

Short communication

Adult survival and avian cholera in Common Guillemots *Uria aalge* in the Baltic Sea

HENRIK ÖSTERBLOM,^{1*} HENK P. VAN DER JEUGD² & OLOF OLSSON³

¹Bird Ringing Centre, Swedish Museum of Natural History, PO Box 50007, SE-104 05 Stockholm, Sweden
²Edward Grey Institute of Field Ornithology, Department of Zoology, University of Oxford, Oxford OX1 3PS, UK
³Mistra, Gamla Brogatan 36–38, SE-111 20 Stockholm, Sweden

Common Guillemots *Uria aalge* are long-lived seabirds with a low annual reproductive output; hence annual adult survival is a significant parameter for the sustainability of the population (Harris & Birkhead 1985, Hudson 1985). Oiling, bycatches, and large-scale oceanographic and food-web changes are commonly considered to be potential major threats to adult Common Guillemot survival (Takekawa *et al.* 1990, Vader *et al.* 1990, Piatt & Anderson 1996, Bakken & Falk 1998, Olsson *et al.* 1999, Österblom *et al.* 2002).

Avian cholera epizootic (caused by the bacteria *Pasteurella multocida*) is characterized by affecting a large number of species, annual recurrence of epizootics and an increasing geographical area of occurrence (Botzler 1991, Hindman *et al.* 1997, Friend *et al.* 2001). To our knowledge, avian cholera has only been documented once before in the Common Guillemot (Macdonald 1963), but in that case the basis of bacterial identification was not clear (cf. Botzler 1991). The first registered avian cholera epizootic in Scandinavia was noted in 1996 in Denmark (Christensen *et al.* 1997), but previous, undetected outbreaks cannot be excluded. In Sweden, Common Eiders *Somateria mollissima*, Herring Gulls *Larus argentatus*, Great Black-backed Gulls *L. marinus* and Barnacle Geese *Branta leucopsis* were all confirmed killed by *Pasteurella multocida* (avian cholera) in 1998 (Persson 1998, R. Mattson, Swedish National Veterinary Institute, pers. comm.). An estimated 5000 seabirds, on the island of Västergarns utholme (57°26'N, 18°06'E; 19 km north of the Common Guillemot colony at Stora Karlsö), were killed between 1996 and 1998, probably as a result of avian cholera. The findings of avian cholera in Common Guillemots reported in this

study were probably part of this outbreak. In 1998, Common Guillemots from Stora Karlsö were confirmed killed by avian cholera (necropsy report: Jansson 1998). The disease may have been transmitted from the Netherlands via Denmark by migrating Common Eiders (Christensen *et al.* 1997, Persson 1998).

The aim of this study is to estimate the annual adult survival probability of Common Guillemots ringed as breeding adults, and to discuss different factors that may affect this in the Baltic Sea, in particular avian cholera.

METHODS

Ringling and resighting

The study was performed on the island of Stora Karlsö (57°17'N, 17°58'E) off the west coast of Gotland in the Baltic Sea. This island hosts about 10 000 breeding pairs of Common Guillemots, about two-thirds of the Baltic Sea population. In 1997, 47, 30 and 34 breeding birds were colour-ringed in three different areas (areas 1–3) on the west coast of the island.

Searches for these birds were made each year between 1998 and 2002. Observations were made from above the breeding ledges with minimal disturbance using binoculars or a 20–60 × 70 telescope. Because chicks are ringed annually on the island, a certain proportion of the breeding birds are ringed with metal rings only. On the focal ledges, we checked almost all these rings annually to eliminate the possibility that a ringed bird that had lost its plastic ring was counted as being dead. We detected loss of plastic rings in only six birds.

Survival analysis

On only two occasions, both in 1999, was an unobserved individual later found to be alive. Therefore, the resighting rate in this study was equal to one in all years but 1999. This had the great advantage that survival could be estimated very accurately. The computer program MARK (White & Burnham 1999) was used to model resighting rate and survival. Although birds were only resighted rather than being physically recaptured, we refer to birds that were resighted in a particular year as having been 'released' during that year. We started the analyses from a model considering the effects of all variables of interest, plus interactions. Starting with the largest dataset, we modelled survival using the principle of parsimony, i.e. by gradually reducing the number of parameters in such a way that the model still provided a good representation of the data (Lebreton *et al.* 1992). Model selection was performed on the basis of a Quasi-Akaike's Information Criterion (QAICc), calculated as the deviance (–2 log likelihood) of the model plus twice the number of parameters, weighted for sample size and overdispersion (Akaike 1973, Anderson *et al.* 2000). The variance inflation factor,

*Corresponding author.
Email: henrik.osterblom@nrm.se

c-hat, equalled 1.072, indicating a very good fit and little overdispersion. We performed likelihood ratio tests (LRT) to test for the effects of different variables on survival by comparing two models, one including and one omitting the variable of interest. Model notation follows Lebreton *et al.* (1992), where the symbol ϕ is used for survival, P for resighting, and subscripts area and y are used to denote effects of area and year, respectively. An asterisk between two subscripts indicates the presence of an interaction between the two effects, and a plus sign denotes that the effects are additive. Particular models with dummy variables were used to address specific questions. For example, the effect of the avian cholera outbreak in 1998 on survival was investigated by replacing the variable time with a dummy variable such that survival was only allowed to be different for birds released in 1998 in two out of the three areas.

RESULTS AND DISCUSSION

Modelling revealed that annual survival was constant and high at 93.7% [95% confidence limits (CL) 90.8–95.7], except after the avian cholera outbreak in 1998, when survival was much lower ($\chi^2_1 = 7.48, P < 0.01$). More specifically, survival was as low as 78.8% (95% CL 68.0–86.6) in areas 1 and 2, whereas birds breeding in area 3 seemed unaffected by the outbreak and survived as well as in normal years. Except for this highly significant effect, differences in survival among years and areas were not significant (see Table 1 for modelling results and Fig. 1 for survival rates).

During the entire study we observed only one bird that changed breeding ledge, confirming the high site fidelity rate in Common Guillemots, which previously has been estimated at 96% (Birkhead 1977) and 91% (Harris *et al.* 1996), and we think that site shift did not bias our estimates of survival. The annual adult survival rate of 93.7% estimated in this study is very similar to estimates from other Common Guillemot studies (Hatchwell & Birkhead

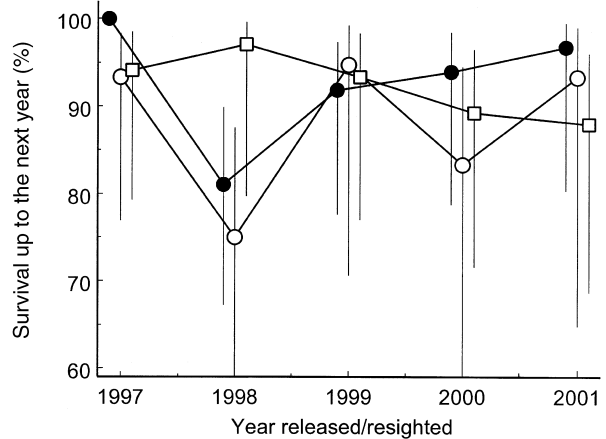


Figure 1. Annual adult survival rates for Common Guillemots *Uria aalge* in the Baltic Sea for three different areas within the breeding colony: (●) Area 1, (○) Area 2, (□) Area 3. Bars denote 95% confidence limits. Values are taken from model ($\phi_{\text{area}^*y}, P_{1999\ 1+3}$) (see text). Differences between areas and years are not significant as the overlapping confidence limits suggest, with the exception of the particularly low survival in areas 1 and 2 for birds released in 1998 owing to an outbreak of avian cholera (see text).

1991, Sydeman 1993, Erikstad *et al.* 1994, Harris *et al.* 2000a, 2000b). However, the estimated adult survival after the avian cholera outbreak in 1998 (see below) was comparatively low, showing that such outbreaks can have very profound effects on the population. Olsson *et al.* (2000) estimated adult Common Guillemot survival in the Baltic Sea by modelling ring recoveries in MARK and found adult (birds 5 years or older) annual survival rates of 87–90% during the period 1962–89 but only 78% during the period 1989–97. However, whereas our study investigated birds ringed as adult breeders, the analyses of ring

Table 1. Analysing annual adult survival of Common Guillemots *Uria aalge* in the Baltic Sea in relation to area and year, using capture–resighting modelling in program MARK. The order of models reflects the order in which they were run. Quasi-AICc and AICc weight for the most parsimonious models for P and ϕ are shown in bold type.

Model name	QAICc	QAICc weight	NP	LRT
Modelling P				
1 ($\phi_{\text{area}^*y}, P_{\text{area}^*y}$)	320.102	0.001	27	
2 ($\phi_{\text{area}^*y}, P_{1999\ 1+3}$)	297.975	0.001	17	P in area 1 + 3 similar in 1999: 2 vs. 1: $\chi^2_{10} = 0.02, P = 1.00$
3 (ϕ_{area^*y}, P)	302.338	0.000	16	Lower P in 1999: 3 vs. 2: $\chi^2_1 = 6.52, P = 0.01$
Modelling ϕ				
4 ($\phi_{\text{area}^*y}, P_{1999\ 1+3}$)	293.557	0.004	9	Interaction area*year: 4 vs. 2: $\chi^2_7 = 12.58, P = 0.08$
5 ($\phi_{\text{area}}, P_{1999\ 1+3}$)	296.109	0.001	5	Effect of year: 5 vs. 4: $\chi^2_4 = 10.82, P < 0.05$
6 ($\phi_y, P_{1999\ 1+3}$)	292.052	0.010	7	Effect of area: 6 vs. 4: $\chi^2_2 = 2.65, P = 0.27$
7 ($\phi, P_{1999\ 1+3}$)	294.675	0.002	3	Effect of area and year: 7 vs. 4: $\chi^2_6 = 13.47, P < 0.05$
8 ($\phi_{1998}, P_{1999\ 1+3}$)	289.228	0.040	4	Survival 1998 lower: 8 vs. 7: $\chi^2_1 = 7.48, P < 0.01$
9 ($\phi_{1998\ 1+2}, P_{1999\ 1+3}$)	282.930	0.941	4	

recoveries by Olsson *et al.* (2000) mainly investigated birds ringed as chicks. They therefore addressed a somewhat different subsample of the population, including non-breeders and dispersers. Non-breeding adult Common Guillemots appear to have a lower annual survival than breeders (Harris & Wanless 1995). Moreover, if survival probability increases with age well beyond the age of 5 years (Anderson *et al.* 1985, Martin 1994, Van der Jeugd & Larsson 1998), this can explain the lower survival found in recent years by Olsson *et al.* (2000).

Avian cholera

We found four of the individually ringed birds dead on one breeding ledge in study area 1 in 1998. They had shown signs compatible with avian cholera during the preceding few days (Rosen 1971, Rhoades & Rimler 1984). Two of these birds (one male and one female) were sent to the Swedish National Veterinary Institute, where the bacterium *P. multocida* was isolated from the liver and/or bone marrow. Histological examination showed congestion in most internal organs, polyserositis and a large number of circulating bacteria in ovary, air sacs and pleura (necropsy report: Jansson 1998).

Avian cholera is rare in Scandinavia and epizootics similar in magnitude to those of North America have so far been absent (see Botzler 1991). It is currently unclear to what extent adult survival in Common Guillemots could be affected by a major outbreak of avian cholera. Mortalities in some local Common Eider populations in Denmark were as high as 95% of the breeding females (Christensen *et al.* 1997).

However, stochastic events such as avian cholera have the potential to alter a population (size and/or structure) unpredictably. Other variable but predictable mortality factors can have an equally large impact on a population. Because avian cholera may never have occurred in Scandinavia prior to 1996 (Christensen *et al.* 1997), the decrease in adult survival between 1989 and 1997 observed by Olsson *et al.* (2000) probably resulted from some other factor (see below).

Sustainability

Common Guillemot adult survival in the Baltic Sea is probably influenced by a number of interactive factors that may be important at different times of the year, in different years and in different geographical areas (this study, Olsson *et al.* 1999, 2000, Österblom *et al.* 2002).

In conclusion, adult survival is high in the absence of avian cholera, which suggests that the population is sustainable at the current level of additional mortality caused by bycatches and oiling. However, unpredictable catastrophic events such as large avian cholera outbreaks or other diseases, or a large oil spill in the vicinity of the colony, migration routes or wintering area could have a large deleterious

impact on the population. Knowledge of age at first breeding and survival to breeding age are vital factors for population modelling and future management decisions.

J. Arrendal, K. Bäck, L. Engström and J. Sundberg performed a substantial part of the fieldwork in this study. We are grateful for the support from D. Jansson, R. Mattson and C. Bröjer at the Swedish National Veterinary Institute, who performed the necropsy and/or assisted with discussions. We would like to thank F. Sigsarve and Karlsö Jagt- och Djurskyddsförening AB, who provided logistic support. Drs A.G. Gosler, P. Rothery and an anonymous referee provided valuable comments on the manuscript. This project was funded by WWF Sweden. H.P.vdJ. was supported by a grant from the Swedish Foundation for International Cooperation in Research and Higher Education (STINT) while in Oxford.

REFERENCES

- Akaike, H.** 1973. Information theory and an extension of the maximum likelihood principle. In Petran, B.N. & Csáki, F. (eds) *International Symposium on Information Theory*: 267–281. Budapest: Akadémiai Kiadó.
- Anderson, D.R., Burnham, K.P. & Thompson, W.L.** 2000. Null hypothesis testing: problems, prevalence, and an alternative. *J. Wildl. Manage.* **64**: 912–923.
- Anderson, D.R., Burnham, K.P. & White, G.C.** 1985. Problems in estimating age-specific survival rates from recovery data of birds ringed as young. *J. Anim. Ecol.* **54**: 89–98.
- Bakken, V. & Falk, K. (eds)** 1998. *CAFF Technical Report no. 1, Circumpolar Seabird Working Group: Incidental Take of Seabirds in Commercial Fisheries in the Arctic Countries*. Akureyri, Iceland: CAFF International Secretariat.
- Birkhead, T.R.** 1977. The effects of habitat and density on breeding success in the common guillemot (*Uria aalge*). *J. Anim. Ecol.* **46**: 751–764.
- Botzler, R.G.** 1991. Epizootiology of avian cholera in wildfowl. *J. Wildl. Dis.* **27**: 367–395.
- Christensen, T.K., Bregnballe, T., Andersen, T.H. & Dietz, H.H.** 1997. Outbreak of Pasteurellosis among wintering and breeding Common Eiders *Somateria mollissima* in Denmark. *Wildl. Biol.* **3**: 125–128.
- Erikstad, K.E., Anker-Nilssen, T., Asheim, M., Barrett, R.T., Bustnes, J.O., Jacobsen, K.-O., Johnsen, I., Sæther, B.-E. & Tveraa, T.** 1994. Hekkeinvestering og voksendødelighet hos norske sjøfugler (Parental investment and adult survival in Norwegian seabirds). *NINA Forskningsrapport* **49**: 1–25.
- Friend, M., McLean, R.G. & Dein, F.J.** 2001. Disease emergence in birds: challenges for the twenty-first century. *Auk* **118**: 290–293.
- Harris, M.P. & Birkhead, T.R.** 1985. Breeding ecology of the Atlantic Alcidae. In Nettleship, D.N. & Birkhead, T.R. (eds) *The Atlantic Alcidae: the Evolution, Distribution and Biology of the Auks Inhabiting the Atlantic Ocean and Adjacent Water Areas*: 155–204. London: Academic Press.
- Harris, M.P. & Wanless, S.** 1995. Survival and non-breeding of adult Common Guillemots *Uria aalge*. *Ibis* **137**: 192–197.
- Harris, M.P., Wanless, S. & Barton, T.R.** 1996. Site use and fidelity in the Common Guillemot *Uria aalge*. *Ibis* **138**: 399–404.
- Harris, M.P., Wanless, S. & Rothery, P.** 2000a. Adult survival rates of Shag *Phalacrocorax aristotelis*, Common Guillemot

- Uria aalge*, Razorbill *Alca torda*, Puffin *Fratercula arctica* and Kittiwake *Rissa tridactyla* on the Isle of May 1986–96. *Atlantic Seabirds* **2**: 133–150.
- Harris, M.P., Wanless, S., Rothery, P., Swann, R.L. & Jardine, D.** 2000b. Survival of adult Common Guillemots *Uria aalge* at three Scottish colonies. *Bird Study* **47**: 1–7.
- Hatchwell, B.J. & Birkhead, T.R.** 1991. Population dynamics of Common Guillemots *Uria aalge* on Skomer Island, Wales. *Ornis Scand.* **22**: 55–59.
- Hindman, L.J., Harvey, W.F.I.V., Costanzo, G.R., Converse, K.A. & Stein, G. Jr** 1997. Avian cholera in Osprey: first occurrence and possible mode of transmission. *J. Field Ornithol.* **68**: 503–508.
- Hudson, P.J.** 1985. Population parameters for the Atlantic Alcidae. In Nettleship, D.N. & Birkhead, T.R. (eds) *The Atlantic Alcidae: the Evolution, Distribution and Biology of the Auks Inhabiting the Atlantic Ocean and Adjacent Water Areas*: 233–261. London: Academic Press.
- Jansson, D.S.** 1998. *Necropsy report. Assignment Number 980611258*. Uppsala: Swedish National Veterinary Institute, SVA.
- Lebreton, J.D., Burnham, K.P., Clobert, J. & Anderson, D.R.** 1992. Modelling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol. Monogr.* **62**: 67–118.
- Macdonald, J.W.** 1963. Mortality in wild birds. *Bird Study* **10**: 91–108.
- Martin, K.** 1994. Patterns and mechanisms for age-dependent reproduction and survival in birds. *Am. Zool.* **35**: 340–348.
- Olsson, O., Fransson, T. & Larsson, K.** 1999. Post-fledging migration of Common Murre *Uria aalge* in the Baltic Sea: management implications. *Ecography* **22**: 233–239.
- Olsson, O., Nilsson, T. & Fransson, T.** 2000. *Long-Term Study of Mortality in the Common Guillemot in the Baltic Sea*. Report 5057. Stockholm: Swedish Environmental Protection Agency.
- Österblom, H., Fransson, T. & Olsson, O.** 2002. Bycatches of Common Guillemot (*Uria aalge*) in the Baltic Sea gillnet fishery. *Biol. Conserv.* **105**: 309–319.
- Persson, L.** 1998. Fågelkolera på ejder och andra fåglar på Västergarns utholme (in Swedish). *Bläcku* **3**: 91–93.
- Piatt, J.F. & Anderson, P.** 1996. Response of Common Murres to the Exxon Valdez oil spill and long-term changes in the Gulf of Alaska marine ecosystem. In Rice, S.D., Spies, R.B., Wolfe, D.A. & Wright, B.A. (eds) *Proceedings of the Exxon Valdez oil spill symposium. American Fisheries Society Symposium* **4**: 720–737.
- Rhoades, K.R. & Rimler, R.B.** 1984. Avian Pasteurellosis. In Hofstad, M.S., Barnes, B.W., Calnek, B.W., Reid, W.M. & Yoder, H.W. Jr (eds) *Diseases of Poultry*, 8th edn: 141–156. Ames, Iowa: Iowa State University Press.
- Rosen, M.N.** 1971. Avian cholera. In Davis, J.W., Anderson, R.C., Karstad, L. & Trainer, D.O. (eds) *Infectious and Parasitic Diseases of Wild Birds*: 59–74. Ames, Iowa: Iowa State University Press.
- Sydemann, W.J.** 1993. Survivorship of Common Murres on Southeast Farallon Island, California. *Ornis Scand.* **24**: 135–141.
- Takekawa, J.E., Carter, H.R. & Harvey, T.E.** 1990. Decline of the Common Murre in Central California, 1980–86. *Stud. Avian Biol.* **14**: 149–163.
- Vader, W., Barrett, R.T., Erikstad, K.E. & Strann, K.-B.** 1990. Differential responses of Common and Thick-billed Murres to a crash in the capelin stock in the southern Barents Sea. *Stud. Avian Biol.* **14**: 175–180.
- Van der Jeugd, H.P. & Larsson, K.** 1998. Pre-breeding survival of barnacle geese *Branta leucopsis* in relation to fledging characteristics. *J. Anim. Ecol.* **67**: 953–966.
- White, G.C. & Burnham, K.P.** 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* **46** (Suppl.): 120–139.

Received 29 May 2003; revision accepted 11 November 2003.