

# Using a stochastic model to examine the ecological, economic and ethical consequences of population control in a charismatic invasive species: mute swans in North America

MARTHA M. ELLIS\* and CHRIS S. ELPHICK

*Ecology and Evolutionary Biology, University of Connecticut, 75 North Eagleville Road, U-43, Storrs, CT 06269–3043, USA*

## Summary

1. Although invasive species are widely recognized as a threat to native ecosystems, control or eradication plans can create controversy, particularly when target species are considered attractive or desirable by members of the public. Detailed consideration of both biological and non-biological criteria when evaluating management proposals can better inform managers working with controversial species.
2. In this study, alternative strategies for controlling introduced populations of mute swans *Cygnus olor* during the first few decades of population growth were compared in terms of ecological, economic and ethical considerations using a simple population model.
3. By quantifying parameter uncertainty with a stochastic model, we identified, in quantitative terms, management strategies that were predicted to have a high certainty of succeeding. Survival rates should be reduced by more than 17% to be 90% certain of a decline; reproductive rates would need to decline by more than 72% to achieve the same goal. Populations in which density dependence occurs are expected to need even greater effort for management to work.
4. Reducing survival rates was also more efficient economically; reducing population growth via reduced reproduction required three to four times more person-days within the first year across a range of simulated growth rates.
5. Prolonging timelines for implementing management increased the number of swans that would have to be killed and the costs that would be required for reaching target population sizes.
6. *Synthesis and applications.* Because of controversy surrounding swan management, various considerations must be addressed when weighing control options. Our modelling suggests that, if a population is to be controlled, a period of intensive culling of adults will be the most efficient option in terms of biological effectiveness, economic costs and minimizing the total number of swans that ultimately are killed.

*Key-words:* avian eradication, demographic modelling, ecological ethics, invasive species, mute swan, pest control, stochasticity

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## Introduction

Biological invasions by non-native species pose a serious threat to native ecosystems and biodiversity (Mooney

*et al.* 2005; Hulme 2006). Human activities have dramatically increased the movement of species around the globe, greatly increasing the frequency of introductions (Mack *et al.* 2000). As awareness of the problems caused by these new populations has increased, so too has the attention given to the management and eradication of potentially problematic species (Bomford & O'Brien 1995). While methods for determining the

most biologically efficient route for control have become increasingly sophisticated, deciding a course of action can still be controversial because of the economic costs of control and concerns over killing the invasive organism. Such ethical considerations are greatest when the species has aesthetic or emotive value in society, independent of its ecological role.

Although growing emphasis has been placed on the importance of alternative criteria in decision-making (Minteer & Collins 2005), it remains rare to address explicitly societal concerns alongside analyses of biological efficacy in studies of invasive species control. One recent exception involved the use of a simple model to determine the feasibility and economic consequences of eradicating ruddy ducks *Oxyura jamaicensis* from the UK (Smith, Henderson & Robertson 2005). Here, we address another highly controversial case, where societal considerations, particularly the ethics of population control, have greatly influenced the course of action. We demonstrate how conventional methods for analysing the biological efficiency of management alternatives can also be used to quantify and describe the broader consequences of different strategies in ways that can directly contribute to more informed decision-making.

Mute swans *Cygnus olor* Gmelin (1789) were first brought to North America in the late 1800s (Ciaranca, Allin & Jones 1997). Released or escaped mute swans have established populations in several parts of North America, and their numbers are rapidly increasing (Ciaranca, Allin & Jones 1997; Petrie & Francis 2003). Today, there are three main populations, each isolated from the others and originating from separate introductions. The largest population extends along the Atlantic coast from Virginia to New Hampshire (Ciaranca, Allin & Jones 1997; Atlantic Flyway Council 2003). Annual Christmas Bird Counts (CBC; Butcher 1990) first recorded mute swans in New York in 1922. By 2002, approximately 10 000 swans were recorded along the east coast of North America (National Audubon Society 2004). In the Great Lakes region, the number of swans reported grew from two in 1945 to more than 5000 in 2002, with estimates of the population growth rate ranging from 10% to 18% year<sup>-1</sup> (Petrie & Francis 2003). A third population, near the USA–Canada border on the Pacific coast, became established in the late 1960s and has shown irregular population growth since that time, with fewer than 100 swans seen in 2002. Isolated observations and breeding also occur elsewhere across the continent, suggesting that other population foci might develop. Mute swan introductions are not restricted to North America, and populations have been established in South Africa, New Zealand, Australia and elsewhere (Long 1981; Ciaranca, Allin & Jones 1997).

Introduced swans pose potentially serious threats to native species by overgrazing aquatic plants and displacing other waterbirds with their aggressive behaviour. Other concerns include deposition of faecal material, conflicts between humans and swans and damage to crops (Ciaranca, Allin & Jones 1997; Atlantic Flyway

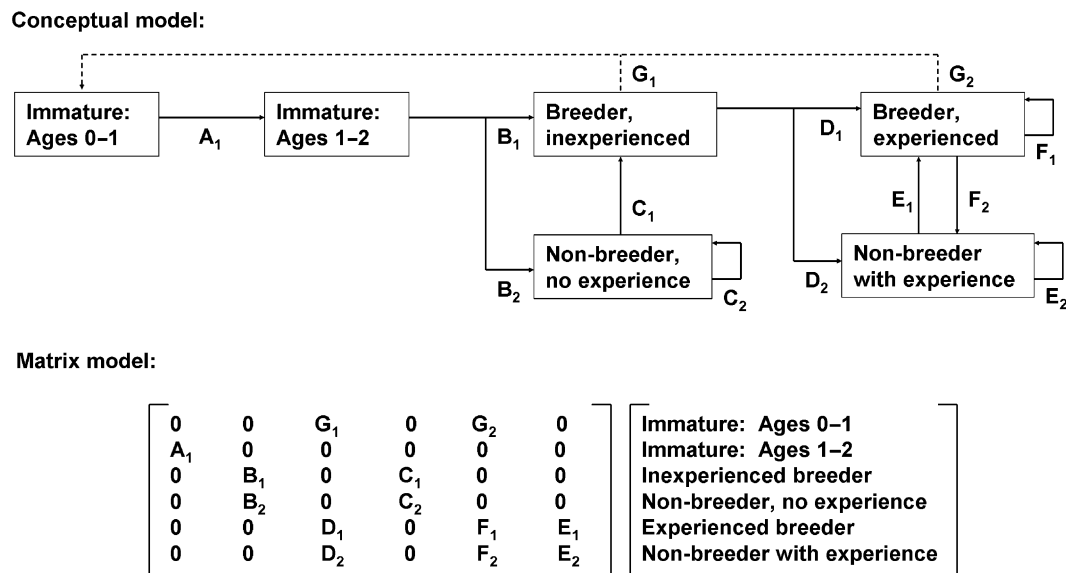
Council 2003). Deciding how managers should respond to population growth, however, has been hampered by the limited literature describing conclusively the effects of swans on native species (Conover & Kania 1994; Allin & Husband 2003). Grazing studies have either been inconclusive or have produced conflicting results. Experiments conducted during the breeding season tend to show few effects (Conover & Kania 1994; although see Allin, Chasko & Husband 1987) while those with post-breeding flocks tend to show local depletion (Cobb & Harlin 1980; Allin & Husband 2003). Even studies of flocking birds, however, can show great variation in the amount of depletion within a site (Allin & Husband 2003) and it is unclear whether local depletion translates to regional patterns of vegetation loss.

Nesting swans can also be very aggressive (Allin, Chasko & Husband 1987). Despite observing high rates of aggressive interactions with other species, however, Conover & Kania (1994) found no evidence that swans caused nesting failures or excluded other species from the swans' territories. Isolated problems occur, for example where endangered beach-nesting birds have their nests trampled by swans (Ciaranca, Allin & Jones 1997), but whether population-wide impacts on native species exist is unknown.

The combination of perceived threats and limited data has added to the controversy as managers seek to reduce mute swan numbers (Atlantic Flyway Council 2003; Perry 2004), while other organizations have brought and won legal challenges to restrict population control (Hindman & Harvey 2004). Such conflicts are not unusual when charismatic species are introduced to new areas and subsequently impact native species. For instance, controversies have developed in response to attempts to control feral horse *Equus caballus* populations in the USA and New Zealand (Mack *et al.* 2000) and ruddy ducks in England (Central Science Laboratory 2002). Minimizing such conflicts presents a clear challenge for applied ecologists.

Improving our understanding of a species' population dynamics can inform such debates (cf. Hughes, Kirby & Rowcliffe 1999). Previous models have shown that control focused on reducing adult swan survival will be more effective than efforts to reduce reproductive success (Harvey 2000; Watola *et al.* 2003; Allin & Husband 2004; Hindman & Harvey 2004), as expected for a long-lived species. These earlier studies have used deterministic models and have generally focused on local population dynamics within a relatively small area. Watola *et al.* (2003) also raised concerns about the ability to generalize results without detailed field data from the areas of interest, and pointed out that such data do not exist for many areas.

We have built on previous analyses by creating a stochastic stage-based matrix model. We used the model to predict population growth during the early stages of an invasion, when control is likely to be most effective, and compared scenarios for managing growth. A limitation of deterministic models, or model results that



**Fig. 1.** Conceptual and matrix descriptions of population model. Letters denoting transitions between stages in the conceptual description of the model correspond to the relevant values in the matrix.

focus only on average outcomes, is that they do not necessarily provide managers with the desired high level of certainty that specific recommendations will work. For instance, a set of mean parameter values that produce marginally negative population growth may not create a decline if there is considerable uncertainty in the model input. To address these problems, we incorporated estimates of parameter uncertainty in a stochastic framework and conducted a detailed sensitivity analysis, enabling us to place confidence intervals around predictions, identify threshold parameter values at which control has a high chance of success, and assess the importance of data deficiencies. We also structured our analysis to examine a multitude of options, including strategies that combine different forms of management, rather than just looking at a small number of discrete options.

Unlike previous studies, we did not focus on one study area, instead examining a range of parameter values, representative of the species, to determine whether conclusions can be generalized across populations. We did, however, test the model by comparing predictions to data from North America. We also used the model to go beyond purely biological questions. First, we estimated the relative costs of different strategies based on the number of person-days required to reach target growth rates. Then we assessed the ethical consequences of different options in terms of the number of swans that would need to be killed or removed under different scenarios. Our analysis provided detailed information on the set of management alternatives that would allow populations to be controlled during the initial period of growth; identified simple ways in which modelling results can be used to distinguish strategies that have a high likelihood of achieving a given result; and provided a quantitative means of addressing economic

and ethical concerns within the same modelling framework used to examine population dynamics.

## Methods

### MODEL STRUCTURE

We built a stochastic, stage-based model using data from the literature. The model had six stages representing different groups of swans: first-year immatures, second-year immatures, mature birds that have never bred, first-time (inexperienced) breeders, birds that have reproduced but skip a year of breeding, and experienced breeders (Fig. 1). The mathematical model consisted of a  $6 \times 6$  matrix, with transition probabilities describing the change in the number of individuals in each stage at each time step. The number of swans in each stage in any given year was determined by multiplying the transition matrix by a vector describing the number of swans in each stage in the previous year. Each iteration of this multiplication was equivalent to a 1-year interval, beginning in April. The model assumed a single annual birth pulse, that the number of individuals in each stage was counted immediately after breeding, and no density dependence.

Cygnets entered the first stage (immature, age 0–1; Fig. 1) at fledging. A proportion of these birds survived to the next year and entered the next stage of the model (immature, age 1–2) based on the first-year survival rate. After their second year, a swan may be physically capable of breeding but not all swans breed immediately (Birkhead & Perrins 1986). In the model, we simulated these alternatives by allowing a proportion of the birds in the ‘immature, age 1–2’ class to start to breed (inexperienced breeders) while the remainder entered a pool of mature non-breeding birds (non-breeders, no

experience), based on the probability that a mature non-breeder begins to breed. Each year a proportion of the birds in the inexperienced non-breeder group also became first-time breeders, while the remainder continued in the non-breeding pool. Each year, all swans that entered the inexperienced breeder group in the previous year moved into a loop for experienced breeders, in which they either continued to breed (breeder, experienced) or entered a second pool of non-breeding birds (non-breeders, experienced). In addition to moving between stages, swans were removed from each stage through mortality. The rate at which swans entered the population depended on the number of individuals in each of the two breeder stages and the corresponding reproductive rates.

#### MODEL PARAMETERS

##### *Survival rates*

Survival can vary by age, sex, breeding status and year, although differences among classes can be small (Birkhead & Perrins 1986; Ciaranca, Allin & Jones 1997; Coleman *et al.* 2001; Watola *et al.* 2003). We used survival rates from a 20-year study that used mark-recapture methods and the program MARK to estimate survival (Watola *et al.* 2003). This study found that the best-fitting model included an increase in survival with age and higher survival for breeders than for non-breeders (Table 1) but no difference between sexes. These results are similar to those from other studies, including from North America (Reese 1980). We included stochasticity by selecting survival values for each year from truncated normal distributions (limited to values between 0 and 1) based on information reported by Watola *et al.* (2003).

##### *Reproductive rates*

The number of young produced per breeding pair was calculated as the product of the average clutch size and the probability of an egg surviving to become a fledged

cygnet. Clutch sizes are distributed relatively symmetrically around their mean (Perrins & Reynolds 1967) but means vary among populations. Means from North American studies range from 4.3 to 6.5 eggs clutch<sup>-1</sup> (Ciaranca, Allin & Jones 1997). In our simulations, we used a clutch size for experienced breeders taken randomly from a normal distribution with mean 5.9 and standard deviation 2.2, truncated to eliminate negative values. These values were calculated from a distribution reported by Perrins & Reynolds (1967) that had a much larger sample than most other available studies and were representative of the data reported for North American populations.

Birkhead, Bacon & Walter (1983) found that both the mean clutch size and the number of cygnets fledged were higher for experienced pairs [ $7.0 \pm 0.2$  (SE) and  $2.8 \pm 0.4$ , respectively] compared with inexperienced pairs ( $5.7 \pm 0.6$  and  $1.7 \pm 0.8$ ). Based on these results, we fixed the clutch size for inexperienced breeders at 81% of that selected for experienced breeders, and set the percentage of eggs that survived to enter the first immature pool at 30% for inexperienced breeders and 40% of eggs for experienced breeders.

##### *Probability of breeding*

To determine the number of birds that breed each year, we estimated the rate at which inexperienced swans begin to breed (probability of first breeding; Table 1) and the frequency with which swans continue to breed once they have begun (probability to repeat breeding). Although swans are capable of breeding after their first year and most swans have begun breeding by their third year, some do not breed until they are older (Reese 1980; Birkhead & Perrins 1986; Ciaranca, Allin & Jones 1997). Using data from several populations (Reese 1980; Birkhead & Perrins 1986; Ciaranca *et al.* 1997), we determined cumulative probability distributions for the age at which a swan starts to breed and calculated the expected age of a non-breeding bird in the population. We then took the difference in the proportions of

**Table 1.** Parameter values used in the basic model to predict mute swan population dynamics

| Parameter  | Value           | Source                          |
|--|-----------------|---------------------------------|
| Juvenile survival ( $\pm$ SE)<br>(fledging to April of first year)             | $0.68 \pm 0.04$ | Watola <i>et al.</i> (2003)     |
| Immature survival ( $\pm$ SE)<br>(April of first year to April of second year) | $0.73 \pm 0.02$ | Watola <i>et al.</i> (2003)     |
| Non-breeder survival ( $\pm$ SE)   | $0.71 \pm 0.02$ | Watola <i>et al.</i> (2003)     |
| Breeder survival ( $\pm$ SE)   | $0.90 \pm 0.02$ | Watola <i>et al.</i> (2003)     |
| Annual mean clutch size ( $\pm$ SE)  | $5.9 \pm 2.2$   | Perrins & Reynolds (1967)       |
| Ratio of average clutch sizes of<br>inexperienced to experienced breeders      | 0.81            | Birkhead, Bacon & Walter (1983) |
| Survival from eggs to fledging:<br>inexperienced breeder nests                 | 0.30            | Birkhead, Bacon & Walter (1983) |
| Survival from eggs to fledging:<br>experienced breeder nests                   | 0.40            | Birkhead, Bacon & Walter (1983) |
| Probability of first breeding  | 0.45            | Birkhead & Perrins (1986)       |
| Probability of continuing breeding   | 0.90            | see text                        |

birds breeding between the expected age and the following year to find the average proportion of non-breeding birds that begin breeding each year. This estimate ranged from 15% to 45% for different populations. In preliminary analyses, we found that values less than 40% underestimated the population growth observed in North American populations. We therefore set the probability of first breeding at 45% to reflect the fact that age of first breeding is likely to be at the younger end of the range for introduced populations in which density-dependent competition is unlikely to play a role (cf. Newton 1998).

Available information suggests that, once a swan has bred, the probability that it will breed in the subsequent year is very high. For instance, Reese (1980) found that 98% of females and 89% of males aged 6–20 nested each year in Chesapeake Bay, USA. Birkhead & Perrins (1986) suggest that up to 20–30% of pairs do not breed each year, but this figure includes inexperienced birds that have paired but not yet attempted to breed. We set the probability of repeat breeding at 90%.

#### TESTING THE MODEL

To test the model's accuracy, we conducted an initial set of simulations to determine how well we could predict growth of newly established populations. Population data came from the CBC, which has been conducted annually since 1900 and involves thousands of birdwatchers across North America (Butcher 1990; National Audubon Society 2004). The CBC does not exhaustively census populations but, for a large, conspicuous, aquatic species that forms concentrated flocks during winter, it probably provides a good index of population growth. In certain areas, such as the state of Connecticut and southern New York, the CBC covers much of the coastline, where most swans occur in winter, and a large proportion of the swan population is probably counted. The CBC also dates back to the years before swans became established and provides the only quantitative record of the species' entire population history in North America.

For our projections, we assumed an initial population of 15 experienced breeders, because CBC population data suggest that mute swan populations do not show consistent growth until populations contain 15–20 individuals (National Audubon Society 2004). As we were interested only in the growth of established populations, we did not start simulations until after consistent growth could be expected. Initial analyses showed that projections were most accurate if all of the starting individuals were placed in the experienced breeder stage. We later tested the effect of this assumption in our sensitivity analysis. Using these initial conditions, we ran 500 simulations of our basic model and calculated, for each year, a mean population size and the interval containing 95% of the obtained population sizes. We then compared the predicted growth to the observed CBC data.

#### SENSITIVITY ANALYSIS

We first tested the sensitivity of the exponential growth rate ( $r$ ) predicted by our model to error in the parameters for which estimates were based on limited data, inferred or measures of uncertainty were unavailable. These parameters included both of the breeding probabilities, both of the probabilities that influence whether an egg survives to enter the model, and the percentage difference in average clutch size between experienced and inexperienced breeders. For each of these parameters, we determined the growth rate across all plausible values by changing the parameter value in 0.01-increments between 0 and 1. For each possible value, the growth rate was calculated at every time step by solving an exponential growth equation then averaging 500 simulations, each of which started with 10 000 individuals in a stage distribution corresponding to the largest eigenvalue. We also tested the sensitivity of the model's predictions to changes in the distribution of individuals among stages. We randomly arranged the starting individuals among the groups and projected population growth with the original matrix. We ran simulations for 500 random arrangements and calculated the maximum and minimum population sizes predicted in each year over a 40-year interval.

In the second phase of our sensitivity analysis, we varied the parameters that provide information about the effectiveness of proposed management options. To examine the effects of changing survival rates, we calculated the predicted growth rate over the entire range of plausible values (0–1) in 0.01 increments. To test the effect of changes in the average clutch size, we systematically decreased the mean value in 1% increments from the original value of 5.9–0. For each scenario, we calculated the predicted growth rate from 500 simulations. These changes simulated the effects of culling (or removing; Sladen & Rininger 2004) swans or preventing successful nesting, respectively.

Because management options are not limited to one control method, we also examined the effectiveness of strategies that combined methods. We estimated the effect of reducing survival and reproduction simultaneously by calculating the growth rate under different combinations of decreased reproduction and survival. Survival decreases were applied to all stages equally to reflect the situation where managers cannot selectively cull individuals based on age or breeding status. For this analysis, the parameters were sequentially reduced in 1% increments from the current value to 0. We ran 100 simulations for each combination of parameter values, then found the points at which 10%, 50% and 90% of the simulations had final population sizes that were smaller than the initial population size. The 90% threshold was considered to be appropriate for making management recommendations because it represents conditions at which a set of proposed actions can be expected to have a 90% chance of success.

EVALUATING OPTIONS FOR REDUCING  
POPULATION SIZE

Our sensitivity analysis tested the efficacy of different management options by comparing population growth rates arising from changes in one or more parameter values. Other factors, however, are involved in determining the ultimate success of a management strategy. For example, if decreases in one parameter are difficult or costly to achieve, then another method that is simpler or cheaper might be more desirable, even if it is less biologically efficient. Using cost estimates from the Connecticut Department of Environmental Protection (M. Huang, personal communication), we evaluated the cost efficiency of culling swans compared with destroying nests. It was estimated that a team of four or five officials could cull *c.* 50 swans day<sup>-1</sup> and that a team of two people could initially destroy 10–15 nests day<sup>-1</sup>. The rate of nest destruction, however, was estimated to decline to around five nests day<sup>-1</sup> after the first *c.* 40 nests had been destroyed because of increased travel and searching times. To calculate the costs required to achieve a certain growth rate, we first calculated the percentage reduction in survival or reproduction required to reach a given target growth rate. We then applied that percentage to a population of 2000 birds, to most closely replicate the situation from which our cost estimates were constructed, and used these estimates to calculate the cost for each management plan in terms of the number of person-days required to reach these goals in the first year. We repeated this calculation for target growth rates of 0.05, 0, -0.05, -0.1 and -0.15.

Given public concerns over the killing of swans (Feral 2004), we also estimated the cumulative mortality that would be needed to achieve a given population size under different culling regimes. This information could be used to identify regimes that minimize the number of birds that need to be killed to meet certain goals. For this analysis, we examined four hypothetical scenarios. In the first two scenarios, populations were reduced from 500 individuals to a target population of 200 individuals within either 5 or 20 years. We calculated the maximum (i.e. the least negative) growth rate needed to reach the target population size within the given time period using an exponential growth equation. Using results from our sensitivity analysis, we selected the lowest mortality rates that would achieve the management goal. We then ran 500 simulations for each scenario and determined the number of individuals removed from the population in each year of the simulation. In each case, management switched to maintain the target population size as soon as the target was reached. During this maintenance phase, breeder survivorship had to be 14.6% below the natural level to prevent renewed population growth. In the second two scenarios, we simulated eradication from an initial population of 200 individuals within either 5 or 20 years. We used the growth rate used in the maintenance phase for the previous two scenarios and distributed additional deaths randomly

among the model's six stages. Using 500 simulations, we calculated the mean number of swans that must be removed to eradicate the population under each strategy.

## Results

## MODEL EVALUATION

The model predicted an exponential growth rate (*r*) of  $0.133 \pm 5.7 \times 10^{-3}$ , implying that an introduced mute swan population has a doubling time of approximately 5 years in the initial growth phase after establishment. The growth predicted by the model matched that shown by the Atlantic Coast population for approximately 35 years after establishment (Fig. 2a), after which growth of actual populations slowed. Data from southern New England, where colonization began and thus where density dependence is probably strongest, suggested that growth slows after 25–30 years at more local scales (Fig. 2b).

## SENSITIVITY ANALYSIS

For the first part of the sensitivity analysis, we systematically altered the model to test whether it was robust to uncertainty in parameter estimates. For five variables describing whether a swan breeds and how many young they produce, we found little evidence that small errors in parameter values would influence our results (Fig. 3). Our analysis showed a non-linear relationship between the growth rate and both the probability of first breeding and the probability of continued breeding. Small changes made near the current values did not

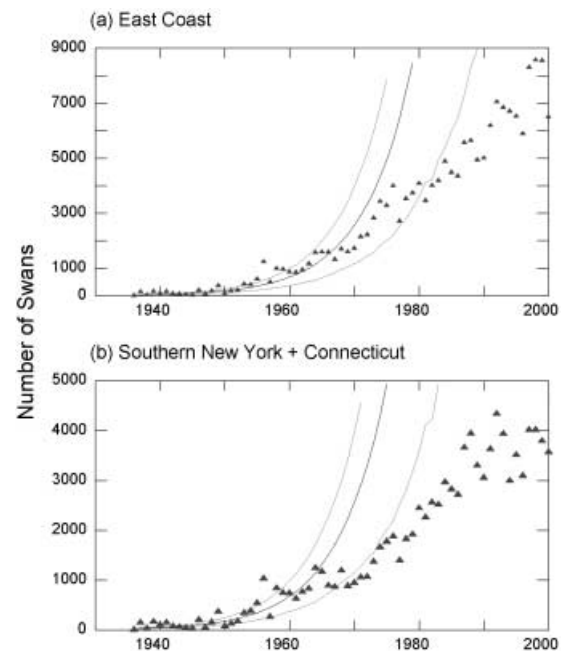
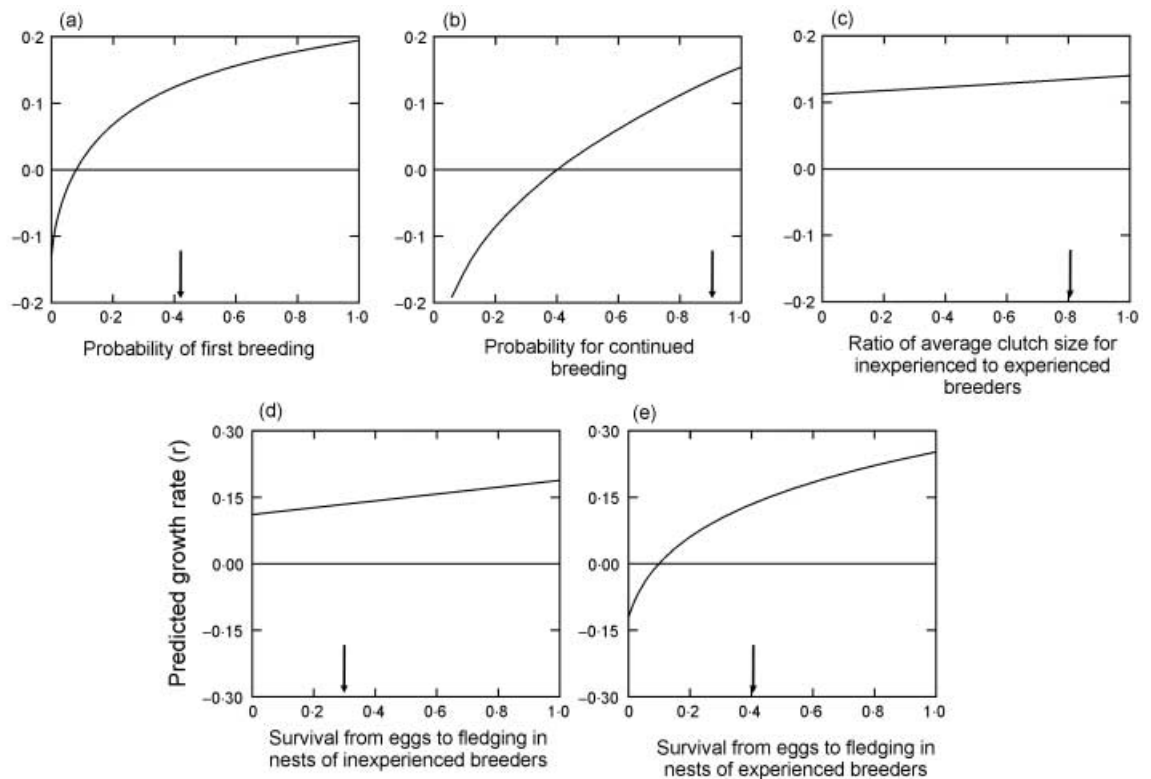


Fig. 2. Mean population sizes (solid line) predicted by the model with a 95% prediction interval compared with the CBC population data (triangles) from (a) the entire Atlantic coast and (b) southern New York and Connecticut between 1930 and 2000.



**Fig. 3.** Sensitivity of population growth rate to changes in the (a) probability of first breeding, (b) probability of continued breeding, (c) ratio of mean clutch sizes in the nests of inexperienced vs. experienced breeders, (d) survival of eggs to fledging in nests of inexperienced breeders and (e) survival of eggs to fledging in nests of experienced breeders. The predicted growth rate for each value of a parameter is shown, with arrows pointing to the value used in our basic model.

greatly affect predicted growth rates for either parameter, and substantially lower breeding probabilities were required to achieve population declines (Fig. 3a,b). Varying clutch size differences between inexperienced and experienced breeders or the survival of eggs to fledglings from the nests of inexperienced breeders had almost no effect on the predicted growth rate (Fig. 3c,d), suggesting that first-time breeders have little effect on population trajectories. Not surprisingly, changing the probability of an experienced breeder's egg surviving to enter the model had a greater impact on the growth rate, although small changes still had only a limited effect. This probability would have to decline from our estimate of 0.4 to 0.1 to produce a stable population.

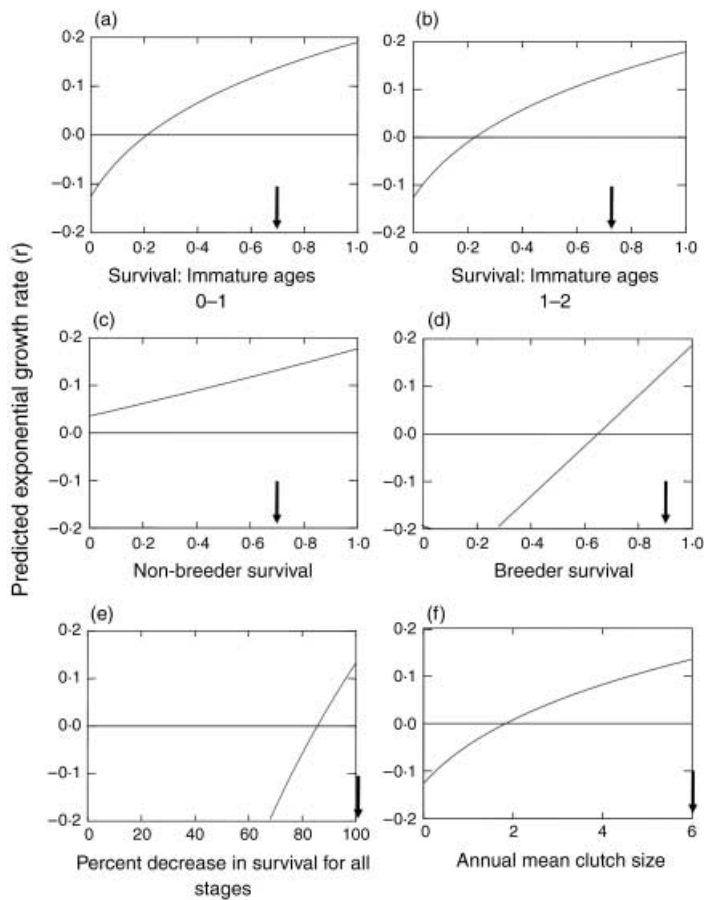
The initial distribution of individuals across stages only affected growth rates for the first few iterations of our model, but predicted population sizes were affected for the entire simulation. Population estimates were highest when all individuals started in the experienced breeder stage, because this stage contributed most to future generations.

In the second part of our analysis, we systematically lowered parameter values for the average survival and reproduction rates to simulate management actions designed to reduce population growth (Fig. 4). These simulations showed that growth was most sensitive to breeder survival rates, with a decrease from 0.90 to 0.65 required to stabilize growth (Fig. 4d). Immature survival (for ages 0–1 and ages 1–2) and mean clutch size needed to be reduced more substantially to achieve

similar results (Fig. 4a,b,f). Non-breeder survival had little effect on growth rate; even if reduced to zero, the population would still increase (Fig. 4c). Decreasing survival in all stages simultaneously created large changes in the predicted growth rate (Fig. 4e); on average, a decrease of 14.6% (90% confidence interval 13.0–16.3%) was needed to stabilize a population. The combined effects of changing survival and clutch size parameters simultaneously, to examine the trade-off between management alternatives, are shown in Fig. 5a. As uncertainty in parameter values creates uncertainty in the placement of each contour, we constructed a 90% confidence interval around the  $r = 0$  contour (Fig. 5b). To have high confidence that control measures will be successful, managers need to achieve combinations of survival and reproduction rates that lie above and to the right of this interval's upper bound. Similar uncertainty is associated with all contours, but these confidence intervals are not shown for visual clarity. Deterministic population projections based on the growth rates associated with each contour are also shown in order to illustrate how long it would take to achieve control under different management scenarios (Fig. 5c).

#### EVALUATING OPTIONS FOR REDUCING POPULATION SIZE

Using cost estimates from the Connecticut Department of Environmental Protection, we found that reducing



**Fig. 4.** Sensitivity of population growth rate to changes in (a) immature ages 0–1 survival, (b) immature ages 1–2 survival, (c) non-breeder survival, (d) breeder survival, (e) decreased survival in all groups and (f) mean clutch size. The predicted growth rate for each value of a parameter is shown, with arrows pointing to the value used in our basic model.

the growth rate for a population of 2000 swans via nest or egg destruction would require three to four times as many person-days within the first year as the same reduction through culling individuals. For the highest target growth rate that we tested ( $r = 0.05$ ), the number of person-days needed to reach the target was four times greater for nest destruction than for culling (73 vs. 18). For a target of  $r = -0.1$ , the ratio decreased to 3:1, with 159 person-days for nest destruction compared with 56 for culling. The lowest growth rate we tested ( $r = -0.15$ ) could not be achieved via nest destruction alone.

To estimate the cumulative mortality under different culling regimes, we reduced survival in all groups simultaneously because the sensitivity analysis showed that survival had the greatest effect on growth rate. We found that we could reduce the population from 500 to 200 individuals within 20 years by lowering the average survival in all classes by 19.7%, producing  $r = -0.046$ . To reach the target population size within 5 years, the average survival had to be reduced by 32.5% ( $r = -0.183$ ). After a 20-year period, 37% (260) more swans would have been killed under the 20-year plan compared with the 5-year plan. To eradicate a population of 200 swans within 5 years, our model predicted that a

total of 210 birds would need to be killed or otherwise removed. Taking a less aggressive approach, and spreading the mortality over 20 years, would increase the number of swans that need to be removed by 78%, to a total of 373 birds.

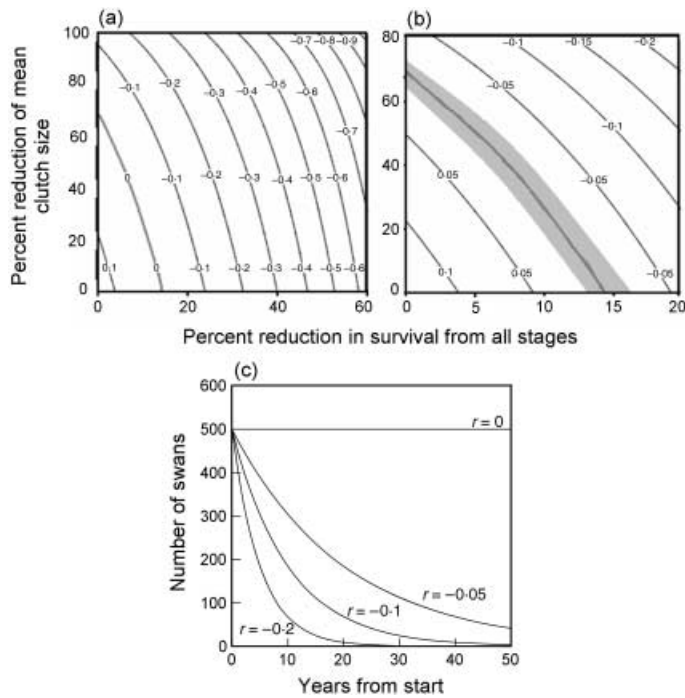
## Discussion

By their very nature, invasive species are hard to control. To become invasive, species are likely to have life-history characteristics that predispose them to population persistence and rapid population growth. Moreover, species are typically not identified as invasive until they have achieved large populations and spread across a considerable area (Mack *et al.* 2000). Limiting or reversing population growth therefore is usually hard to accomplish and may require considerable economic resources (Mack *et al.* 2000; Simberloff, Parker & Windle 2005). For charismatic and attractive species, implementing control is further complicated by the competing views that some introduced species provide aesthetic or other value to society, or because there are ethical concerns over the killing of large numbers of animals (Feral 2004).

Proposed control programmes can therefore benefit from a thorough evaluation of the likely consequences of their implementation. Given the economic costs and ethical concerns, it is paramount that any proposed programme has a high chance of succeeding if implemented. Managers, for example, need to know how much effort will be required to achieve their goals, so that they can evaluate what resources are needed to ensure success. Equally, to balance ethical concerns with management objectives, one would wish to minimize the numbers of individuals that are killed and ensure that culling actually reduces the threat to native ecosystems. We thus recommend the routine use of stochastic models that account fully for parameter uncertainty and allow the identification of confidence intervals around the location of important thresholds. Determining the boundaries of such intervals will provide managers with far greater confidence that management will work than if they rely on results based only on average conditions.

Analysis of our model shows that management that reduces reproductive rates, without changing survival rates, is unlikely to be an efficient strategy for reducing mute swan populations. On average, our simulations suggest that at least 72% of the nests would need to be destroyed annually to ensure a 90% chance of a decline (Fig. 5). Alternatively, the same goal could be reached by culling or removing at least 17% of the individuals in the population annually. To reduce populations substantially, the number of individuals targeted must be even greater and will require a long-term commitment from managers. For instance, to reduce a population of 500 individuals to 200 individuals within 10 years will require managers to find and destroy more than 95% of the nests every year (Fig. 5a,b). Removing birds from





**Fig. 5.** (a) Contour plot showing the population growth rates ( $r$ ) predicted for each combination of decreased survival (all age classes) and decreased mean clutch size. For example, if a manager was to lower both survival and mean clutch size by 20%, the model predicts a growth rate of approximately  $-0.1$ . Assuming that both management strategies require equal amounts of effort, a given growth rate is achieved most efficiently when the distance between the origin (which represents the values used in the basic model) and the contour for that growth rate is minimized. (b) Enlarged portion of plot (a) to illustrate the 90% prediction interval (shaded region) around the contour that represents no population growth ( $r = 0$ ). To ensure at least a 90% chance of stabilizing population growth, combinations of parameter values that lie to the right of this interval's upper boundary must be used. Graph (c) relates the predicted growth rates found in (a) to the number of years to extinction for a population starting with 500 individuals.

a population is often considered impractical except for very small populations, because of the limited options for relocating birds. Eradication is therefore unlikely to be possible without killing birds, and even this option is likely to require a long-term commitment unless high mortality rates can be achieved. For example, even if managers reduced survival by a third, it would still take at least 20 years to eradicate a population of 500 swans (Fig. 5c). Hughes, Kirby & Rowcliffe (1999) provide similar results from other systems.

The costs and number of swans targeted will depend on the period of time allotted to reach management goals. As expected, increasing the time frame increases the overall number of individuals that must be targeted. In our simulations, the number of swans that must be killed to reach target population sizes was increased by nearly 80% when management was spread over 20 years compared with a 5-year scenario.

The growth rate predicted by our model agrees quite closely with estimates for recently established populations from different parts of North America (Reese 1980; Allin, Chasko & Husband 1987; Petrie & Francis 2003; National Audubon Society 2004; Fig. 2). This result suggests that, although our data come from various

sources and several populations, they can be generalized and should apply to many swan populations during the first few decades after establishment. In contrast, current estimates for growth rates in the long-established Atlantic coast population are distinctly lower than our model predicts (Atlantic Flyway Council 2003). CBC data from New York and Connecticut suggest that these populations have become relatively stable within the last decade, while survey data for the entire USA east coast show reducing rates of increase (National Audubon Society 2004). These findings suggest that our results may be less accurate after the initial few decades of population growth.

Presumably, the difference between the predicted growth rates and estimates from populations that have been established for several decades results from negative density dependence in demographic rates. Data on density dependence in mute swans have only recently become available (Nummi & Saari 2003) and the relationship between the absolute number of swans in an area and the effective density, after correcting for the amount of suitable habitat within a broad study area, is not well characterized. Thus we lacked adequate data to include density dependence in our model. Based on our sensitivity analysis (Figs 3–5), however, likely changes in certain parameters as a result of density dependence could easily produce growth rates that match those currently found in Atlantic coast populations. For example, Nummi & Saari (2003) reported that the number of fledged young per pair decreased from 5 to  $< 1$  as the number of pairs in their study population increased. This decrease (in place of clutch size and egg to fledging survival in our model) produces a growth rate of 0.036, which is similar to current growth rates. Lower values for the probability of first breeding calculated from Birkhead & Perrins (1986) produce a similar effect (Fig. 3a).

Although the omission of density dependence is a well-founded criticism of many demographic models (Morris & Doak 2002), our results are consistent with actual population dynamics during the first few decades of population growth. The presence of density dependence would mean that our model underestimates the number of individuals that would have to be affected by management in more established populations, as removing individuals from a population would cause an improvement in demographic rates that had been depressed by density. This result is illustrated empirically by an egg-addling programme implemented in Rhode Island, USA. From 1979 to 2000 (after density dependence appears to have begun to slow population growth; Fig. 2), eggs from approximately 79% of nests were destroyed and yet the population continued to grow (Allin & Husband 2004). Similarly, as the availability of breeding territories becomes more limiting, the effect of removing breeders will probably have much less of an impact on growth rates, as removed breeders would simply be replaced by non-breeders (Watola *et al.* 2003). Therefore for well-established populations, even

greater management efforts than our model predicts are likely to be needed for control to work.

As is the case for many charismatic species, population control for mute swans has been controversial. The problems caused by invasive species have only recently begun to gain public attention and, frequently, this awareness is limited to isolated or local situations (Simberloff, Parker & Windle 2005). Even among biologists, there can be conflict over the most appropriate way of dealing with introduced species (Soule 1990; Bomford & O'Brien 1995). Long-term success of control projects therefore often depends on building strong support both from management staff and the public (Bomford & O'Brien 1995; Courchamp, Chapuis & Pascal 2003). Faced with this challenge, it becomes increasingly important to build a solid biological basis behind arguments for control. A greater use of stochastic models that describe model uncertainty will help to ensure that control efforts actually achieve their intended goals. Doing this is important, not only because of the need to avoid wasted management efforts, but also because ethical concerns are only exacerbated when a cull fails to provide its intended benefits. Unsuccessful control efforts, such as the attempted eradication of European blackbirds *Turdus merula* from Tasmania in the 1940s (Guiler 1982), are not only regretful because of the loss of funds and the killing of animals to no effect, but also because they often make it more difficult to build public support in future situations where control is necessary and appropriate. Addressing economic and ethical concerns as part of the management assessment process might also lessen controversy. For instance, when culling is the only method that is likely to achieve management goals, it would be valuable to identify strategies that minimize the number of animals that must be killed (e.g. by altering the time line or by combining culls with other control methods; Fig. 5). Population models, as used here, provide a means to investigate both the probable success of proposed control efforts and social issues that impinge on their acceptance within a broad spectrum of society.

#### MANAGEMENT RECOMMENDATIONS

Evidence that introduced mute swan populations harm native species is limited but population control is often considered necessary because of the potential for detrimental effects on native species. If control is to be implemented, our model suggests that reducing adult survival (e.g. through culling) will be much more effective and less costly than reducing reproductive rates (e.g. through nest destruction). Moreover, imposing high mortality over a short period will minimize the total number of swans that need to be killed to meet a given population target.

To ensure a high chance that a growing swan population will decline, our models predict that managers will need to destroy more than 72% of the nests every year, or kill at least 17% of the adults. Unless this effort

can be sustained over many years, control is unlikely to work and perhaps should not be considered.

Our model describes the effects of management implemented during the early phase of population growth. Based on the empirical data used to test our model predictions, we anticipate that density dependence will begin to occur after two to three decades of growth. At this point the extent to which the management methods examined in this paper will reduce growth rates is unknown. It is expected, however, that the effort required to stabilize or reduce growth rates will greatly increase as a population becomes more established. Consequently, an even greater commitment will be required to control populations than is shown by our results, and the concomitant costs, both economic and in terms of the number of birds that must be killed, will be far greater.

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