# ADULT SURVIVAL OF THE BLACK GUILLEMOT IN ICELAND[1]

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*Abstract.* We studied adult survival of the Black Guillemot (*Cepphus grylle*) based on a capture-recapture data set collected in 1974–1995 in a colony in western Iceland. A total of 1,483 individuals were observed once or more as breeders; some of these were local or immigrant recruits. There was no evidence that adult survival varied over time; the estimated constant survival was 0.870 (95% confidence limits 0.855–0.884). This was similar to previous estimates for this species, but precision was very high. Because many guillemots drowned in fishing nets near our study site, we attempted to model survival as a function of local fishery effort; we were unable to do this because of excessive variation in capture effort. The final model also included a separate survival estimate for the first year after the first capture as breeder. This apparent first-year survival declined over time from 0.900 to 0.562. Both the lower apparent first-year survival and the negative trend were likely due to the presence of low-capturability individuals in the data set. We suggest that some birds were very difficult to capture because their nests were in shorebird or tern territories. The lower adult survival of Black Guillemots compared to other Atlantic alcids (murres, puffins) is presumably related to their inshore feeding habits, which also allow this species to raise two chicks to fledging.

*Key words: adult survival, Black Guillemot, capture-recapture, Cepphus grylle.*

## INTRODUCTION

Adult survival is a key parameter of vertebrate population dynamics. In long-lived species, population multiplication rate is more sensitive to changes in adult survival than it is to changes in any other demographic parameter (Lebreton and Clobert 1991). As a consequence, any understanding of population dynamics in such species requires a good estimate of adult survival and preferably some information on factors affecting survival, e.g., age, sex, and external factors. Generally, seabird life histories are characterized by high adult survival, delayed recruitment, and low reproductive output (Furness and Monaghan 1987, Croxall and Rothery 1991).

With the major advances in capture-recapture theory (Lebreton et al. 1992, Nichols 1992) and software (Cooch et al. 1997) over the last decade, it has become relatively easy to obtain information on survival and the factors affecting it, given the availability of adequate data sets. As a rule of thumb, such data sets should span

at least twice the mean life expectancy of the species (J.-D. Lebreton, pers. comm.); for a long-lived species, 20–30 years of data may be required. The collection of relevant data is helped by the fact that most seabirds are colonial breeders, making it possible to mark and observe large numbers of birds. Some long-term studies of seabirds have been conducted (Jouventin and Weimerskirch 1991, Wooller et al. 1992), but for many species no pertinent information on adult survival is available.

The Black Guillemot (*Cepphus grylle*) is an inshore-feeding, cavity-nesting alcid seabird widely distributed in the North Atlantic and Arctic (Nettleship and Evans 1985). Several short-term studies have investigated its breeding biology and population dynamics, including adult survival (Asbirk 1979, Petersen 1981, Ewins 1989), but as yet no one has analyzed survival using capture-recapture models on a long-term data set.

Here, we report the results of a survival analysis of a long-term capture-recapture data set collected in a colony of Black Guillemots on the island Flatey in western Iceland (Fig. 1). The study started in 1974 (Petersen 1981) and has been running continuously ever since, although
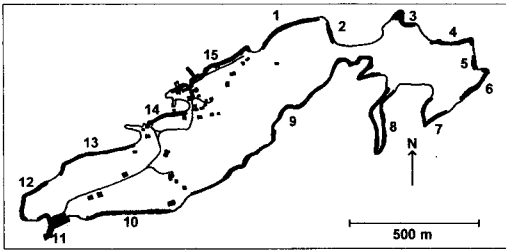
FIGURE 1. Map of Flatey island, western Iceland, showing the location of the 15 subcolonies of Black Guillemots. 1: Lunda, 2: Sunda, 3: Brull, 4: Skelja, 5: Salt, 6: Torta, 7: Nátt, 8: Kjóa, 9: Str-Dugg, 10: Yzti, 11: Bryggja, 12: Tröll, 13: Tein, 14: Vest, 15: Eyj-Hj.
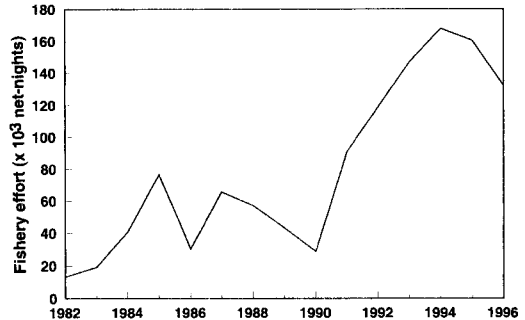


FIGURE 2. Fishery effort (number of net-nights) 1982–1996 in the lumpsucker fishery in Breiðafjörður quadrats 5221 and 5232 (Marine Research Institute, Reykjavík), including the known foraging areas of Black Guillemots breeding on Flatey Island (Petersen 1981).

with a large annual variation in the effort invested.

The main aim of our analysis was to provide a robust baseline estimate of adult survival in the Black Guillemot. Such an estimate is needed for population modeling in a basic or applied (management) context (Lebreton and Clobert 1991, Frederiksen and Petersen, in press b), and also for comparative studies of life-history evolution.

We also wanted to examine the link between survival and external factors affecting the population. Drowning in fishing gear has been implicated as the cause of increased mortality and population declines in other seabirds, particularly albatrosses (Weimerskirch and Jouventin 1987, Weimerskirch et al. 1997). During the early part of the Black Guillemot breeding season (May–June), increased fishing for lumpsucker (Cyclopterus lumpus) has taken place near the study colony (Fig. 2). Many Black Guillemots get entangled in monofilament nylon nets and drown, including an increasing number of birds banded on Flatey (A. Petersen, unpubl. data). We predicted that increased fishery effort might affect adult survival at our colony, and we therefore attempted to model survival as a function of local fishery effort.

In view of the nonstandardized capture effort in the field study, a further objective of our analysis was to assess the effect of extensive variation in capture effort over space and time.

## METHODS

### STUDY AREA

The Black Guillemot colony on Flatey in the Breiðafjörður bay, western Iceland (65°22′N, 22°55′W) has been studied since 1974. The

study was particularly intensive in 1975–1978 (Petersen 1981). Flatey is a flat, basaltic, grass-clad island, approximately 2 km from end to end, strongly indented and only about 50 ha in area (Fig. 1). The western part of the island is inhabited by less than 10 persons year-round and by about 100 people during the summer, whereas the eastern part is a bird reserve with restricted admittance. Flatey has a rich birdlife dominated by a large Arctic Tern (Sterna paradisaea) colony (Petersen 1979). Several shorebird species also are numerous, particularly Common Redshank (Tringa totanus) and Common Snipe (Gallinago gallinago) (both > 50 pairs). Black Guillemots breed in holes and crevices along all rocky parts of the coastline, and also in stone walls and other human artifacts.

### FIELDWORK

In 1975–1977, the colony was studied intensively for the entire breeding season (Petersen 1981). In almost every year since then (see below), two visits were made to the colony, one during late incubation (mid–late June) when most adults were captured, and one during chick rearing (mid July). Generally, the whole coastline of the island was explored on every visit (except as below), and practically all nests were found. All newfound nests were marked with a unique sequential number using an engraved Darvic tag glued to a nearby rock. Furthermore, a description of the location of the nest in relation to landmarks was made. The state of every previously known nest was ascertained. It is thus known in which years each nest was suitable for

TABLE 1. The 15 subcolonies of Black Guillemots on Flatey island, western Iceland.

| Subcolony | Maximum size (occupied nests) | Year of maximum size | Total nests used 1974–1995 |
|---|---|---|---|
| Lunda | 135 | 1985 | 315 |
| Sunda | 14 | 1988 | 26 |
| Brull | 30 | 1987 | 45 |
| Skelja | 46 | 1991 | 61 |
| Salt | 8 | 1990, 1991, 1993 | 9 |
| Torta | 49 | 1985, 1993 | 71 |
| Nátt | 23 | 1990, 1992 | 43 |
| Kjóa | 19 | 1985 | 31 |
| Str-Dugg | 38 | 1991 | 56 |
| Yzti | 30 | 1994 | 47 |
| Bryggja | 20 | 1991 | 38 |
| Tröll | 23 | 1986 | 33 |
| Tein | 84 | 1989 | 183 |
| Vest | 16 | 1985, 1991 | 31 |
| Eyj-Hj | 56 | 1992 | 114 |
| Total | 534 | 1985 | 1,103 |

nesting (as judged by the human eye). Missing number tags were replaced.

The presence, number, and age of eggs and/ or chicks were noted. All chicks older than approximately 10 days were banded with steel bands from the Icelandic Institute of Natural History. These bands are readable up to 23 years, and band loss did not seem to be a problem. In a few cases, it was impossible to catch or even see the chicks, and their presence was inferred from excrement stains (highly visible, especially in large chicks). A nest was scored as occupied if eggs and/or chicks (or their remains) were found, or if an adult was captured in or seen leaving the nest. Chicks older than approximately three weeks were considered to have fledged (unless proven to have died before fledging), because mortality has been shown to be very low after this age (Petersen 1981).

Any adults present in the nest cavity were captured (if possible) and banded or band numbers read. In 1975–1978, color band combinations were used in some parts of the colony, otherwise only steel bands. In some years and areas, adults also were captured using traps placed in the nest entrance. Neither chicks nor adults could be sexed from morphological characters.

The island was divided into 15 subcolonies of varying sizes (Table 1, Fig. 1). In most years, all subcolonies were visited. However, in 1981, Lunda, Sunda, Brull, Vest, and Eyj-Hj were not visited, and from 1993 onwards, Sunda, Nátt,

Kjóa, Bryggja, Vest, Eyj-Hj, and a part of Lunda were dropped from the study. Capture effort for adults has varied among subcolonies. In 1975–1978, it was particularly high for Torta and a part of Lunda, because many birds were color-banded and a high-intensity study of breeding biology, chick feeding, etc. was carried out here (Petersen 1981). Since about 1985, Yzti and Tröll have been worked intensively, partly because most nests are more accessible here than in the rest of the colony.

In 1980, 1981, 1984, and 1988, no early visit was made and therefore very few adults were captured.

DATA ANALYSIS

The data set consisted of the capture histories of 1,483 individuals captured at least once as breeders during 1974–1995, excluding birds captured only in 1995. Of these, 341 were known local recruits (i.e., banded as chicks on Flatey—almost 9,000 chicks were banded from 1974–1994; Frederiksen 1998) and 30 were known immigrants banded as chicks in nearby colonies, whereas the remaining 1,112 were banded as adults. For the recruits and immigrants, we only considered the capture histories from first recapture as breeder. Here, "age" for all birds means number of years elapsed since first capture as breeder.

Because of the known heterogeneity of capture effort among subcolonies, we initially split the data into 15 subsets according to subcolony. Birds were assigned to the subcolony in which they were first captured as breeders; in this analysis, we ignored the few known cases of intersubcolony breeding dispersal (see Frederiksen and Petersen, in press a). Because analyzing 15 groups would involve estimating a huge number of parameters, and because some of the sub-datasets were quite small (25 individuals), we pooled them into four groups. This pooling was mainly based on the known variation in capture effort over time (see Fieldwork). We checked the validity of the pooling both by goodness-of-fit tests and by checking for a sub-group effect in initial SURGE analyses.

Goodness-of-fit tests were carried out in a modified version of RELEASE (Burnham et al. 1987), which incorporates Yates' correction for continuity and may be more useful for sparse data sets. For model fitting and parameter estimation, we used SURGE 5.1 (Cooch et al.

1997), which can handle higher numbers of groups and constraints than previous versions. The survival analysis followed standard capture-recapture procedures (Lebreton et al. 1992), the output being estimates of survival and recapture probabilities.

Briefly, the first step is to test the goodness-of-fit of the Cormack-Jolly-Seber (Cormack 1964, Jolly 1965, Seber 1965) model with time-dependent survival and recapture parameters for each data set, thereby assessing whether the assumptions of this model are met (Lebreton et al. 1992). Next, based on the results of this test, one selects a general model as a starting point for further analysis. If a particular component of the RELEASE test (test 3.SR) is significant, such a general model should include a two age-class effect on survival (Pradel et al. 1997), age here meaning number of years since first recapture as breeder. A number of less general models are then fitted, and the object is to select the model that provides the most parsimonious description of the data while still retaining an adequate fit. We used Akaike's Information Criterion (AIC; calculated automatically by SURGE 5.1) for model selection (Lebreton et al. 1992, Burnham et al. 1995). The model with the lowest AIC was selected. Because the absolute value of AIC has little meaning, we here report $\Delta$AIC values, i.e., the differences in AIC between the model in question and the best model.

Model notation follows Lebreton et al. (1992). A model is described by subscripts indicating its structure regarding survival ($\phi$) and recapture ($p$) probabilities. As an example, the Cormack-Jolly-Seber model is denoted ($\phi_t$, $p_t$). Following Prévot-Julliard et al. (1998), we use a more extended notation for models with two age-classes having different structure for survival parameters; e.g., model ($\phi^*_g$, $\phi$, $p_{t*g}$) has a group effect on apparent first-year survival, constant adult survival, and time and group effects (with interaction) on recapture probabilities. Subscripts used here are $t$: time-dependence, $g$: group effect, $a2$: two age-class effect, and $T$: logistic-linear time trend. An asterisk between two subscripts indicates a multiplicative effect (with interaction between the terms) and a plus sign an additive effect (no interaction).

Parameter values reported here are means and 95% confidence intervals.

TABLE 2. SURGE analyses checking for subcolony effects on survival and recapture probabilities for subcolony groups A (low effort), B (intermediate effort), and D (high effort 1975–1978). Values shown are $\Delta$AIC obtained automatically from SURGE 5.1.

| Model | Group A | Group B | Group D |
|---|---|---|---|
| $\phi_g$, $p_{t*g}$ | 82.06 | 83.42 | 28.43 |
| $\phi$, $p_{t*g}$ | 73.32 | 79.53 | 26.89 |
| $\phi_g$, $p_t$ | 4.74 | 3.22 | 4.62 |
| $\phi_{a2*g}$, $p_t$ | 0 | 0 | 2.30 |
| $\phi_{a2}$, $p_t$ | 1.98 | 0.31 | 0 |
| $\phi$, $p_t$ | 7.15 | 1.23 | 4.36 |

## RESULTS

### POOLING AND GOODNESS-OF-FIT TESTS

We chose to use four groups of subcolonies. Group A was characterized by a low capture effort, with almost no effort in 1993–1995 (Lunda, Sunda, Nátt, Kjóa, Vest, Eyj-Hj). Group B had a medium effort (Brull, Skelja, Salt, Str-Dugg, Bryggja, and Tein), group C had a very high effort 1975–1978 (Torta), and group D had a high effort since 1985 (Yzti, Tröll). The groups obtained were not geographically contiguous (see Fig. 1).

We checked the validity of the pooling by running a SURGE analysis with six simple models for each of the three groups containing multiple subgroups (Table 2). In no case was a model with recapture probabilities unique for each subgroup needed. For groups A and B, the model with a subgroup effect on survival (and two age-classes) was preferred, but the difference in AIC was so small ($\Delta$AIC < 2) that we nevertheless accepted model ($\phi_{a2}$, $p_t$) (no subgroup effect). This model was also preferred for group D (Table 2).

Goodness-of-fit tests showed that the four groups were homogeneous, particularly when corrected for sparseness of data by the use of Yates' correction (Table 3). However, for groups A and D, test component 3.SR was quite significant, and examination of the pattern of residuals of this test for all four groups showed that more individuals than expected among the "newly marked" were never recaptured. Newly marked birds were a mixture of newly marked adults and recruits/immigrants captured for the first time as breeders. This indicated an age effect on survival, with newly marked individuals having a lower apparent survival than others. The high $\chi^2$ value for group C was caused by the aberrant cap-

TABLE 3. RELEASE goodness-of-fit tests for groups A, B, C, and D. The top value in each cell for $\chi^2$ and $P$ is for the standard $\chi^2$ test, the bottom value incorporates Yates' correction for continuity. The first three columns show the goodness-of-fit test for the standard Cormack-Jolly-Seber model with time-dependent parameters ($\phi_t$, $p_t$), the middle three test for a relative age effect on apparent survival (Test 3.SR), and the last three show the goodness-of-fit test for the model including a two age-class effect ($\phi_{a2*t}$, $p_t$).

| Group | Number of individuals | $\phi_t, p_t$ | | | Test 3.SR | | | $\phi_{a2*t}, p_t$ | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | $\chi^2$ | df | $P$ | $\chi^2$ | df | $P$ | $\chi^2$ | df | $P$ |
| A | 552 | 108.3 | 84 | 0.04 | 32.7 | 14 | 0.003 | 75.6 | 70 | 0.30 |
| | | 93.0 | | 0.24 | 28.2 | | 0.01 | 64.8 | | 0.65 |
| B | 577 | 94.7 | 81 | 0.14 | 16.3 | 15 | 0.36 | 78.4 | 66 | 0.14 |
| | | 83.5 | | 0.40 | 15.8 | | 0.39 | 67.7 | | 0.42 |
| C | 147 | 69.8 | 52 | 0.05 | 8.1 | 13 | 0.84 | 61.7 | 39 | 0.01 |
| | | 27.6 | | 1.00 | 2.0 | | 1.00 | 25.6 | | 0.95 |
| D | 207 | 77.1 | 56 | 0.03 | 28.1 | 15 | 0.02 | 49.0 | 41 | 0.18 |
| | | 53.6 | | 0.56 | 21.6 | | 0.12 | 32.0 | | 0.84 |

ture history of one individual and disappeared completely when Yates' correction was applied (Table 3). Model ($\phi_{a2*t}$, $p_t$) thus fit the data adequately for all four groups.

SURVIVAL ANALYSIS

We started from model ($\phi_{a2*t*g}$, $p_{t*g}$) and fitted progressively simpler models (Table 4). It was impossible to achieve more parsimony in the description of recapture probabilities (models 1–4). Time and group effects on survival could be discarded (models 5–7); however, a two age-class effect was needed (models 7, 9). Models with a logistic-linear time trend in survival improved the fit (models 10–13); a group effect was still not needed (models 10–12). A model with a logistic-linear time trend in first age-class survival and a constant adult survival had the lowest AIC (model 13), but the model including a trend in adult survival was nearly as good

TABLE 4. Models fitted in SURGE for all four groups (A, B, C, and D) combined.

| Model | Deviance | No. of parameters | ΔAIC |
|---|---|---|---|
| (1) $\phi_{a2*t*g}, p_{t*g}$ | 7,009.68 | 218 | 145.41 |
| (2) $\phi_{a2*t*g}, p_{t+g}$ | 7,135.56 | 169 | 173.29 |
| (3) $\phi_{a2*t*g}, p_t$ | 7,274.34 | 164 | 302.07 |
| (4) $\phi_{a2*t*g}, p$ | 8,132.79 | 150 | 1,132.52 |
| (5) $\phi_{a2*g}, p_{t*g}$ | 7,137.31 | 91 | 19.04 |
| (6) $\phi^*_g, \phi, p_{t*g}$ | 7,139.20 | 88 | 14.97 |
| (7) $\phi_{a2}, p_{t*g}$ | 7,142.40 | 85 | 12.13 |
| (8) $\phi_g, p_{t*g}$ | 7,154.35 | 87 | 28.08 |
| (9) $\phi, p_{t*g}$ | 7,158.69 | 84 | 26.42 |
| (10) $\phi_{a2*T*g}, p_{t*g}$ | 7,117.64 | 99 | 15.40 |
| (11) $\phi^*_{T*g}, \phi, p_{t*g}$ | 7,123.61 | 92 | 7.34 |
| (12) $\phi_{a2*T}, p_{t*g}$ | 7,127.07 | 87 | 0.80 |
| (13) $\phi^*_T, \phi, p_{t*g}$ | 7,128.27 | 86 | 0 |

(model 12; ΔAIC = 0.80), and we base our inferences to some extent on both models.

We also attempted to fit models describing first age-class and/or adult survival as a function of fishery effort around Flatey (measured as number of net-nights). Unfortunately, this attempt failed due to severe problems of non-identifiability, i.e., SURGE was unable to estimate parameters independently of each other. This was probably related to the complex variation in recapture probabilities over time and groups.

The final model (model 13) included an estimated constant survival probability of 0.870 (95% confidence interval: 0.855–0.884); the estimates of apparent first-year survival $\phi^*$ declined from 0.900 in 1974–1975 to 0.562 in 1994–1995. Estimated recapture probabilities for all four groups are shown in Figure 3.

DISCUSSION

ADULT SURVIVAL

Our study provides the first robust estimate of adult survival in the Black Guillemot (0.870 [0.855–0.884]); that is, an estimate derived by maximum likelihood estimation from capture-recapture data under an appropriate statistical model, and including a measure of the precision of the estimate (Clobert and Lebreton 1991). However, several other estimates are available, all calculated as return rates, that is the proportion of marked birds recaptured or resighted the following year: 0.804 (Preston 1968), 0.82–0.89 (Asbirk 1979), 0.87 (Petersen 1981), and 0.94 (Ewins 1989). The estimates of Asbirk, Petersen, and Ewins were based on intensive, short-term (4, 5, and 2 years, respectively) studies of color-banded populations. Asbirk (1979) and Petersen
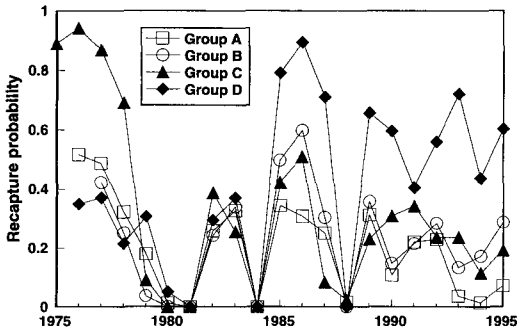
FIGURE 3. Recapture probabilities in the four groups of subcolonies 1975–1995. Values based on recaptures of 1–3 marked individuals in the early years have been omitted. Near-zero recapture probabilities in 1980, 1981, 1984, and 1988 were caused by very limited field effort. Groups A—D were characterized by different patterns of capture effort over the study period (see text for details).

(1981) corrected for the presence of birds missed in one year, but resighted later. Preston's study (1968) was similar, but involved physical recapture of marked individuals. For the closely related Pigeon Guillemot (*Cepphus columba*), only one estimate is available: 0.80, from a 5-year study of color-banded birds with no correction for missed individuals (Nelson 1991).

Contrary to what has been found in other species (e.g., Fig. 2 in Prévot-Julliard et al. 1998), our estimate is not markedly higher than the previous ones. This is probably because intensive studies of color-banded birds can achieve resighting probabilities close to 1 (Fig. 3, Group C 1975–1978). As noted by Martin et al. (1995), the negative bias in return rate estimates of survival is a decreasing function of recapture/resighting probability. It is therefore not surprising that studies using color-banded individuals provided higher estimates than the one depending on physical recaptures, because it is generally easier to resight than to recapture individuals. Bias can be further reduced by correcting for missed individuals. Thus, the estimate of Petersen (1981) is identical to the one we present here for the same population. Actually, Petersen's data were a subset of the first 5 years of our data set, namely the color-banded birds. We analyzed the whole 1974–1978 data set as one group. As expected, there was a pronounced lack of fit, but when we ignored that, we found that model ($\phi$, $p_t$) gave an estimated $\phi$ of 0.870.

## APPARENT FIRST-YEAR SURVIVAL

As predicted, a two age-class model provided the best description of the data. Prévot-Julliard et al. (1998) showed by simulation of a Common Black-headed Gull (*Larus ridibundus*) data set that this could be expected when individuals with both high and low capturability were present in the same data set. Low-capturability individuals will often only be captured once in their (breeding) lifetime, and the apparent first-year survival will be biased low because they appear to have died following their first capture as breeders (Prévot-Julliard et al. 1998). Significance of RELEASE test 3.SR should alert one to the possibility of such an age effect (cf. also transient models; Pradel et al. 1997). Further simulations of the Common Black-headed Gull data showed that a negative time trend in apparent first-year survival $\phi^*$ also is expected in such a situation (J.-D. Lebreton, pers. comm.). This occurs because the probability of an animal with low capturability being captured more than once in its breeding lifetime will decline with the number of years remaining in the study, i.e., there are simply fewer opportunities for being recaptured.

We expected this particular type of capture heterogeneity in our data, because we had pooled the original 15 subcolonies into four groups, thereby mixing individuals that had experienced different patterns of capture effort over time. Test 3.SR was significant in two of the four groups, and we accordingly started from a two age-class model. However, some heterogeneity was present already in the original subcolony data sets. When subcolonies were analyzed separately, a model with a two age-class structure was preferred in 4 out of 15 cases (data not shown), in every case with a lower $\phi^*$.

There are several possible biological explanations for this heterogeneity. If transients were present in the colony, a lower $\phi^*$ would result, because such individuals are by definition only observed once (Pradel et al. 1997). In our study, all animals captured were breeders, and because breeding dispersal was quite rare (Frederiksen and Petersen, in press a), it is not likely that there were many transients in the data set. Furthermore, the presence of transients would not induce a negative trend in $\phi^*$, precisely because they are never observed more than once. It is more likely that individual variation in captura-

bility was responsible for this effect. This might be related both to variation among individuals in shyness and to variation in nest-site characteristics. We suggest that the latter factor was the most important. Black Guillemots react strongly to the warning calls of Common Redshanks, Eurasian Oystercatchers (*Haematopus ostralegus*), and Arctic Terns by leaving their nests (pers. observ.). Birds nesting within shorebird or tern territories were therefore much more difficult to capture than others, and we conclude that this was responsible for at least part of the within- and among-subcolony heterogeneity in recapture probabilities. A contributing factor may have been that capture effort was not necessarily uniform within subcolonies.

An important question is whether neglecting the relative age effect would seriously bias the resulting estimate of adult survival. Pradel et al. (1997) showed for transient models that the relative bias in $\phi$ increases with higher proportion of transients and with lower $p$. In our study, the bias was not very severe. When the model ($\phi$, $p_{t*g}$) was fitted, $\phi$ was estimated as 0.862, well within the confidence interval of the estimate from the more general model. In general, our estimate of adult survival was very robust to violations of assumptions and fitting of inappropriate models. Even when we used the simplest possible model [($\phi$, $p$), $\Delta$AIC = 1,347.97], ignoring heterogeneity and variation over time and space in recapture probabilities, the estimate of $\phi$ was 0.837, only 3.8% lower than our best estimate. The long duration of our study probably contributed to this robustness.

## EFFECTS OF VARIATION IN CAPTURE EFFORT

Because capture effort was not standardized among years and subcolonies, and because no records were kept of the number of man-days spent every year, it was impossible to achieve parsimony beyond our initial pooling of the 15 subcolonies into four groups, and we had to use 83 parameters to model recapture probabilities (Fig. 3). If not for this, the confidence interval of $\phi$ would have been even narrower, given the same number of individuals and years. More importantly, the variation in capture effort prevented us from assessing the impact of external factors such as fishery on adult survival. It was not possible to fit a model with a link between fishery effort and survival in SURGE. Given the increasing fishery effort (Fig. 2) and the large

number of Black Guillemots drowning in fishing nets in recent years (A. Petersen, unpubl. data), we believe that adult survival has been affected negatively. Some support for this can be found in the low AIC value ($\Delta$AIC = 0.80) of the model ($\phi_{a2*T}$, $p_{t*g}$) with a trend in adult survival as well (Table 4, model 12). This trend was negative, even though $\phi$ only declined from 0.889 in 1974–1975 to 0.850 in 1994–1995. Such a trend might well be related to a change in some external factor; the increasing lumpsucker fishery is a good candidate. However, this is just speculation, and the fact remains that we would have been much better equipped to investigate such possible effects if capture effort had been standardized.

Years with no or almost no observations are particularly problematic when trying to establish a link between survival and some external factor. The reason is that if there are no observations in year $i$, the year-specific survival estimates of $\phi_{i-1}$ and $\phi_i$ cannot be calculated—only their product. It is therefore impossible to relate these estimates to the value of some external factor. This was probably the cause of the severe non-identifiability problems we experienced in SURGE when we tried to fit models of this type.

We advise researchers to keep records of the effort expended trying to capture animals every season. It will then be possible to model $p$ as a function of the effort (Lebreton et al. 1992). If effort is the main factor influencing recapture probability, this may allow a much more parsimonious model to be selected. Resulting survival estimates will have increased precision without a concurrent increase in bias, and power to detect small effects on survival will be increased. If capture effort is kept constant, a model with a constant $p$ may even be selected, thus achieving ultimate parsimony on the recapture side.

We conclude that when designing and carrying out a long-term capture-recapture study, one should, in order of priority: (1) avoid years with no capture effort, (2) keep records of capture effort (e.g., number of man-days per season), and (3) try to maintain a constant capture effort.

## ALCID LIFE HISTORIES

It is well known that Black Guillemots have a lower adult survival than the other Atlantic alcids (e.g., Hudson 1985). The best available estimates for these species are: Common Murre

(*Uria aalge*) 0.949 (Harris and Wanless 1995); Thick-billed Murre (*Uria lomvia*) 0.95 (Erikstad et al. 1994); Razorbill (*Alca torda*) 0.90 (Chapdelaine 1997); Atlantic Puffin (*Fratercula arctica*) 0.924 and 0.975 (two time periods) (Harris et al. 1997).

The lower survival is correlated with a number of other differences in life history, e.g., the Black Guillemot is the only Atlantic alcid that normally lays a two-egg clutch (Harris and Birkhead 1985). Like the other *Cepphus* guillemots, it also is less strictly colonial and more of an inshore feeder than other alcids (Gaston and Jones 1998). The key ecological difference is probably inshore feeding, which, through higher availability of food and/or shorter transit times between nest and foraging habitat, allows guillemots to achieve higher chick growth rate and fecundity than most other alcids. For example, a Black Guillemot pair is able to raise two chicks to fledging weight in shorter time than a pair of Atlantic Puffins—a bird of similar size—can raise one chick (Gaston 1985). The lower adult survival of guillemots is presumably the result of an evolutionary trade-off between reproduction and survival. The inshore foraging habitat is probably in some way associated with higher mortality risks, e.g., predation. However, very little is known about natural mortality factors affecting alcids, so it is too early to draw definite conclusions regarding the causes of variation in alcid life histories.

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