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Net-entrapment of great cormorants *Phalacrocorax carbo sinensis* in relation to individual age and population size

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Population control of great cormorants *Phalacrocorax carbo sinensis* has been suggested as a tool to mitigate fish losses by cormorants foraging in pound nets, gill nets and fykes. The objective of our study was to quantify the difference between first-year birds and older birds in the risk of drowning in fishing gear, and to explore the influence of population size on the proportion of individuals drowning. An index of the proportion of first-year birds and older birds that drowned was obtained for cormorants ringed in the Danish Vorskø colony using resightings of colour-ringed individuals and ring recoveries of individuals found dead. First-year birds were approximately 10 times more likely to drown than older birds. We used ring recoveries of cormorants ringed in Denmark and found dead in Denmark, North Germany and South Sweden (i.e. in the main post-breeding area) to reveal changes over a 25-year period in the proportion drowned among those recovered. Among first-year birds the proportion drowned declined from 66% in 1978-1984 to 24% in 2000-2002, and among older birds the proportion declined from 46% in 1978-1984 to 26% in 1999-2002. During 1978-2000, breeding numbers in Denmark increased from 1,400 to 42,500 nests, and the proportion of cormorants drowned among those recovered was significantly negatively correlated with population size. This suggests that the proportion of the population foraging in nets declined as the population increased. The damage caused by cormorants foraging in pound nets is, therefore, unlikely to decrease in proportion to reductions in population size reached through population control.

Key words: bycatch, cormorants, drowning, fykes, management, pound nets

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In many parts of the world, fishing with standing gear takes place in areas preferred by diving birds during part of their annual cycle. The overlap in area use leads to drowning of huge numbers of birds of many species of diving birds (e.g. van Eerden et al. 1999). In some regions, drowning has even led to or accelerated declines of seabird populations (Tull et al. 1972, Evans & Waterston 1976, King et al. 1979, Straty & Haight 1979, Piatt et al. 1984, Piatt & Gould 1994). For example, the loss of seabirds in fishing nets in Norway probably caused or added to the decrease of some Norwegian seabird populations (Strann et al. 1991, Follestad & Strann 1991).

In some areas cormorants *Phalacrocorax* sp. forage inside pound nets or fyke nets and along gill nets with the consequence that some individuals eventually get trapped and drown (Craven & Lev 1987, Follestad & Runde 1995, Engström 1998, Bregnballe 1999). Bregnballe (1999) found that among recovered great cormorants *P. carbo sinensis* (hereafter referred to as cormorants) ringed in Denmark, 42% of first-year birds and 23% of older birds were reported drowned in fishing gear, suggesting net-entrapment to be a potentially important mortality agent that could influence population development. The impact of this extra mortality on population development depends not only on the number of individuals drowned, but also on the proportion drowning within each age class, and whether or not the size of the population is regulated by factors acting in a density-dependent fashion (cf. Schaub & Pradel 2004).

Cormorants exploit nets as feeding patches and predate and injure fish trapped or caught in pound nets, fyke nets and gill nets (Bildsøe et al. 1998). To reduce impacts of cormorants on fish catches in pound nets and elsewhere, legal as well as illegal measures are taken to control sizes of local breeding populations in many areas of Europe (Engström 2001, Bregnballe et al. 2003). However, the applicability of population control to reduce cormorant predation of fish caught in nets depends on the relationship between population size and predation pressure in nets.

Bildsøe et al. (1998; pers. comm.) found that cormorants arriving at pound nets 'late' in the morning were more likely to move on to feed elsewhere than individuals arriving 'early'. This suggests that pound nets can be viewed as feeding patches that start to decline in value after a short period of exploitation early in the morning, and that each net is only able to support a limited number of cormorants. The implication is that the proportion of individuals foraging in pound nets will decline as the population of cormorants increases, unless the number of pound nets increases as well.

The aim of this paper is to quantify the risk of net-

entrapment of cormorants ringed in Denmark in relation to individual age, year and population size over a 25-year period. We discuss how drowning has affected the development of the breeding population of cormorants, as well as the applicability of population control as a tool to reduce fish losses caused by cormorants foraging in nets.

Material and methods

The risk of net mortality among first-year birds relative to that of older birds was quantified by use of recoveries of cormorants ringed in the well-studied breeding colony on Vorsø (55°52'N 10°01'E). Ringing took place some time before fledging, and the annual number of ringed young (375-1,144 chicks/year) that actually fledged from the colony during 1982-1992 was estimated by use of resighting data from daily searches for colour-ringed birds in the colony (see Frederiksen & Bregnballe 2000b). Of the chicks ringed, 77-97% were resighted as fledged, and we assumed that on average 3% of the fledged young left the colony without being observed as fledged. From the recoveries made throughout Europe between 1 June 1983 and 31 May 1993, we extracted the number of individuals known to have drowned before the age of one year. It was then possible to estimate the minimum proportion drowned in the first year of life. For older birds, we estimated the number of individuals alive at the beginning of each year (i.e. 1 June each year), using estimates of annual survival for each cohort (Frederiksen & Bregnballe 2000b). To reduce the effect of a low resighting probability on Vorsø early in the period and a recent decline in the proportion of first-year birds reported drowned, we only included recoveries made between 1 June 1983 and 31 May 1993.

From the recoveries of 35,135 cormorants ringed as chicks in 19 Danish breeding colonies during 1972-1998 (of which 39.2% were ringed in the Vorsø colony), we calculated the annual proportion of cormorants that drowned. During 1972-1976, 636 chicks were ringed with large aluminium rings, but during 1977-2002, 79.2% of 27,303 chicks were ringed with coded colour rings easy to detect on cormorants that drowned or were found dead. The area from which recoveries were included was restricted to Denmark, south Sweden and northeast Germany (for definitions of borders see Bregnballe & Rasmussen 2000). This region constitutes the main post-breeding area for Danish cormorants (Bregnballe et al. 1997a, Bregnballe & Rasmussen 2000). It is also the area in Europe, together with The Netherlands and Germany/Switzerland, which has the highest pro-

portion of individuals recovered drowned (Bregnballe 1999). We included all recoveries from the recovery area (referred to as the 'main post-breeding area') reported between 1 January 1978 and 31 December 2002, except birds from which only the ring was found or birds that were found inside a colony. The last two groups of recoveries were excluded for two reasons: 1) to avoid year-to-year differences in the effort invested in searching for dead birds with rings inside breeding colonies, and 2) to avoid inclusion of recoveries of unfledged young. The proportion that drowned varied significantly between first-year birds from northwest Jutland and first-year birds from south Funen (25.0 vs 52.3%; $\chi^2 = 8.14$, $df = 1$, Yates' correction, $P = 0.0043$, $N = 60$ and $N = 44$, respectively), and all recoveries of birds ringed in northwest Jutland were from the second half of the 25-year period. Therefore, we excluded all recoveries of birds ringed in northwest Jutland (see Bregnballe & Rasmussen 2000 for location of ringing regions). Older cormorants from south Zealand suffered a higher 'risk' of drowning than birds from south Funen (16.1 vs 26.6%; $\chi^2 = 3.86$, $P = 0.0494$, $N = 87$ and $N = 241$, respectively), but there was no reason to consider this difference, because ringing in these colonies took place over the same years. Having excluded some of the recoveries, 1,349 recoveries of first-year birds and 737 recoveries of older birds remained. To explore whether changes observed for the whole post-breeding area were reflected at a lower geographical scale, analyses were also made for recoveries originating exclusively from southwest Kattegat, which was the only subarea with a reasonable number of recoveries from the entire 25-year period (see Bregnballe & Rasmussen 2000 for a definition of 'southwest Kattegat').

We used logistic regression (SAS PROC LOGISTIC, SAS Institute, Inc. 1999) to test for effects of age group, year (modelled either as a factor or as a continuous covariate) and population size on the proportion of recovered cormorants ringed in Denmark and reported to have drowned in 1) the main post-breeding area or 2) in southwest Kattegat. The statistical model providing the best description of data was selected using Akaike's Information Criterion (AIC; Burnham & Anderson 1998). Data on the size of the Danish breeding population were extracted from Bregnballe & Gregersen (1995) and Bregnballe et al. (2003).

Results

Risk in relation to age

The risk of drowning differed between first-year birds

and older birds, with first-year birds running a 10 times higher risk of drowning than older birds. Thus, overall 4.45% of all 5,891 colour-ringed birds estimated to have fledged from the Vorskø colony during 1983-1992 were recorded to have drowned in their first year of life (i.e. before 1 June in the year after ringing), and, overall, 0.46% of the older birds were recovered drowned on a yearly basis during 1983/84-1992/93 ($N = 22,972$ bird-years). The difference in risk between first-year and older birds neither increased nor decreased over the years.

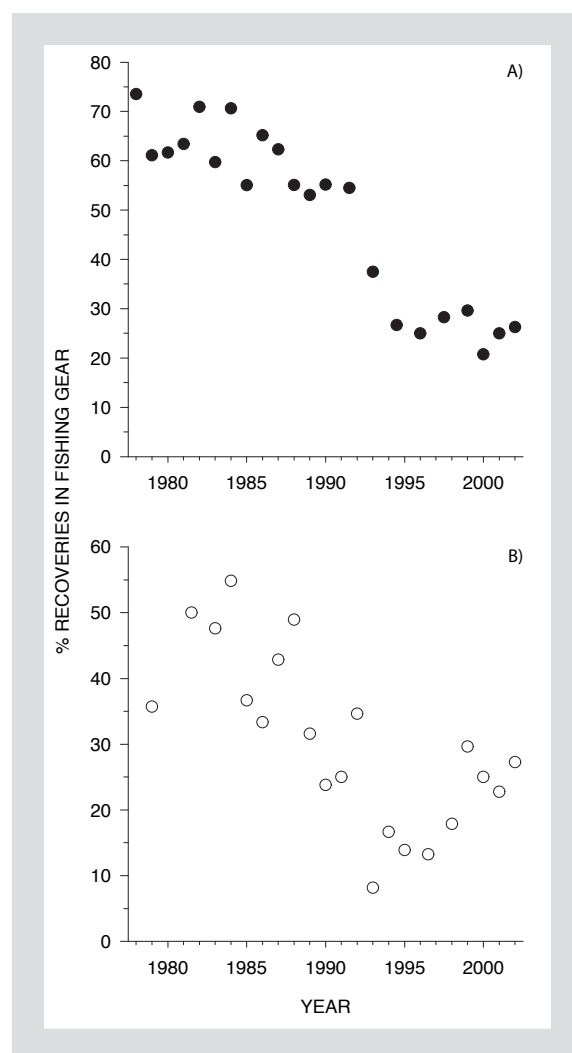


Figure 1. Percentage of cormorants ringed in Denmark and recovered drowned in fishing gear for first-year birds (A; ●) and for older birds (B; ○) in the main post-breeding area during 1978-2002. Data from the following years were pooled to ensure a sample size > 20: 1991-1992, 1994-1995, 1997-1998 for first-year birds, and 1978-1980, 1981-1982 and 1996-1997 for older birds. The numbers of individuals recovered per year were 24-126 (A) and 20-83 (B). Note varying scales of the y-axes.

Table 1. Model selection for logistic regression of the annual proportion of drowned cormorants among all ringed birds recovered, both for the full data set and for southwest Kattegat. Models are ranked according to Δ AIC, i.e. the difference in AIC between the model in question and the best model. Explanatory variables considered were age (juvenile or adult), year (as a factor), YEAR (continuous covariate) and breeding population size (pop). k indicates the number of parameters in the model, including the intercept term.

Models/variables	Full data set			Southwest Kattegat		
	Deviance	k	Δ AIC	Deviance	k	Δ AIC
age pop age*pop	2552.51	4	0	522.28	4	1.32
age pop	2554.71	3	0.23	522.96	3	0
age year	2520.90	26	12.39	490.92	26	13.96
age YEAR	2570.28	3	15.77	530.32	3	7.36
age year age*year	2490.58	50	30.07	459.06	48	16.10
pop	2602.03	2	45.52	528.55	2	3.59
YEAR	2632.42	2	75.91	540.44	2	15.48
age	2761.59	2	205.08	555.37	2	30.41
Intercept only	2843.14	1	284.65	572.34	1	45.44

Changes over 25 years

The proportion of ringed birds reported to have drowned in the main post-breeding area changed over the 25 years covered by our study (Fig. 1). In first-year birds the proportion that drowned decreased from 74% in 1978 to 55% in 1991-1992 (N = 34 and N = 33, respectively), and dropped markedly over a few years reaching 24% (N = 289) in 2000-2002 (see Fig. 1A).

Among older birds, the proportion that drowned decreased from 46% in 1978-1984 to 31% in 1989-1992 (N = 102 and N = 131, respectively; see Fig. 1B). The proportion drowned then dropped markedly over a few years after 1992 to only 14% (N = 214) in 1993-1998, but increased again to 26% (N = 91) in 1999-2002.

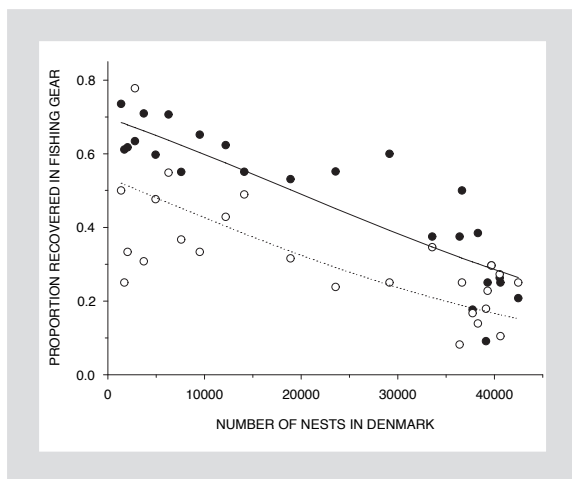


Figure 2. Proportion of cormorants ringed in Denmark and recovered drowned in fishing gear for first-year birds (●) and for older birds (○) in the main post-breeding area during 1978-2002 in relation to the size of the breeding population (number of nests) of cormorants in Denmark. The fit of the additive model is given for first-year birds (—) and for older birds (.....).

Changes with population size

The relationship between the proportion that drowned and population size, year and age was explored using a logistic regression model. The goodness-of-fit of the model for the full data set was assessed by comparing the fit of the full model (with year and age and the interaction between them as factors) to a reduced model with no interaction. The reduced model was accepted (deviance: $\chi^2 = 30.32$, $df = 24$, $P = 0.17$). The model with population size as a covariate performed better than models with year as a factor or continuous covariate (Table 1). The model with the marginally lowest AIC included an interaction between population size and age, but in the interest of model simplicity we preferred the model without this interaction term (as a guideline, models with Δ AIC < 2 are statistically equivalent, and it is often most appropriate to select the simplest model in a set of equivalent models; Burnham & Anderson 1998). The proportion of drowned birds among all recovered birds thus declined with increasing population size and the proportion drowned was higher for juveniles than for adults (Fig. 2, Table 2). Analysis of deviance showed that population size explained 86% of the inter-annual variation additive to age.

For the southwest Kattegat data set, the fit of the model with no interaction was also acceptable (deviance: $\chi^2 = 31.86$, $df = 22$, $P = 0.08$). The same model was

Table 2. Coefficients of the logistic regression model with age (juvenile vs adult) and population size (per 1,000 pairs) as explanatory variables, both for the full data set and for southwest Kattegat.

	Full data set			Southwest Kattegat		
	Coefficient	S.E.	P	Coefficient	S.E.	P
age	0.6968	0.1024	< 0.0001	0.5224	0.2210	0.0181
pop	-0.0438	0.00316	< 0.0001	-0.1664	0.0298	< 0.0001

selected as for the full data set (see Table 1), and the coefficients of the model were similar (the slope of the relationship with population size was necessarily steeper because a similar change in the proportion that drowned occurred over a smaller range of population sizes; see Table 2). Population size explained 50% of the inter-annual variation additive to age.

Discussion

Risk in relation to age

First-year birds from the Vorsø colony were approximately 10 times more likely to get entrapped and drown in fishing gear than older birds. There are at least three different explanations for this difference. First, the number of bird-days spent in regions where pound net fishing is widespread is higher for first-year birds than for older birds during the peak pound net fishing season (Bregnballe et al. 1997a, Bregnballe 1999, Bregnballe & Rasmussen 2000). However, we estimate that the difference in distribution and timing of migration cannot explain more than 5-10% of the age-related difference in the risk of drowning. Second, first-year birds are likely to be less efficient foragers than adults and may therefore be more attracted to the high concentrations of fish in pound nets than older birds, i.e. a larger proportion of first-year birds than of older birds may have attempted to fish in pound nets and fykes. Third, older birds can be expected to be more experienced in foraging in and around nets without getting entrapped. Age-related differences in experience with avoiding entrapment is probably the most important factor.

The two last explanations (or one of them) are supported by the age composition of cormorants found drowned in pound nets and fykes in Sweden and Denmark. H. Engström (unpubl. data) aged 78 cormorants that drowned in lakes and along coasts in southern Sweden during April-September 1994-1996, and he found that 82% were first-year birds. Bregnballe & Hounisen (2003, unpubl. data) aged 546 cormorants that drowned in West Jutland, Denmark, in August-October 2002-2004 of which 86% were first-year birds. During counts of roosting birds in the two fjords in 2003, the mean proportion of first-year birds was 35% (T. Bregnballe, unpubl. data). In this case, first-year birds would have been 60 times more likely to drown in fishing gear than older individuals. In the Danish lake Arresø, 97% of 426 cormorants found drowned in late summer-autumn 1985 were first-year birds (P. Hald-Mortensen, unpubl. data). Hald-Mortensen estimated that approximately 30% of the individuals foraging and loafing in the lake were

first-year birds. In that case, first-year birds would have been 75 times more likely to drown in fishing gear than older individuals. Hence, these two studies from the post-breeding season suggest a much higher risk of drowning for first-year birds than found for the entire year in our study. It might be that older birds experience a higher risk in spring (when breeding) than first-year birds which return later to the breeding areas than older birds (Bregnballe et al. 1997a).

The decline in the proportion drowned

The proportion of cormorants reported drowned was particularly low after 1992 (see Fig. 1). Several changes may have caused this. First, the population had increased from 14,000 nests in 1988 to > 36,000 in 1993. Second, after 1993 an increasing proportion of the cormorants of Danish origin started to disperse to southwest Sweden after breeding or fledging (T. Bregnballe, unpubl. data), and few cormorants have been reported to have drowned in this area (Bregnballe 1999). Third, to avoid entrapment of otters *Lutra lutra* it has been obligatory to use stop grids in fykes in all freshwater areas in Denmark since 1993, and in most fjords in western and northern Jutland since 1994 (the stop grids also prevent cormorants from entering fykes). Fourth, other mortality agents such as starvation are likely to have become increasingly important, especially among first-year birds, after the breeding population stabilised (Frederiksen & Bregnballe 2000a). Fifth, fishermen and fishery researchers have reported that fishing activity with fykes and pound nets owned by professional fishermen has declined in many parts of Denmark, in particular since the end of the 1980s (C. Dieperink, A. Buch, P.C. Rasmussen & T. Hansen, pers. comm.). The number of professional pound net sites officially registered along open coasts around Zealand, Lolland-Falster and Møn declined by 38% during 1979-1994 (Koed & Pedersen 1996). However, the number of non-professional fishermen fishing with fykes and gill nets in late summer and autumn in Danish fjords appears not to have declined (C. Dieperink, pers. comm.). Overall, the information available points to a decline in the number of nets in use over the 25-year study period (particularly in spring), but with geographical variation in the extent of decline. We presume that the sudden decline in the proportion that drowned after 1992 was caused by a combination of the factors mentioned above.

Impacts on population development

It is not possible to estimate the annual number of cormorants that drowned in the post-breeding area from the ringing recoveries. Thus the probability of finding and

reporting a dead cormorant will depend on the cause of mortality, and is likely to be high for causes directly related to humans, leading to a risk of overestimating the importance of human-induced causes. However, new methods based on multi-state capture-recapture models have been developed to correctly estimate the proportion of individuals that die due to a specific cause detected through recoveries (Schaub & Pradel 2004). The bycatch of cormorants in pound nets and fykes in Denmark, Sweden and north Germany has caused substantial mortality among cormorants of Danish origin, probably amounting to > 7,000/year after 1990 (T. Bregnballe, unpubl. data). It would seem reasonable to expect that such an extra mortality had affected the growth rate of the Danish breeding population. However, during 1982-1989, the number of breeding pairs in Denmark increased by 26% per year (Bregnballe & Gregersen 1995), which is close to or above the maximum expected growth rate based on population parameters estimated from the same population (Frederiksen et al. 2001). Three factors may help explain why drowning of primarily juvenile cormorants apparently has had very little effect on the population growth rate. First, the reproductive output in the study population appears to have been very high during the 1980s (Bregnballe 1996, Bregnballe & Gregersen 2003). Second, the population growth rate of long-lived organisms is generally not very sensitive to variation in juvenile survival or other fecundity-related parameters (Lebreton & Clobert 1991, Newton 1998). Third, drowning may have acted as a compensatory rather than additive source of mortality (Williams et al. 2002), so that the mortality rate from natural causes was less than it would have been in the absence of the drowning mortality. At present, we have no results to indicate whether this was the case or not, but new development in the analysis of data from marked birds may soon allow the testing of a hypothesis of compensatory mortality (J-D. Lebreton, pers. comm.).

The observed decline in the proportion of recovered cormorants that were reported drowned in the main post-breeding area correlated well with the increase in the breeding population over the same period (1978-2002). However, this decline may have been affected by the generally declining recovery probability, i.e. the proportion of all dead ringed birds which are reported to the ringing scheme (Frederiksen & Bregnballe 2000b). Thus, the proportion of all ringed fledglings reported dead during their first year of life declined strongly, being high during 1977-1983 (21-46%), lower during 1984-1991 (18-26%) and very low during 1992-1997 (4-11%), although there was no decline in estimated first-year mortality over this period (Frederiksen & Bregnballe 2000a).

It is not known whether the reporting probability of drowned birds has followed this general trend (in which case the trend reported here should be robust), or whether fishermen have shown a less marked decline in their propensity to report ringed cormorants (which would imply that the real decline in drowning mortality has been even stronger than our estimates suggest). All in all, we conclude that drowning has acted as an inversely density-dependent source of mortality over the 25-year period.

The drowning of cormorants continues to have an impact on population size in autumn, but is unlikely to have had more than a marginal effect on the size of the Danish breeding population after breeding numbers stabilised around 38,900-42,500 nests in 1995-2002 (Bregnballe et al. 2003). Thus the size of the breeding population in Denmark is now limited by the availability of new and safe colony sites and by food availability around existing colonies, i.e. density dependent regulation is currently operating (Bregnballe & Gregersen 1997, 2003, Frederiksen & Bregnballe 2000a,b, 2001).

Consequences for management

The number of cormorants foraging in nets in Denmark, Sweden and north Germany increased during the 1980s and early 1990s as the population of cormorants increased. However, the inverse relationship between the proportion reported drowned and the population size (see Fig. 2) suggests that the increase in the number of cormorants foraging in nets was not proportional to the growth of the population. This is also what would be expected if 1) pound nets are attractive feeding sites but hold limited resources (see 'Introduction'), and 2) the number of pound nets is constant or declining (see above) while at the same time population size increases (the number of apparently occupied nests in Denmark increased from 1,375 in 1978 to a maximum of 42,481 in 2000). The implication is that only minor reductions in the extent of damage caused by cormorants in pound nets can be expected if the size of the entire population of cormorants is reduced to, for example, two thirds of its present size (*cf.* Bregnballe et al. 1997b). The validity of this prediction could be tested experimentally or by measuring changes in predation pressure in nets concurrently with changes in numbers of cormorants exploiting regions or areas where pound net fishing is common.

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