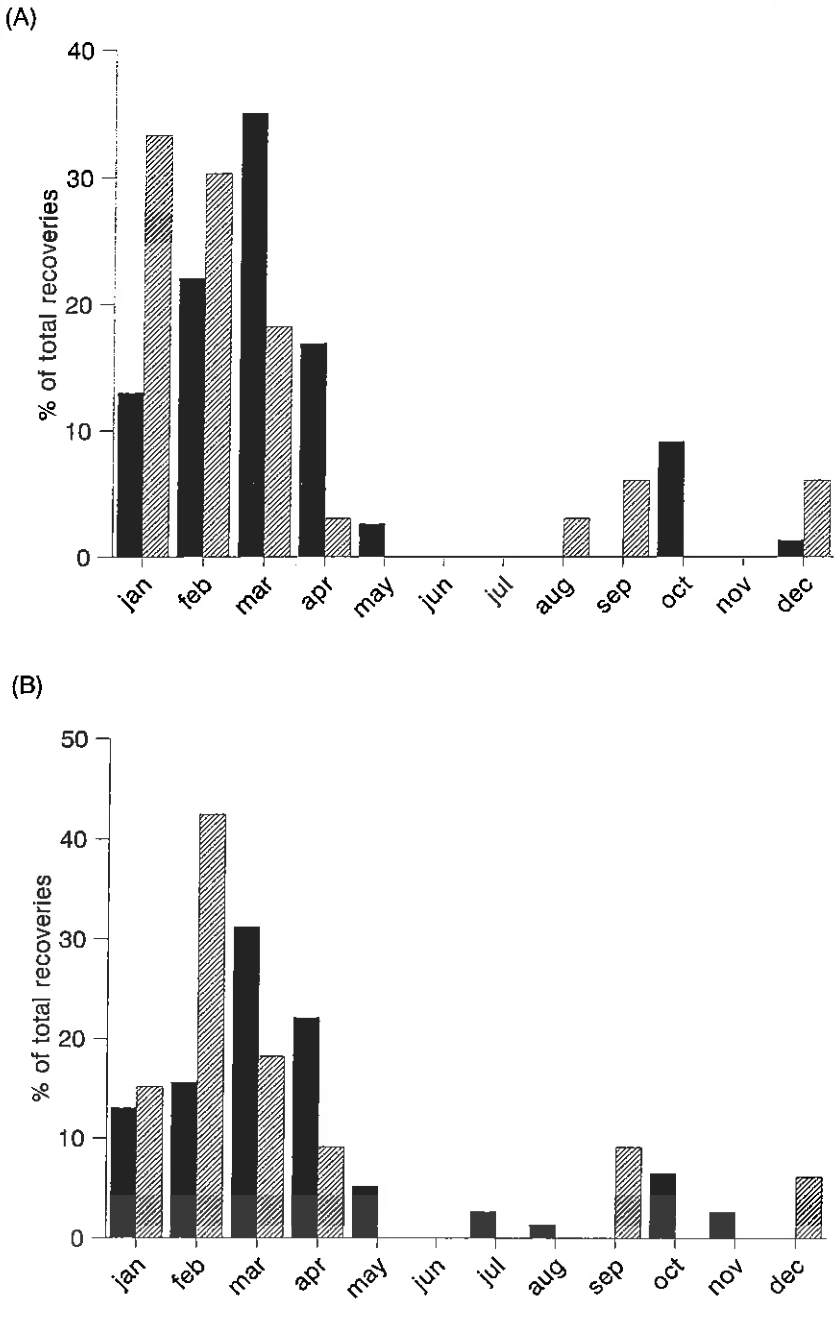


Figure 2 **Comparison of (A) month of ringing and (B) month of recovery between rehabilitated guillemots with oiling mentioned in the ringing details (solid bars) and those without oiling mentioned (striped bars), for guillemots ringed from 1985 onwards. Sample sizes: 77 oiled and 33 non-oiled.**

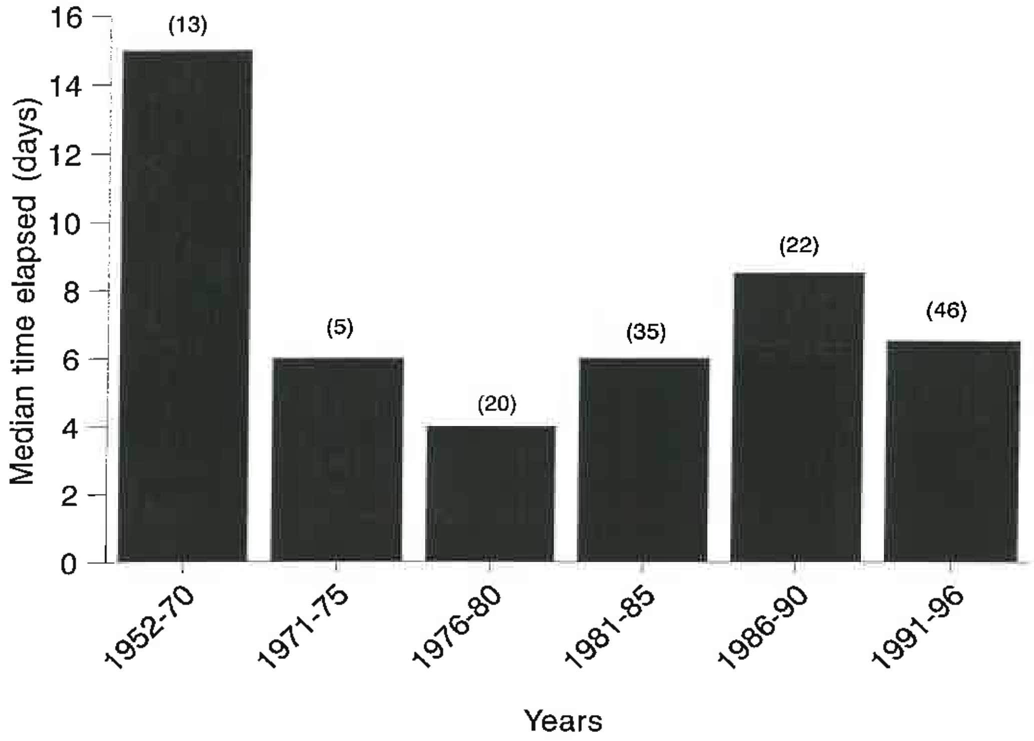


Figure 3 **The median time elapsed between ringing and (dead) recovery of oiled and rehabilitated guillemots between 1952 and 1996. Sample sizes in each block of years are shown in parentheses.**

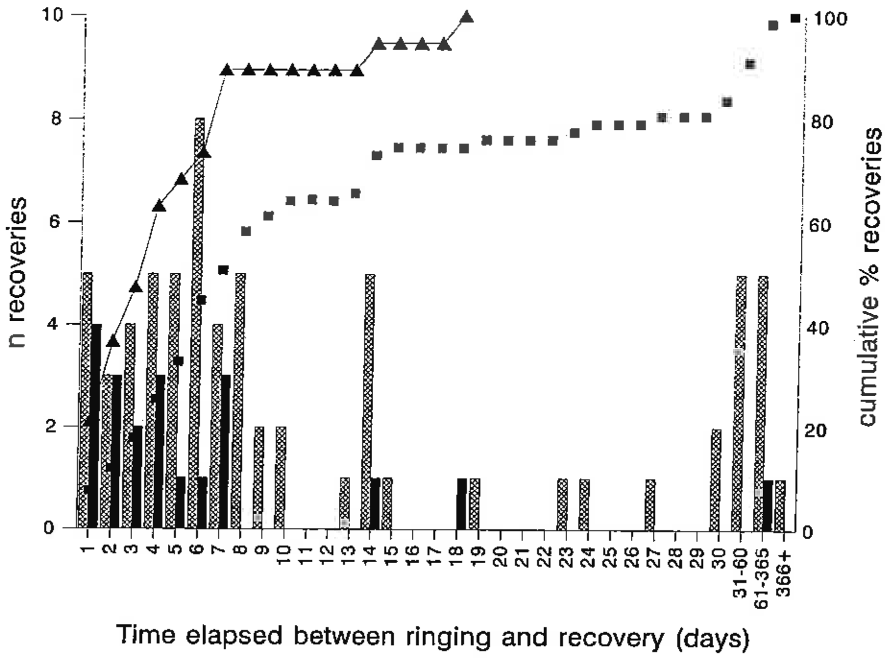


Figure 4 **Distribution of dead recoveries (hatched bars, n=67) and live but 'unwell' recoveries (solid bars, n=19) of oiled and rehabilitated guillemots ringed between 1985 and 1995 with days after release. Note that the x-axis scale is in 1-day intervals up to 30 days and then in blocks. The cumulative percentage of recoveries with time is shown for dead recoveries (square symbols and broken line) and live but 'unwell' recoveries (triangular symbols and solid line).**

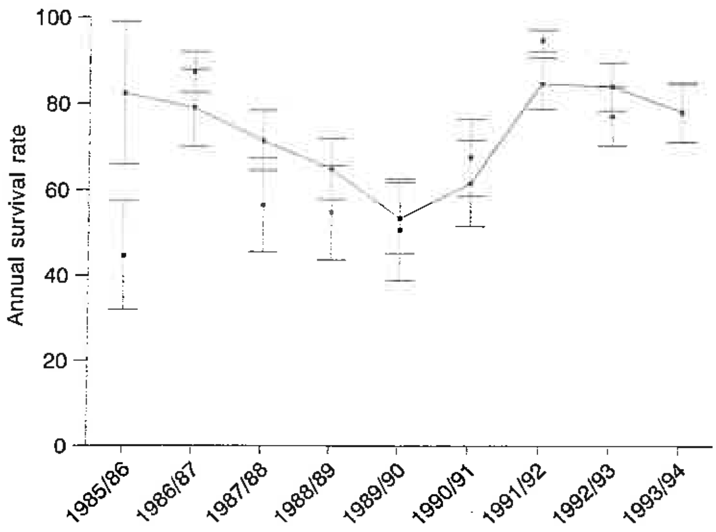


Figure 5 **Annual survival rates of first year (broken line) and fully-grown (solid line) non-RH guillemots from model $\{S_{at}\ \lambda_a\}$. Maximum likelihood estimates (from program SURVIV) are shown with 95% confidence limits.**

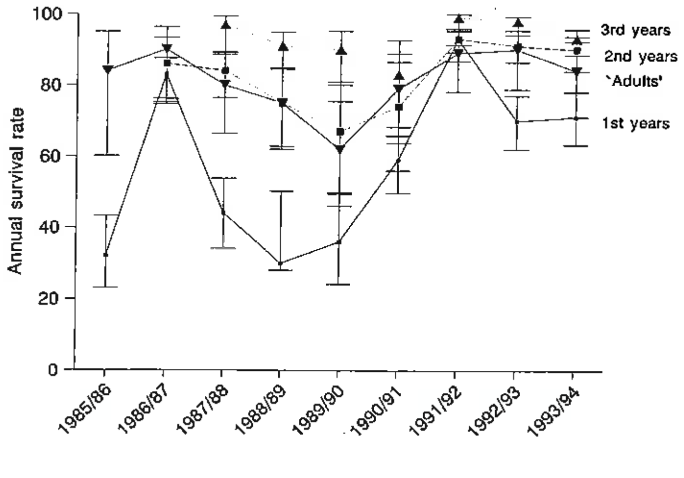


Figure 6 **Annual survival rates of non-RH guillemots from model $\{S_{a4t}\ \lambda_{a2}\}$. Maximum likelihood estimates for each age class distinguished in the analysis (from program MARK) are shown with 95% confidence limits in parentheses. For full details of the modelling process see Section 3.3 of the text.**

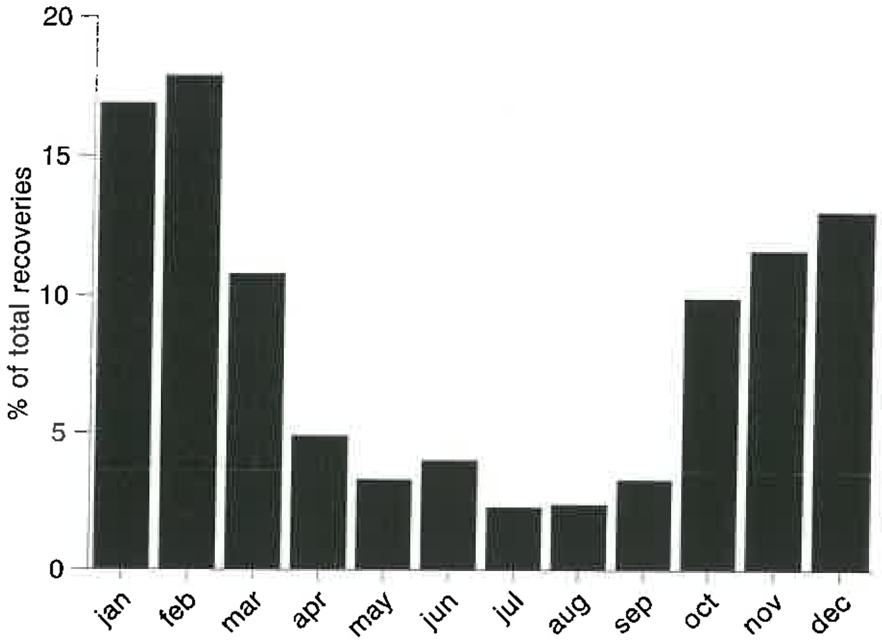


Figure 7 **Seasonal distribution of ring recoveries of non-RH guillemots (all age classes combined) ringed during the breeding season (June & July) from 1985 onwards. Sample size=1865.**