Modelling the Consequences of The New Cormorant Licensing Policy

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Introduction

In September 2004, Defra updated their policy regarding the issuing of licences to prevent serious damage by cormorants to fisheries. Based on CSL's deterministic model of that time, the new policy proposed that the maximum number of birds that might be shot under licence would be increased from 500 per annum to 2,000 per annum with the potential to increase to 3,000 per annum for the first 2 years of the policy. These maximum limits do not advocate that such numbers be removed; rather they provide a limit above which it would be unwise to allow further removal. The policy also changed a number of other aspects of the licensing system which are not relevant to this paper. Defra made a commitment that the model would be refined, updated and expanded as further data became available, and that stochastic elements would be incorporated to explore the uncertainties within the approach. This report provides this further detail and examines the range and uncertainties inherent in the new policy. These findings will inform future policy consideration. It is intended that the model will also form the core of a paper to be submitted for publication in a peer reviewed scientific journal in 2005.

Background To Cormorant Populations

In Europe, over the past 20-30 years there have been marked increases in the populations of the two European subspecies of the great cormorant, the 'Atlantic' race *P. c. carbo* L. and the 'Continental' race *P. c. sinensis* Blumenbach (Debout, Rov & Sellars 1995; Lindell *et al.* 1995; Van Eerden & Gregersen 1995). The UK cormorant population is dominated by the nominate race *P. c. carbo* (Cramp & Simmons 1977). The conservation status of the cormorant in the European Union is described as favourable, its population trend as experiencing a large increase, and its threat status as secure (Birdlife International 2004).

In the UK, increase in the number of birds and in range extension, together with changes in seasonal distribution has increasingly brought cormorants into conflict with inland fisheries. The latest national seabird census (Seabird 2000) estimated the breeding population at 9,133 pairs, during 1998/2002, representing an increase in numbers of coastal breeding pairs of 10% since 1985/88, and 21% since 1969/70 (Mitchell *et al.* 2004). During this period inland breeding colonies have also become established and have increased in size and number. Since first breeding at Abberton Reservoir, Essex in 1981, numbers of cormorants breeding inland in

England increased to 1,437 pairs at 23 inland sites by 1998, a mean increase of 35% per annum (Hughes *et al.* 2000). The most recent estimate for numbers breeding inland is 1,646 pairs (Mitchell *et al.* 2004).

Conflicts With Fisheries Interests

Conflicts between cormorants and UK inland fisheries generally occur during winter when numbers of cormorants inland are greatest. Between 1965/66 and 1993/94, ringing recoveries indicated that the proportion of cormorants wintering inland increased from approximately 16% in 1965 to peak at around 43% in the early 1980s (Wernham *et al.* 1999). National Wildfowl Counts, however, indicated that, during the winters of 1987/88-1990/91, around 50% of cormorants wintered inland, and that movements to inland waters began earlier in the year than previously (Kirby, Gilburn & Sellers 1995). In England and Wales, in addition to increased numbers of birds wintering inland, the number of inland waters occupied by cormorants has also increased (Kershaw & Hughes 1997; Wernham *et al.* 1999). Examination of Wetland Bird Survey (WeBS) data suggests that, on average, around 75% of the GB population winters in England. WeBS data also suggests that the wintering population may have stabilised since 1994/95, where previously numbers had increased by 5-10% per annum between 1987/88 and 1994/95 (Wernham *et al.* 1999).

Fisheries interests claim that increased predation by cormorants has had, and is continuing to have, a detrimental impact on inland fisheries. Case studies of impact assessment at still waters and rivers in England and Wales have described predation levels that cause serious damage at some fisheries (Feltham *et al.* 1999). Similar concerns over the impact of cormorants on fisheries are widespread throughout Europe (Carss 2002; Marquiss & Carss 1994).

Application To The New Cormorant Licensing Policy

In Britain, the Wildlife and Countryside Act (1981) implements the European Community Directive on the Conservation of Wild Birds and allows the Government to issue licences to kill a limited number of cormorants strictly “for the purposes of preventing serious damage to ... fisheries.” Until recently, the role of licensed shooting was to aid scaring. In England and Wales, during 1997/98-2001/02, licences were issued to shoot between 443 and 545 cormorants annually, with between 139 and 225 actually killed. In September 2004, however, amendments to the cormorant licensing policy were introduced. Defra may now grant a licence that allows the shooting of a specified number of birds, both to reinforce the effects of scaring measures and to limit bird numbers visiting a specific site. Under the new policy, licences may be issued to shoot up to a total of 2,000 cormorants annually, with up to 3,000 for the first 2 years of the policy. The amount of birds actually licensed to be shot under the policy will depend on the number of legitimate applications which are made under the licensing system. The new policy does NOT include any provision for a national cull. With an increase in the maximum number of cormorants that may be legally shot under licence each year, it is important to know the potential effect of such levels of removal on the overall population. These maximum limits do not advocate that such numbers be removed; rather they provide a limit above which it would be unwise to allow further removal. The policy also includes specific commitments to monitor the response of the cormorant population to change, to review the maximum number of birds which may be licensed to be shot, and if necessary to cease to issue future licenses, should the conservation status of the cormorant appear to be threatened.

A synthesis of cormorant-fisheries interactions across 25 European countries (Carss 2002) indicated that shooting adult cormorants in the non-breeding season represented the most common control method. Cormorants are fully protected under the European Community Directive on the Conservation of Wild Birds (79/409/EEC), however, Member States are able to derogate from this protection in certain circumstances provided that specified conditions are met. In 14 of the 25 countries there was legislation that allowed, in effect, the culling of cormorants. In a further 6 countries (including the previous licensing policy within the UK) licences could be issued for the killing of a limited number of cormorants at specific sites to enhance scaring activities. In most countries, however, there was no assessment of the effects of shooting on the population (Frederiksen, Lebreton & Bregnballe 2001).

Predicting the effects of wildlife management is of critical importance in attempting to balance the conflicting demands of the interest under threat and the conservation concerns of maintaining a viable status of the species concerned. In this regard, population models have been used with some success in predicting or evaluating the impact of management measures (Bedard, Nadeau & Lepage 1995; Middleton, Nisbet & Kerr 1993; Wanless *et al.* 1996). Frederiksen *et al.* (2001) developed a predictive model for the north European breeding population of *P. carbo* to investigate the interaction between culling and density-dependence, with emphasis on evaluating the effects of culling. It was concluded that if culls were carried out in a density-dependent manner they could stabilise numbers near a desired level. Subsequent extension of their model to include geographical variation in culling intensity, however, showed that the effects of culling are highly dependent on the extent of immigration into the control area (Frederiksen, Lebreton & Bregnaballe 2003).

This new policy was supported by a deterministic model with a commitment to update and expand the model as further data became available, and to incorporate stochastic elements to explore the uncertainties within the approach. This report provides this further detail and examines the range and uncertainties inherent in the new policy. The report assesses the effect of different annual regimes of licensed removal, permissible under the new licensing policy, on the cormorant population wintering in England, using a number of different predictive population models. The aim is that such a modelling approach would be continually refined, in order to meet the policy's objectives, as new information on numbers of birds shot under licence and population response become available.. We anticipate that information on the number of birds shot issued under the new policy will be available within one year, and WeBS counts available within two years. Thus, for it to be a useful policy tool, the model will need to predict cormorant responses to changes in licensing over the coming three years to allow for delays in the availability of new data following each licensing season.

Methods

The models below were all constructed in Crystal Ball®, an add-on to Microsoft® Excel, which allows a stochastic population growth model to be produced with annual time steps to match the annual winter estimates of cormorant numbers. A stochastic model is necessary to calculate the probability of a given event occurring. The approach taken followed Smith, Henderson & Robertson (in press July 2004) to construct a variety of population models, with different assumptions on initial population size and population growth rate. There is much discussion in the literature on how to find evidence for density-dependence in a time series of population estimates, and how to calculate the finite annual growth rate (λ) and determine the variation in this rate when there is natural (environmental) variation and observational error (McCallum 2000; Staples, Taper & Dennis 2004). Because of this uncertainty we have used a variety of models and compared the output projections. Estimates of the population size at the start of each year were predicted by:

$$N_{t+1} = \lambda(N_t)N_t - c_t,$$

where N_t and N_{t+1} are the population size in years t and $t+1$ respectively, $\lambda(N_t)$ is the finite annual growth rate which may be a function of population size in year t, and c_t is the number of birds culled during each year. For density-independent models $\lambda(N_t)$ simplifies to λ.

Data

The data used were the Wetland Bird Survey (WeBS) annual peak cormorant counts for England, from 1986 to 2001 (Table 1); cormorants were first recorded by the WeBS scheme in the winter of 1986/87. These data relate to over-wintering birds and will include over-wintering non-breeders. If we assume that a single population supplies the birds available to be counted, then population growth rates between years can be calculated. This single breeding population need not be the English (or GB) population; some of the birds that over-winter may migrate from the continent. (Wernham *et al.* 1999) estimated that 3.5% of the GB wintering population comes from outside UK and Ireland. This will not affect the growth rate estimates, as long as the numbers migrating into England increase consistently with the calculated population growth rate. For each year an estimate of the annual finite growth rate was made, based on the population size in year t and $t+1$. The value for 1986 is believed to be biased due to under-recording of cormorants when first added to the WeBS species list (Kershaw & Hughes 1997). This is clear in Table 1, where the growth estimate for 1986 is 2.37. As a result of this, the data for 1986 was excluded from analyses. There has also been discussion of whether the 1987 data was also under-recorded. The inclusion of this data point is discussed further below.

Due to bias in the wetland habitat covered, it is recognised that WeBS under records species which are dispersed widely over rivers, non-estuarine coast or small inland waters (e.g. (Kershaw & Cranswick 2003; Pollitt *et al.* 2003); these species will include the cormorant. However, WeBS provides a consistent measure of trend and will continue to do so in its current form. A further constraint is that there are gaps in coverage as a result of not all sites being covered on each count date (e.g.(Kershaw

& Cranswick 2003; Kirby 1995). WeBS counts will thus underestimate the true size of the cormorant population. As long as this underestimate is approximately stable across years, then the annual growth rate of the population can be calculated from the WeBS count data directly. If the logarithm of the annual population data is plotted then a population undergoing exponential growth should reveal a straight line (Figure 1). This shows that the data for 1986 and, potentially, 1987 are unlikely to lie on such a line. The increased rate of growth seen could be due to poor recording on some WeBS sites in these early years, or could be due to increased immigration. In either case it would therefore be conservative to ignore the data from 1986.

A number of published sources provide estimates (or data from which estimates can be derived) for the magnitude of under-reporting by WeBS of the 'true' national population size (Table 2). Early estimates for this 'extrapolation factor' have varied from 1.24 to 1.67, whereas later estimates have been higher. The most recent estimate of the GB population is provided by the WeBS Dispersed Waterbirds Survey, conducted in 2002/03 (Jackson & Austin 2004), and is the first to give a confidence range. In the absence of the published 2003 WeBS data, an extrapolation factor between 1.51 and 3.88 was calculated based on the latest available (2000-01) WeBS count and by data extraction from the published graphs. [Note –a manuscript based on this survey has been submitted for peer review]

Estimates of Initial Population Size

A recent estimate of the wintering GB cormorant population, based on WeBS data from the late 1990s (Kershaw & Cranswick 2003), gave an estimate of 23,000 birds. As WeBS data indicates that on average the English population accounted for about 75% of the total GB WeBS count, this would suggest that there are about 17,500 cormorants in England. This is approximately halfway between the population estimates based on the first two WeBS correction factors (see Table 2). We could therefore assume that an estimate of the current English population can be drawn randomly from a triangular distribution with limits derived by the first two correction factors (minimum 15338, best estimate 17500, maximum 20656). Examination of the summary graphical data from the recent WeBS Dispersed Waterbirds Survey (Jackson & Austin 2004) indicates a GB population of around 44,400 (or 33,300 in England). This suggests a triangular distribution based on their confidence interval (minimum 18677, best estimate 33300, maximum 47992). This gives us two potential initial population distributions.

Growth Rates

There are two main approaches to simulating population growth: density-dependent or density-independent. If the current population is constrained by density-dependence, the population growth rate will increase if the population is culled. If the population growth is density-independent, then it has been growing at a constant rate since the late 1980s: these rates should vary about a constant value and every estimate of population growth can be used to determine the variation around that fixed annual growth rate.

The annual growth rate of the English cormorant population is significantly correlated with population size (Figure 2). However these data are not independent. If the population growth is plotted on a log scale over time (Figure 1) then the axes are independent: this linear relationship is also significant ($p < 0.05$). Both of these relationships hold if the WeBS counts are ‘corrected’ to estimate national population size. For a population model, it is necessary to estimate the degree of density-dependence. Three approaches are taken below. As a conservative approach it would also be useful to predict the population growth under the assumption of density-independence, as this would be a worst-case scenario. Four density-independent models are considered below. For each density-dependent model the equations are given for two mean extrapolation factors, halfway between the values given above: 1.455 and 2.695. The deterministic model on which the new policy was based is effectively the same as the linear density dependent growth model described below, although this now incorporates stochastic elements.

Linear density-dependent growth model. The annual growth rates from 1987 to 2000 were regressed against the English WeBS extrapolated population size giving the following equations:

Finite Annual growth = 1.646 - 0.000039 * population size (1)
Finite Annual growth = 1.646 - 0.000021 * population size (2)

The residuals were then used to define the variation around these equations, giving a standard deviation of 0.08647. For each year the mean finite growth rate was calculated from the above equations dependent upon population size, and a growth rate was chosen at random from a normal distribution (mean =0) with the above standard deviation.

Bootstrap density-dependent growth model. Following the model of (Dennis & Taper 1994) the intercept, slope and residual error (natural variation in growth rate) were calculated for $\ln(\lambda)$, along with the standard deviations in these estimates. Since the errors of the estimates are autoregressive, bootstrap estimates were made following (McCallum 2000). The 95% confidence interval for the slope was between -0.000105 and –0.000010. This gives clear evidence that density-dependence is operating as the confidence interval does not include zero. However, this is a more data demanding method, which means that the confidence intervals will be relatively wide. The bootstrap values were used to define the distributions for the relevant parameters. This gave the following values to be used in the model:

Constant, normal distribution (mean 0.645677, standard deviation 0.225532)
(mean 0.646178, standard deviation 0.224748);
Slope, extreme values distribution (mode –0.000032, scale 0.000018)
(mode –0.000017, scale 0.000010).

In addition, slope and constant were correlated in both sets of bootstrap data at -0.44 and this was reflected in the model. For each simulated year, natural variation around this was produced:

normal distribution (mean 0.081749, standard deviation 0.017784)
(mean 0.081752, standard deviation 0.017782),

which is σ in the model of (McCallum 2000).
Triangular density-dependent growth model. An alternative method to generate a linear density-dependent model with variation is to calculate a minimum and maximum growth rate to define a triangular distribution around the best fitting density-dependent model: equation (1). The minimum growth rate (0.876) was applied regardless of population size, and the maximum was fitted by increasing the constants in equations (1) and (2) to give:

Finite maximum growth rate = 1.78 – 0.000039* population size; min[1.124]
Finite maximum growth rate = 1.79 – 0.000021* population size; min[1.124]

The models below are density-independent:
Custom growth model. The simulated growth rate is drawn randomly for each year from historical data (the growth rate from 1986/87 to 1987/88 was removed from all these models as being too high: 2.37).
Lognormal growth model. The simulated growth rate is drawn randomly from the best-fitting lognormal distribution (i.e. normal on the log scale) defined by the data post-1986/87 (mean 1.0661, s.d. 0.1298).
Normal growth model. As above, but assumes that the underlying distribution is normal (mean 1.0657 s.d. 0.1341).
REML growth model. All of the WeBS counts will include some degree of observational error. A recent paper (Staples *et al.* 2004) presented a restricted maximum likelihood (REML) technique to estimate $\ln(\lambda)$, which should be able to remove the observation error, and leave an improved estimate of the process error (natural variation in growth rates). Using this method the mean finite growth rate was 1.060 (90% confidence limits from 0.990 to 1.134). The model therefore first chose a growth rate at random from a normal distribution defined by these confidence limits. This is the mean value used for one simulation. For each year of that simulation, a random value from a normal distribution (mean 0, s.d. 0.12337) around the mean was chosen to give annual variation.

Various levels of annual cull are simulated. These include the base-line assumption that 2000 birds will be shot in each year, and the exceptional circumstance that 3000 could be shot in each of the first two years. For each scenario 100,000 simulations were performed. During the period 1996/97 to 2002/03, an average of 200 cormorants were shot under licence each year (Table 3). This number is therefore deducted from the scenarios above, as they are already included in the growth rate. Thus, if 2,000 birds were shot under licence in 2004, this would be an increase of 1800.

Levels of Population Decline

All of the models predict population declines as a consequence of increased licensed removal. It is useful to place these predicted levels of decline in a broader context. We assess the predictions against two measures, the expected percentage decline over a three year period should the maximum number of birds be removed, and against the risk of the population falling to a level where its numbers would overlap with those likely to have been present in 1979. It is important to emphasise that this does not imply that reducing the number to the probable range of 1979 levels is acceptable or desirable, rather than it would be an undesirable outcome as such, the risk of it occurring needs to be calculated in order to be confident that it can be avoided.

The ‘Birds Directive 1979/409/EEC’ requires Member States to take requisite measures to maintain the populations of all bird species at a level, or to adapt it to a level, which corresponds in particular to ecological, scientific and cultural requirements, while taking account of economic and recreational requirements. The Directive also required that actions taken pursuant to the Directive may not lead to a deterioration ‘in the present situation’ as regards the conservation status of cormorants. Legal advice suggests that this requirement is by reference to the time (1979) when the Directive was implemented. A linear regression of the WeBS counts (ignoring the 1986 count) against year gave a mean predicted value of 4,867 for 1979 (upper 95% prediction interval 7,850). It is important to note that this is not the estimate of the cormorant population at that time, rather an estimate of the WeBS count. A threshold WeBS value drawn from a normal distribution as defined above was therefore used to determine the percentage risk of any policy resulting in the predicted distributions of the English cormorant over-wintering population, as measured by WeBS, overlapping with the range of values predicted for 1979.

It is also useful to note that current monitoring of bird population status is based on the red, amber and green system, with the transition from green to amber reflecting population declines in excess of 25%.

Results

Since the evidence suggests that density-dependence exists in the population, as measured by the WeBS data set, we primarily present the results of the density-dependent models for both levels of WeBS extrapolation factors (results from the latter higher estimate are given in brackets). If the number of birds killed under licence remained unchanged then the three models predict that the mean population size in 2007 would change to, more or less, the carrying capacity for the three models: 16,477 (30,118) for the linear model, 17,972 (34,492) for the triangular model and 17,421 (35,261) for the bootstrap model. This represents a population change of –8% (-9%), +1% (+3%) and –2% (+6%) respectively. However, the distribution of predicted population sizes varies between models, with the bootstrap model producing the greatest variance (Figure 3). For the bootstrap model the upper 95th percentile of the population distribution in 2007 was 39,120 (89,993) birds, much higher than 20-22,000 (36-46,000) predicted by the other two models. This occurred because this model has uncertainty in the slope and intercept of the regression model, in addition to uncertainty in the error structure that all three density-dependent models use. In effect this model is not as precisely defined as the other two models.

If 2,000 birds are killed under licence each year then the population size is depressed for all three models, with a mean population change of -24% (-15%) for the linear model, -25% (-10%) for the triangular model and –20% (-0%) for the bootstrap model: the mean total population size is reduced by some 3-4,000 (1-

5,000) birds. The distribution of predicted population size is similar to the above distributions, with the bootstrap model having a very large variance (Figure 4). Despite the similarity in the mean population size under the above two management scenarios, the difference in variance means that the risk of decline below some threshold varies between the models (Table 4). In this table we would consider that the population is stable where 50% of the simulations are below a given percentage. If we wanted to have zero risk of a particular level of decline, this would be very difficult to obtain. Note that under the current scenario, only the triangular model predicts zero percentage chance of more than a 30% decline. This difference in risk is shown in the effect of different levels of licensed culling on the population in 2007, which results in the population overlapping with the predicted distribution of the 1979 WeBS count. For the original WeBS extrapolation factors of 1.24 and 1.67 and an initial population of 17,500 birds (Table 5a), and for the newly estimated extrapolation factors of 1.51 and 3.88 with an initial population of 33,300 birds (Table 6a) there is a marked difference between the models. These tables show that the greatest risk occurs under the bootstrap density-dependent model (the risk is even greater than any that the density-independent models predict). Indeed, if the current level of licensing is assumed, then the predicted population distribution rapidly expands to be much greater than that recorded historically. As such, we can assume that this model is too poorly parameterised to be useful at this stage – further WeBS count data are required. The other two models predict that the risk of the population overlapping with the predicted distribution of the 1979 WeBS count is less than 10% (Table 5a), or less than 1% (Table 6a) if the more recent WeBS extrapolation factors are used.

A sensitivity analysis of the density-dependent models reveals that the linear and triangular models are most affected by the estimated value of the 1979 WeBS count, whereas the bootstrap model is more affected by the annual growth rates and the slope of the density-dependent function (Table 7). Removing the uncertainty in the slope of the density-dependence dramatically reduced the risk of the numbers of birds being reduced below the 1979 WeBS threshold, and thus reduces the variance in predicted population size.

The four density-independent models all predict very similar population growth over time. For example, even in 2010 with the earlier extrapolation factors, the average predicted population size varies by less than 200 birds, regardless of how many birds are shot under licence. These density-independent models predict a growth of 21% by 2007 if the numbers shot under licence do not change, and a decline of 11% if 2,000 are shot each year. The main difference between these density-independent models is the variance in the growth rates, and this is what accounts for the difference in predicted risk of decline to below the 1979 WeBS count (Table 5b and Table 6b). This risk is least for the custom model, then the lognormal model, the normal model and lastly the REML model. The custom model shows the least risk purely due to the distribution of the actual annual growth rates recorded. The normal model has a greater risk than the lognormal model because the probability of lower than average annual growth rates is greater. The REML model showed the greatest risk as it had the greatest variation in growth rates: it had variation in both the average growth rate per simulation, and in the randomly chosen annual growth rate per year.

The Predicted Consequences of The New Policy

A series of models were constructed to examine the potential short-term effect of increasing the number of cormorants shot under licence each year. We make no attempt to determine whether this number is necessary, or economic. Analysis of the WeBS counts suggests that density-dependence is currently occurring in the English over-wintering cormorant population (i.e. the confidence interval of the slope of the relationship does not include zero).

If the number of birds killed under licence is increased to the maximum of 3000 per year for two years, and 2,000 in the third, then all three models predict a similar mean population decline of 25-35% (earlier extrapolation factors) or 15-20% (later extrapolation factors). The earlier deterministic model suggested declines of 15-30% when re-run for this scenario across the range of extrapolation factors available at that time. Should monitoring suggest that the conservation status of the cormorant is under threat, then reducing the maximum number of birds killed over 3 years to, for example, 3,000, 3,000, 0 would reduce the mean predicted declines to 15-25% (earlier extrapolation factors) or 5-10% (later extrapolation factors). The new policy assumes 2,000 birds killed per annum, with the provision for this to be raised to 3,000 if required in the first two years. If the numbers killed were 2,000 for each of the first three years then the models predict declines of 20-25% (earlier extrapolation factors) or 15-20% (later extrapolation factors). The earlier deterministic model predicted that the annual removal of 2,000 birds would reduce the population by between 15 and 20%. A mechanism to assess the impact on the population of killing birds under licence is already contained within the new policy.

The estimated percentage risk that the distribution of WeBS count, following the maximum of 3,000, 3,000 and 2,000 birds killed, will overlap with the distribution of the 1979 estimated WeBS count was similar under two density-dependent models, and all the density-independent models. All predict that the risk within three years is less than 10%. Should monitoring suggest that the conservation status of the cormorant is under threat, then reducing the number of maximum number of birds killed to, for example, 3,000, 3,000, 0 would reduce the risk to below 5%. The scenario of annually killing 2,000 birds carries a risk of below 5%.

Comparison of Models

Projecting the population for the three density-dependent models indicates that the bootstrap model (following (McCallum 2000) produces very wide confidence intervals, due to the uncertainty in the slope of the density-dependent relationship. This variance is so high that the density-dependent bootstrap model predicted a greater risk of substantial decline than any of the density-independent models, and also a 6% risk that the cormorant annual WeBS count would reduce below the estimated range of 1979 counts under the current licensing levels (see Tables 5 & 6). As such, we can assume that this model is too poorly parameterised to be useful at this stage – further WeBS count data are required.

The main advantage of a stochastic model is not an improved prediction of mean results, but the prediction of the potential variance in results. Two density-dependent models, and all the density-independent models, predict similar levels of risk that the population will fall below the 1979 threshold. Indeed, all the density-independent models agree very closely, with the most advanced of these, the restricted maximum likelihood (REML) model (Staples *et al.* 2004) predicting the highest risk. In this particular situation, there seems to be very little to choose between these density-independent models. However, since the REML model predicts the highest risk, we would recommend its use, since (1) it should be the least biased, and (2) with other datasets the difference between the REML model and the other models could be greater.

The difference in risk of population decline was greater between the density-dependent models, than between the density-independent models. This demonstrates that the correct choice of the density-dependent function is important. For similar modelling exercises, we therefore recommend that a variety of methods are employed to determine the density-dependent function, and that these different models are critically compared. For the bootstrap model presented her, a longer time series of cormorant counts would greatly improve the precision of the estimated risk.

Adaptive Resource Management

Natural resource managers are frequently presented with scenarios where there are uncertainties regarding the effects of policy decisions on complex biological systems. (Williams, Nichols & Conroy 2002) describe Adaptive Resource Management (ARM) as a particularly powerful tool for scientific management in these cases. In ARM, emphasis is placed on decision-making to reach a long-term resource goal. The key to ARM is that decision-making accounts not only for the current resource goals, but also for the information needed to improve management in the future. Thus, information is gathered continuously about system responses to management as decisions are being made, and this information is used to revise understanding of the system processes and thus to improve decision-making.

This approach links decision-making to improving the understanding of the system in question through an iterative process. A good example of the use of ARM is the annual assessment and setting of North American wildfowl harvest regulations, where an annual decision is made based on resource status and model predictions. Once this decision is made, its effects are predicted through the use of a model. The effects of the decision are then monitored, and the information used to refine the original model. This revised model is then used to start another iteration of the process. The overall system of monitoring, modelling and regulations is designed to identify optimal regulatory choices for particular resource states and simultaneously track measures of model reliability over time (Johnson *et al.* 1997).

ARM provides a tool directly applicable to the proposed policy on cormorants. A model has been produced which predicts population responses to changes in the number of licences based on existing count data. This model is based on the best available data but the strength of its predictions remains untested and there remain uncertainties in many of the key parameters. Application of ARM to this issue would involve the annual prediction of the effects of granting licences to meet an established goal. This would guide the policy decision to set the appropriate number of licences, the effects of this on the population would be monitored through WeBS and the predicted and observed effects compared. This information would be used to improve the model and the process repeated each year.

The models predict the likely range of impacts of an increase in the number of licences issued on the over-wintering cormorant population. As this policy is implemented, further data will become available which will allow the model to be refined and the accuracy of its predictions improved. Data to support this process include actual figures for the numbers of birds licensed to be shot, figures for the actual number of cormorants removed under licence and updated counts of the wintering cormorant population, which may take one or two years to become available. As a consequence, there will be a staggered sequence of data becoming available over a two-year period relating to the number of birds removed and population status in any one winter. It is recommended that the model is re-run on at least an annual basis to incorporate new data on numbers of birds shot and winter counts as they become available. This process will produce a recommendation for the maximum number of licences to be considered in the coming year, annually refined to reflect improving knowledge and changing circumstances. This process is inherent in the new cormorant policy.

A predictive model for the north European breeding population of *P. carbo* (Frederiksen *et al.* 2001) has proposed that removals should be planned to operate in a density dependent manner between years to stabilise numbers near a desired level. This is consistent with the approach taken in the new policy, where a larger number of licences may be considered in the early years of the policy, with this number being reduced in subsequent years. This is reflected in the 3,000, 3,000, 2,000 maximum limits modelled for the first three years of the new policy. These limits would be reviewed in the light of observed numbers of birds removed and the response of the population in order to direct, in a density dependent manner, any reduction in future upper limit recommendations, if required, in order to stabilise the population.

Future Monitoring

It is recommended that the effects of the new policy on wintering cormorant numbers and population trend be monitored through the existing WeBS count scheme, which provides the only nationally representative and annually repeated survey of cormorant population trend. As the majority of licensed removal also takes place in the winter, this is the appropriate time of year at which to monitor the effects for modelling. However, WeBS is only an index of population size, it is not an absolute count and the model has been shown to be sensitive to the assumptions underlying the extrapolation to the national population size. Additional data on how WeBS counts relate to actual winter population size should be collected, for example through the Dispersed Waterbirds Survey. Should this provide a robust method of assessing total population size it should be periodically repeated, possibly every three to five years, to allow a regular correction to the WeBS counts for the purposes of modelling.

Both the model and WeBS relate to winter populations and information on the status of the breeding population should also be collected to inform future policy. There are current schemes which produce annual estimates of cormorant breeding numbers at different sites, together with periodic national counts of breeding birds such as Seabird 2000, which produce estimates of total breeding numbers. Continued use should be made of these to provide further information on the effects of the new policy.

The model is based on England and treats the population as a whole. Local concentrations of removal could lead to greater local declines, and the current, non-spatial, model cannot accommodate such regional effects in its current form. However, guidance issued to licensing officers includes advice on acceptable numbers of licences to be considered within individual areas, and measures to prevent undue licensed removal impacting on a particular locality or site of interest.

Conclusions

We therefore conclude that the potential maximum increase to 3,000, 3,000, 2,000 birds per annum in the number of cormorants killed in England under licence each year would, most likely, produce a mean population decline of 15-35% by 2007. When applied to this scenario, the earlier deterministic model, published on the Defra web site in September, predicts declines of 15-30%, which is broadly consistent with this more detailed analysis. The risk of the resultant population distribution overlapping with the predicted distribution of 1979 counts is less than 10%. These figures represent the worst case scenarios. The annual reassessment of the model, as data on the effects of the new policy become available, will allow the risk of more substantial declines to be assessed and managed on an iterative basis, and the number of birds licensed to be shot managed to stabilise the population at a particular level. For example, lowering the maximum number of birds shot under licence, or ceasing to issue new licences for a period would substantially reduce the risk of adverse population consequences were this thought necessary.

Modelling should continue to consider a variety of stochastic density dependent and density independent approaches to examine the sensitivity of the predictions to the assumptions inherent in each approach. The models should be re-run as new information on numbers of licences, birds killed and cormorant population figures become available to guide future policy.

References

Bedard, J., Nadeau, A. & Lepage, M. (1995) Double-crested cormorant culling in the St. Lawrence River estuary. Colonial Waterbirds, 18 (special publication 1), 78-85.
Carss, D. (2002). Reducing the conflict between Cormorants and fisheries on a pan-European scale. Report of a Concerted Action funded by the European Union, Rep. No. Study contract no. Q5CA-2000-31387. Natural Environment Research Council Centre for Ecology & Hydrology, Banchory, Scotland.
Cramp, S. & Simmons, K.E.L., eds. (1977) Handbook of the birds of Europe, the Middle East and North Africa. The birds of the Western Palearctic. Vol. 1. Oxford University Press, Oxford.

Debout, G., Rov, N. & Sellars, R.M. (1995) Status and population development of cormorants *Phalacrocorax carbo carbo* breeding on the Atlantic coast of Europe. Ardea, 83, 47-59.
Dennis, B. & Taper, M.L. (1994) Density dependence in time series observations of natural populations: estimation and testing. Ecological Monographs, 64, 205-224.
Feltham, M.J., Davis, J.M., Wilson, B.R., Holden, T., Cowx, I.G., Harvey, J.P. & Britton, J.R. (1999). Case studies of the impact of fish-eating birds on inland fisheries in England and Wales. Ministry of Agriculture, Fisheries and Food, London.
Frederiksen, M., Lebreton, J.D. & Bregnaballe, T. (2003) Modelling the effect of winter culls on Great Cormorant *Phalacrocorax carbo sinensis* population size in Europe: the importance of spatial variability in culing intensity. Die Vogelwelt, 124 (Supplement), 325-330.
Frederiksen, M., Lebreton, J.D. & Bregnballe, T. (2001) The interplay between culling and density-dependence in the great cormorant: a modelling approach. Journal of Applied Ecology, 38, 617-627.
Hughes, B., Bruce, J., Ekins, G. & Newson, S. (2000). Movements and distribution of inland breeding cormorants in England. Wildfowl & Wetlands Advisory Service.
Hughes, B., Kirby, J. & Rowcliffe, J.M. (1999) Waterbird conflicts in Britain and Ireland: Ruddy Ducks *Oxyura jamaicensis*, Canada Geese *Branta canadensis*, and Cormorants *Phalacrocorax carbo*. Wildfowl 50: 77-99. Wildfowl, 50, 77-99.
Jackson, S. & Austin, G. (2004). The WeBS Dispersed Waterbirds Survey 2002/03, Rep. No. WeBS News: Newsletter of the Wetland Bird Survey, Issue no. 20 Summer.
Johnson, F.A., Moore, C.T., Kendall, W.L., Dubovsky, J.A., Caithamer, D.F., Kelley, J.R.J. & Williams, B.K. (1997) Uncertainty and the management of mallard harvests. Journal of Wildlife Management, 61, 202-216.
Kershaw, M. & Cranswick, P.A. (2003) Numbers of wintering waterbirds in Great Britain, 1994/1995-1998/1999: I. Wildfowl and selected waterbirds. Biological Conservation, 111, 91-104.
Kershaw, M. & Hughes, B. (1997). Trends in the numbers of cormorants *Phalocrocorax carbo*, goosanders *Mergus merganser* and red-breasted mergansers *M. serrator* wintering in the UK. Wildfowl and Wetlands Trust Report to The Britsh Trust for Ornithology, Slimbridge.
Kirby, J.S. (1995) Winter population estimates for selected waterfowl species in Britain. Biological Conservation, 73, 189-198.
Kirby, J.S., Gilburn, A.S. & Sellers, R.M. (1995) Status, distribution and habitat use by Cormorants *Phalacrocorax carbo* wintering in Great Britain. Ardea, 83, 93-102.
Lindell, L., Mellin, M., Musil, P., Przybysz, J. & Zimmerman, H. (1995) Status and population development of breeding cormorants *Phalacrocorax carbo sinensis* of the central European flyway. Ardea, 83, 81-92.
Marquiss, M. & Carss, D.N. (1994). Fish-eating birds: Assessing their impact on freshwater fisheries, Rep. No. Unpublished R&D Report 15. National Rivers Authority, Bristol, UK.
McCallum, H. (2000) Population parameters: estimation for ecological models Blackwell Science, Oxford.
Middleton, D.A.J., Nisbet, R.M. & Kerr, A.J. (1993) A mathematical model of the effect of shooting barnacle geese wintering on Islay. Journal of Applied Ecology, 30, 1-12.
Mitchell, P.I., Newton, S.F., Ratcliffe, N. & Dunn, T. (2004) Seabird Populations of Britain and Ireland T & A.D. Poyser, London.

Pollitt, M., Hall, C., Holloway, S., Heran, R., Marshall, P., Musgrove, A., Robinson, J. & Cranswick, P. (2003) The Wetland Bird Survey 2000-01: Wildfowl and Wader Counts BTO/WWT/RSPB/JNCC, Slimbridge, UK.
Smith, G.C., Henderson, I.S. & Robertson, P.A. (press july 2004) A model of ruddy duck *Oxyura jamaicensis* eradication for the United Kingdom. Journal of Applied Ecology, ??, ??
Staples, D.F., Taper, M.L. & Dennis, B. (2004) Estimating population trend and process variation for PVA in the presence of sampling error. Ecology, 85, 923-929.
Van Eerden, M.R. & Gregersen, J. (1995) Long-term changes in the Northwest European population of Cormorants *Phalacrocorax carbo sinensis*. Ardea, 83, 61-79.
Wanless, S., Harris, M.P., Calladine, J. & Rothery, P. (1996) Modelling responses of herring gull and lesser black-backed gull populations to reduction of reproductive output: implications for control measures. Journal of Applied Ecology, 33, 1420-1432.
Wernham, C.V., Armitage, M., Holloway, S.J., Hughes, B., Hughes, R., Kershaw, M., Madden, J.R., Marchant, J.H., Peach, W.J. & Rehfisch, M.M. (1999). Population, Distribution, Movements and Survival of Fish-eating Birds in Great Britain. Report to the Department of the Environment, Transport and the Regions, London.
Williams, B.K., Nichols, J.D. & Conroy, M.R. (2002) Analysis and Management of Wildlife Populations Academic Press, San Diego.

Table 1. The WeBS maximum annual count data for cormorants in England, and the annual finite growth rate for year *t* (calculated by N_{t+1}/N_t).

Year	WeBS count	Finite growth rate
1986/87	2498	2.37
1987/88	5923	1.34
1988/89	7929	1.07
1989/90	8455	1.30
1990/91	11000	0.88
1991/92	9637	1.06
1992/93	10202	1.09
1993/94	11076	0.99
1994/95	10620	1.06
1995/96	11207	0.97
1996/97	10786	0.96
1997/98	10343	1.16
1998/99	12020	1.04
1999/00	12536	0.99
2000/01	12369	N/A

Table 2. Estimated values for the correction factor to estimate the national population from the WeBS count, and the associated estimate with the year for which the estimate was made.

WeBS correction factor	English Population Estimate (2001)	Year correction factor estimated[††]	Reference
1.24	15,338	1990-92	(Kirby 1995)
1.67	20,656	1990-94	(Kershaw & Hughes 1997)
2.19	27,088	1997	(Hughes, Kirby & Rowcliffe 1999)
1.60	19,790	1994-98	(Kershaw & Cranswick 2003)
2.70[†] (1.51-3.88)	33,300[‡] (± 14,660)	2002-03	(Jackson & Austin 2004)

[†]Calculated correction factors assuming that the 2003 WeBS count is identical to the 2001 count. These estimates were calculated from a graph in the reference.
[‡]Estimated population was for GB for 2003. The English population and range (90% confidence limit) were calculated as 75% of the GB total, the average percentage for the years 1993-2001.
[††]The year 1990 refers to the winter of 1990/91, etc.

Table 3. The number of cormorant licences issued, and cormorants shot under licence, for each year since 1996/7.

Year	No Cormorants Licensed To Be Shot	No Birds Actually Shot
1996/7	366	180
1997/8	443	139
1998/9	517	167
1999/2000	485	205
2000/1	506	199
2001/2	545	225
2002/3	603	284
Annual Mean	495	200

Table 4. The estimated percentage extent by which the distribution of WeBS count will overlap with the distribution of the 1979 estimated WeBS count, in 2007, for each of the models, assuming an initial population of about 17,500 English cormorants. The Licences column gives three values: the total number of cormorants killed in 2004, 2005 and each subsequent year under licence. The results show the mean percentage overlap and the range, given extrapolation factors of 1.24 and 1.67.

Table 4a

	Density Dependent Model		
Licences	**Linear**	**Bootstrap**	**Triangular**
3000,3000,2000	3.3 (0.7-9.3)	21.0 (15.8-27.1)	8.5 (3.0-17.7)
2000,3000,2000	2.5 (0.5-7.5)	19.7 (15.3-26.8)	4.4 (1.1-10.8)
2000,2000,2000	1.6 (0.2-5.3)	18.5 (11.8-24.2)	2.1 (0.4- 6.5)
3000,2000,2000	2.0 (0.4-6.4)	19.3 (13.9-25.6)	3.9 (1.0-10.0)
3000,3000,1000	1.4 (0.2-5.0)	17.4 (12.9-22.5)	3.8 (1.0 9.8)
2000,2000,1000	0.6 (0.1-2.8)	12.5 (9.3-18.0)	0.9 (0.1- 3.4)
3000,3000,0	0.7 (0.1-3.0)	14.1 (9.5-19.7)	2.1 (0.5- 6.2)
2000,2000,0	0.3 (0.0-1.6)	10.3 (6.9-14.5)	0.5 (0.0- 2.1)
200,200,200	0.1 (0.0-0.7)	6.3 (3.5-11.5)	0.0 (0.0- 0.2)

Table 4b

	Density Independent Model			
Licences	**Custom**	**Lognormal**	**Normal**	**REML**
3000,3000,2000	7.3 (3.1-13.5)	8.0 (4.0-13.8)	8.8 (4.6-14.4)	10.1 (5.4-15.9)
2000,3000,2000	4.3 (1.4- 8.7)	4.9 (2.2- 9.6)	6.1 (2.9-10.0)	6.4 (3.2-11.5)
2000,2000,2000	2.3 (0.7- 5.4)	3.0 (1.1- 6.2)	3.6 (1.6- 6.9)	4.3 (1.9- 7.9)
3000,2000,2000	4.2 (1.4- 8.8)	4.7 (2.0- 9.3)	6.1 (2.7-10.1)	6.8 (3.1-11.2)
3000,3000,1000	4.0 (1.5- 9.1)	5.1 (2.0- 9.0)	5.6 (2.7-10.0)	6.5 (3.1-11.7)
2000,2000,1000	1.1 (0.2- 3.2)	1.7 (0.5- 4.0)	2.2 (0.8- 4.5)	2.5 (1.0- 5.2)
3000,3000,0	2.6 (0.7- 6.2)	3.3 (1.2- 6.9)	3.9 (1.7- 7.4)	4.6 (1.8- 8.5)
2000,2000,0	0.6 (0.1- 2.1)	0.9 (0.3- 2.6)	1.4 (0.4- 3.1)	1.6 (0.5- 3.8)
200,200,200	0.1 (0.0- 0.2)	0.1 (0.0- 0.3)	0.2 (0.0- 0.5)	0.2 (0.0- 0.6)

Table 5. The estimated percentage extent by which the distribution of WeBS count will overlap with the distribution of the 1979 estimated WeBS count, in 2007, for each of the models, assuming an initial population of about 33,300 English cormorants. The Licences column gives three values: the total number of cormorants killed in 2004, 2005 and each subsequent year under licence. The results show the mean percentage overlap and the range, given extrapolation factors of 1.51 and 3.88.

Table 5a

	Density Dependent Model		
Licences	**Linear**	**Bootstrap**	**Triangular**
3000,3000,2000	0.8 (0.0-15.4)	13.2 (3.2-28.0)	1.0 (0.0-13.3)
2000,3000,2000	0.7 (0.0-14.7)	12.7 (2.7-27.8)	0.7 (0.0-11.4)
2000,2000,2000	0.6 (0.0-13.3)	11.5 (2.2-26.4)	0.5 (0.0-10.1)
3000,2000,2000	0.6 (0.0-13.6)	12.0 (2.6-27.0)	0.7 (0.0-11.2)
3000,3000,1000	0.5 (0.0-12.7)	11.2 (2.2-25.3)	0.6 (0.0-10.8)
2000,2000,1000	0.3 (0.0-10.4)	10.2 (1.5-23.6)	0.3 (0.0- 7.6)
3000,3000,0	0.3 (0.0-10.6)	10.0 (1.8-23.8)	0.5 (0.0- 9.1)
2000,2000,0	0.2 (0.0- 8.7)	8.6 (1.1-22.6)	0.2 (0.0- 6.6)
200,200,200	0.1 (0.0- 6.9)	6.7 (0.6-19.7)	0.1 (0.0- 3.4)

Table 5b

	Density Independent Model			
Licences	**Custom**	**Lognormal**	**Normal**	**REML**
3000,3000,2000	3.0 (0.1-14.5)	3.5 (0.1-14.0)	3.9 (0.2-14.5)	4.1 (0.2-16.0)
2000,3000,2000	2.4 (0.0-12.3)	2.7 (0.1-12.5)	3.0 (0.1-13.3)	3.3 (0.1-13.7)
2000,2000,2000	1.6 (0.0-10.2)	1.9 (0.0-10.5)	2.2 (0.1-10.8)	2.7 (0.1-11.9)
3000,2000,2000	2.3 (0.0-11.8)	2.5 (0.1-12.3)	2.9 (0.1-12.6)	3.3 (0.1-13.5)
3000,3000,1000	2.3 (0.0-11.8)	2.5 (0.1-12.1)	2.8 (0.1-12.7)	3.3 (0.1-14.0)
2000,2000,1000	1.2 (0.0- 8.6)	1.4 (0.0- 8.7)	1.8 (0.0- 9.7)	2.0 (0.0-10.4)
3000,3000,0	1.8 (0.0-10.4)	2.0 (0.0-10.6)	2.4 (0.1-11.3)	2.7 (0.1-12.2)
2000,2000,0	0.9 (0.0- 7.4)	1.2 (0.0- 7.8)	1.4 (0.0- 8.5)	1.6 (0.0- 9.2)
200,200,200	0.2 (0.0- 3.6)	0.3 (0.0- 3.8)	0.5 (0.0- 4.3)	0.5 (0.0- 5.0)

Table 6. The percentage of simulations where the population in 2007 declined by more than a given percentage, from the starting population in 2004 for the three density-dependent models. The Licences column gives three values: the total number of cormorants killed in 2004, 2005 and each subsequent year under licence. Note, that approximately 50% of simulations should lie below any given value if the population is stable at that value.

(a) This assumes an initial population of about 17,500 English cormorants and extrapolation factors of 1.24 and 1.67.

Licences	Linear				Bootstrap				Triangular			
	0	10	20	30	0	10	20	30	0	10	20	30
3000,3000,2000	99.8	97.6	83.5	46.1	71.4	64.4	58.8	49.5	100	100	97.8	71.7
2000,3000,2000	99.7	96.1	78.5	38.6	71.4	65.7	55.2	47.0	100	99.8	90.8	49.8
2000,2000,2000	99.1	92.5	67.1	26.2	70.3	60.8	53.3	44.7	100	98.3	75.0	26.5
3000,2000,2000	99.5	94.6	73.1	32.3	69.6	63.5	56.3	48.4	100	99.7	89.1	46.3
3000,3000,1000	98.4	97.6	83.7	46.6	71.8	66.4	56.8	49.2	100	100	97.7	71.5
2000,2000,1000	96.5	80.9	43.9	10.0	66.5	58.8	49.7	36.7	99.7	90.0	46.8	9.4
3000,3000,0	97.1	82.3	46.1	11.3	64.0	58.2	47.8	40.5	100	97.3	71.1	25.9
2000,2000,0	91.4	66.0	26.0	3.9	61.0	53.6	45.4	36.6	97.8	74.2	26.2	3.1
200,200,200	76.8	40.7	10.6	0.9	56.9	50.5	40.0	28.9	48.0	9.6	0.3	0.0

(b) This assumes an initial population of about 33,300 English cormorants and extrapolation factors of 1.51 and 3.88.

Licences	Linear				Bootstrap				Triangular			
	0	10	20	30	0	10	20	30	0	10	20	30
3000,3000,2000	85.2	70.8	48.8	24.9	64.0	57.1	49.0	39.2	90.4	70.0	30.6	4.4
2000,3000,2000	83.8	69.5	47.7	23.5	63.2	56.2	48.0	38.9	87.5	63.3	23.3	2.2
2000,2000,2000	81.6	66.0	44.6	20.5	62.6	55.5	46.6	37.7	83.3	53.8	16.0	1.1
3000,2000,2000	82.8	67.3	45.5	21.8	63.1	55.6	47.7	38.0	86.6	61.4	22.3	2.0
3000,3000,1000	80.9	64.4	41.8	18.6	61.4	54.3	46.2	36.5	85.6	59.1	19.7	1.8
2000,2000,1000	77.2	59.9	37.4	15.6	60.4	53.1	43.9	34.5	76.5	41.3	9.0	0.4
3000,3000,0	77.3	59.1	36.7	14.8	59.9	52.3	43.5	34.1	81.0	50.0	13.4	0.9
2000,2000,0	73.3	54.9	32.6	12.3	58.2	51.0	42.0	32.3	68.8	32.5	4.8	0.1
200,200,200	67.5	48.0	26.9	9.0	56.0	47.9	39.0	29.4	38.3	8.5	0.3	0.0

Table 7. Results of the sensitivity analysis for the density-dependent models. The percentage probability that the WeBS count will fall below the 1979 estimated WeBS count, in 2007, for each of the models. The percentage contribution to the variance in the risk is also presented for each variable. In these results the sensitivity to starting conditions is examined. Licences are 2000 in all years; the extrapolation factors used are 1.24 and 1.67.

	Density Dependent Model		
Variable fixed	**Linear**	**Bootstrap**	**Triangular**
None	1.6 (0.2-5.3)	18.5 (11.8-24.2)	2.1 (0.4-6.5)
1979 WeBS estimate	0.0 (0.0-0.0)	16.6 (8.6-21.6)	0.0 (0.0-0.0)
Initial pop size	1.5 (0.2-5.1)	16.0 (13.6-22.5)	0.5 (0.1-2.4)
Growth rates	0.6 (0.0-3.3)	18.0 (12.1-21.4)	0.5 (0.0-2.8)
Sigma		15.7 (13.4-21.8)	
Slope		7.6 (5.0-11.2)	
Constant		15.1 (12.5-20.3)	
Correlations		25.4 (19.0-32.0)	
	1979 WeBS estimate 86%	Growth rates 64%	1979 WeBS estimate 76%
	Growth rates 14%	Slope 25%	Growth rates 15%
	Initial pop size 0.0%	1979 WeBS estimate 7.9%	Initial pop size 8%
		Intercept 6%	
		Initial pop size 0%	
		Sigma 0%	

Figure 1. The logarithm of the English cormorant WeBS count against year.

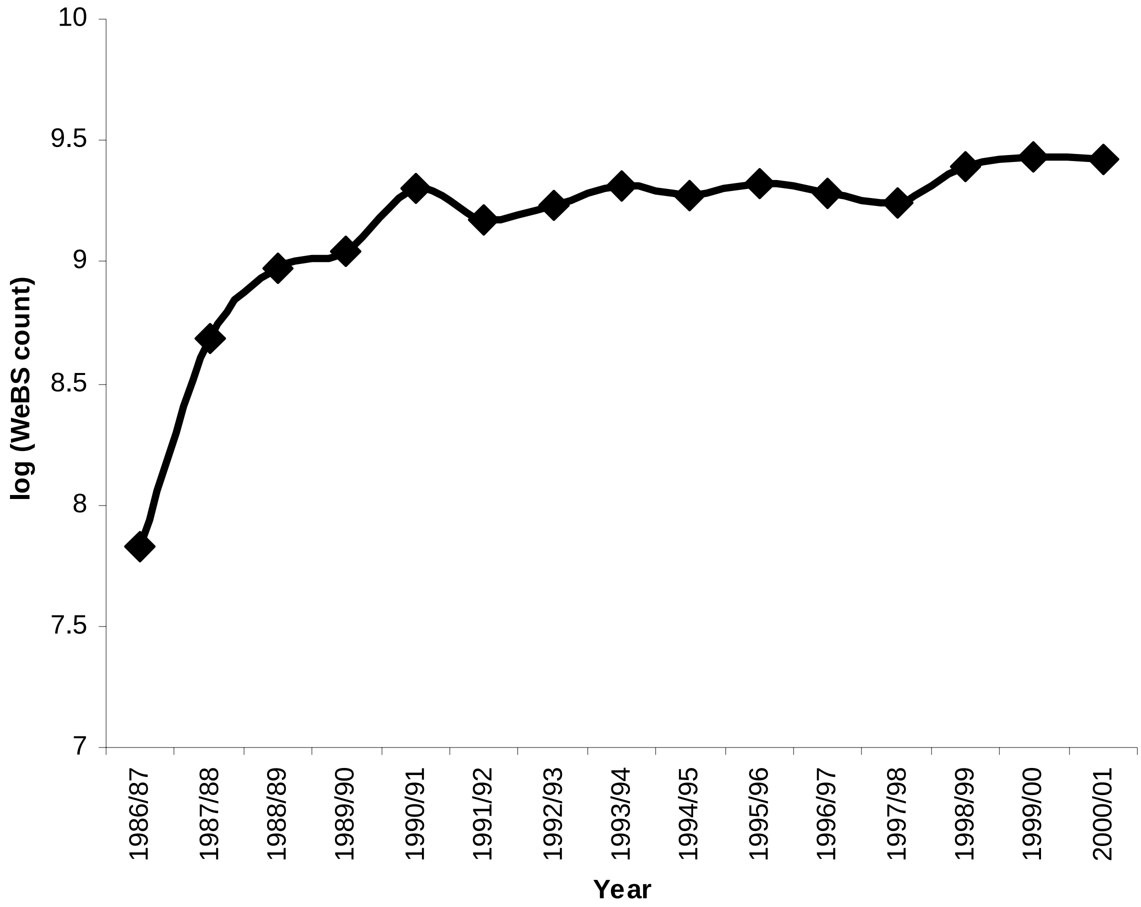


Figure 2. The estimated annual growth rate of the English cormorant population, derived from Table 1, plotted against the 'peak annual WeBS count' population size. The regression line is shown for the data, and is significant (p<0.005).

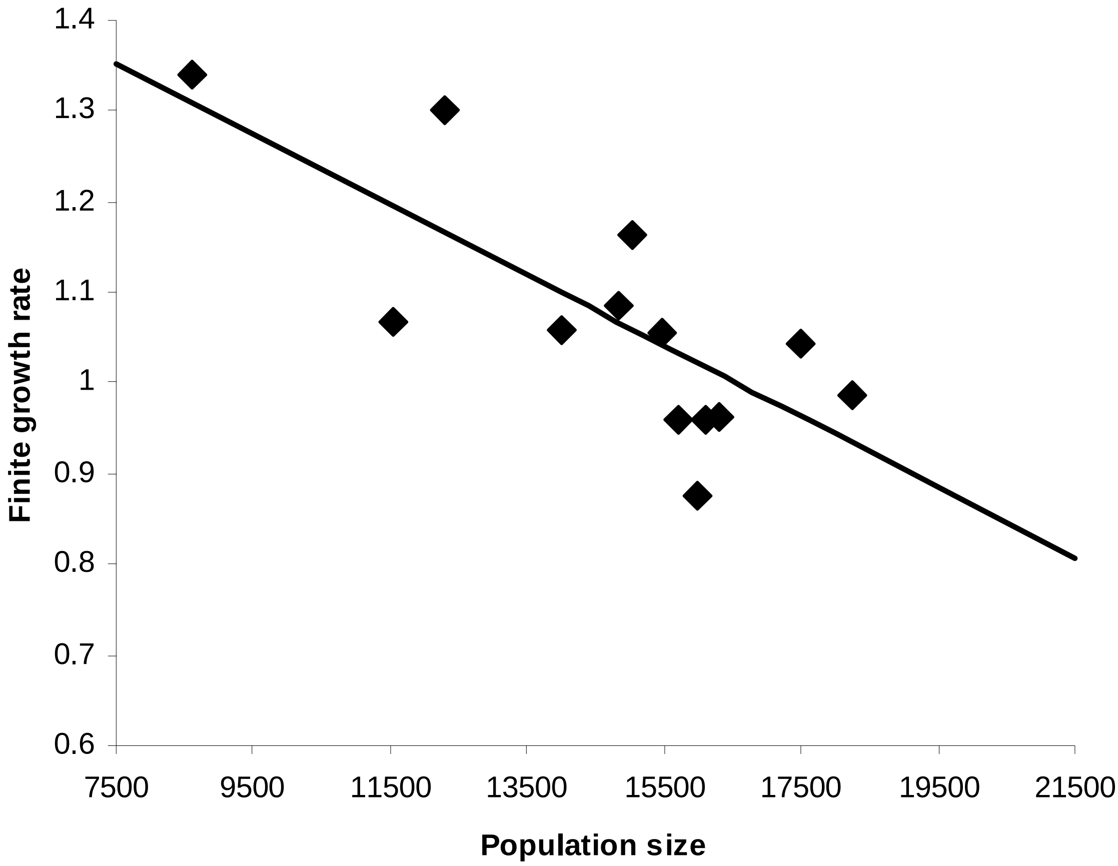
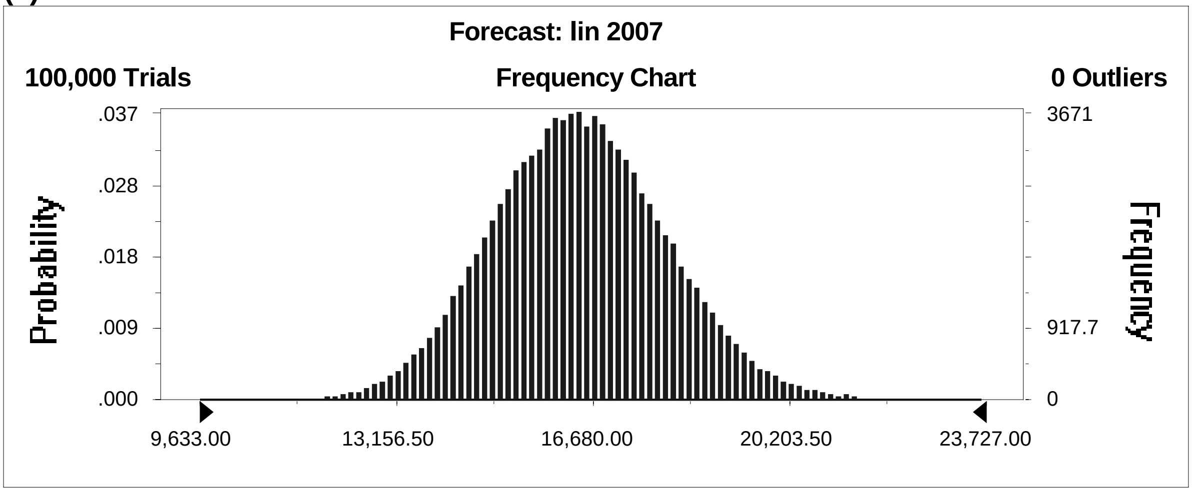
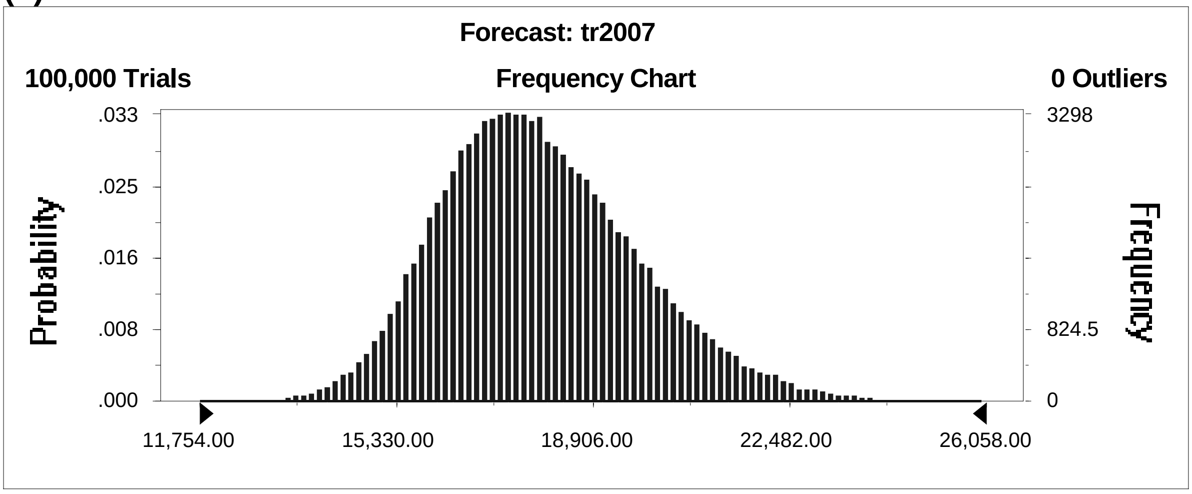


Figure 3. Predicted population size in 2007, assuming no change in the average number of birds shot under licence for the three density-dependent models: (a) linear, (b) triangular and (c) bootstrap.

(a)



(b)



(c)

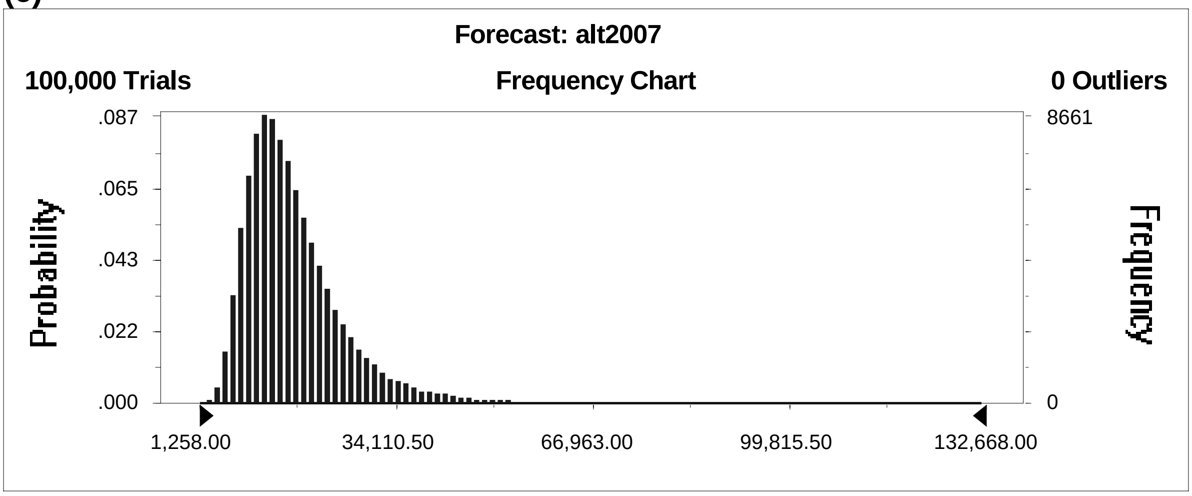
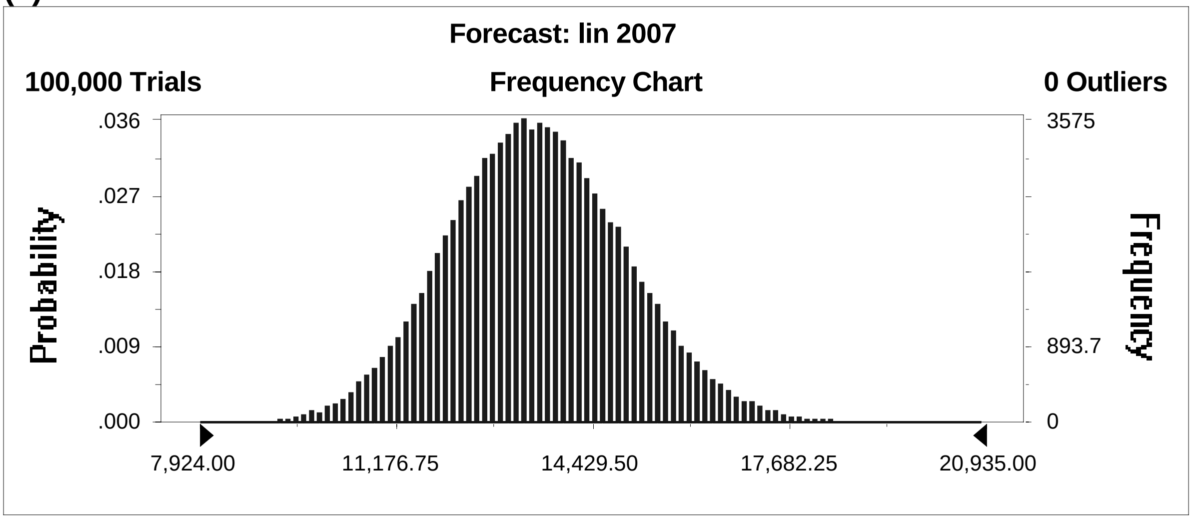
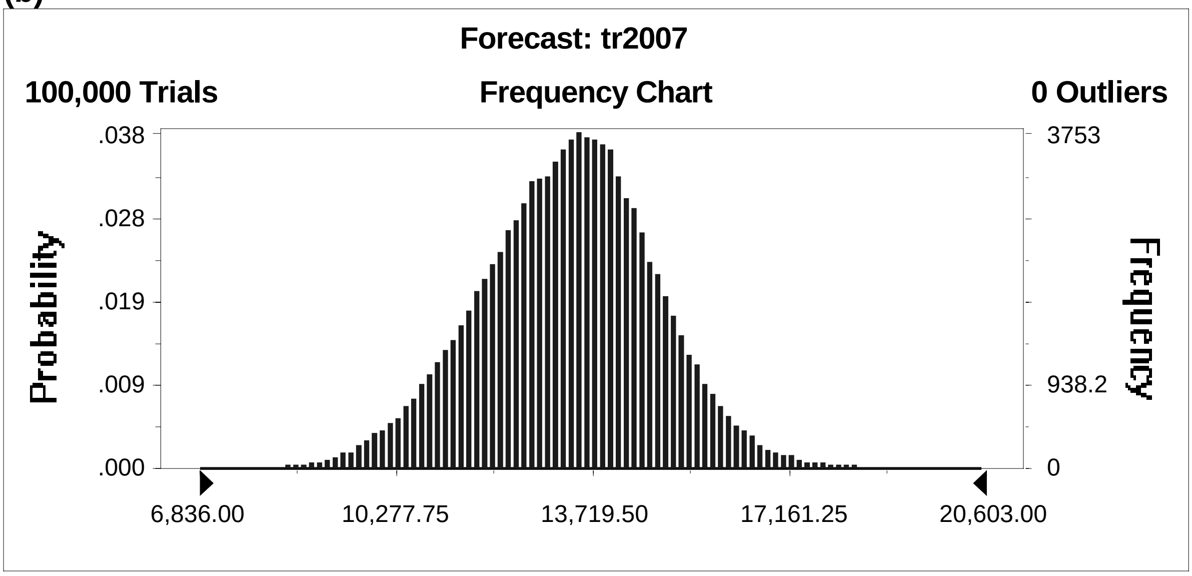


Figure 4. Predicted population size in 2007, for 2000 birds shot annually under licence for the three density-dependent models: (a) linear, (b) triangular and (c) bootstrap.

(a)



(b)



(c)