The introduction and naturalisation of birds

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Population models and their relevance to prediction of trends in naturalised populations and management implications

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Mathematical models can be useful in the analysis of the processes that regulate animal populations but are often avoided due to their apparent complexity. This paper reviews the approaches to modelling with regard to the amount and quality of available data. Models may be used to estimate rates of population growth and geographical spread, effort needed to constrain a pest population at a given level, the amount of damage a species may cause, and the likelihood that a naturalised population might become extinct. In addition, simple models can and should be used to verify the accuracy of data on population processes, to ascertain what degree of accuracy is required for data that have yet to be collected, and to determine the relative importance of parameters such as fecundity, mortality and dispersal in the establishment or maintenance of particular populations. Relevant examples and approaches are given for various problems in avian and mammalian population biology. It is hoped that a greater understanding of such models will lead to greater use, and a more critical scepticism of their findings.

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Introduction

Mathematical models are simplifications of complex systems. Ideally they should be produced on the principle of parsimony, including essential components only, and following Occam's razor by using the minimum number of assumptions. Although most mathematical notation cannot be considered 'simple', the growth of many populations can be described by a single equation.

All models and their results should be considered with a healthy scepticism, and neither blindly accepted nor dismissed out of hand. Models are generally produced for a limited number of purposes and their use should be limited to these areas. It is important to express models in plain English so that their assumptions are open to criticism, and their limitations may be understood (Bross 1971). Verification and validation are necessary steps during model production, and sensitivity analysis of more complex models should be performed to help understand limitations of the output based on the accuracy of the input data. Current computing power is such that computer models of all types are now very easy to produce and analyse, where previously this would have been a truly Malthusian task. One important aspect when considering computer models of populations, is the reliance that can be placed upon their results. Where sufficient information is available exact confidence intervals can be produced (Alvarez-Buylla & Slatkin 1991). If information is more limited, or such mathematical precision is not required, then a confidence range can be considered. For example, in estimating population growth rates, the lowest estimate at time *0* and the highest estimate at time *t* (and *vice versa*) can be used to calculate two growth rates which identify extreme limits.

Models

Population models can take various approaches and there are a number of good introductions to population modelling (e.g. Jeffers 1978; Starfield & Bleloch 1986). In general, such models can be classified into three areas: statistical models (e.g. analysis of variance), mathematical models (e.g. differential and difference equations) and simulation models (e.g. Monte Carlo models).

Holling (1978) recognised four classes of modelling problems (Figure 1). Area 1 is the region of good data but little understanding. This is the area of statistical modelling to analyse data and search for relationships. Area 3 has both good data and understanding. Many aspects of the physical sciences belong here, and exact reliable models are routinely used. Areas 2 and 4 are characterised by limited data and various degrees of understanding of the structure of the problem, and are thus more pertinent to biological problems. It is these areas where computer modelling can be invaluable. It is a

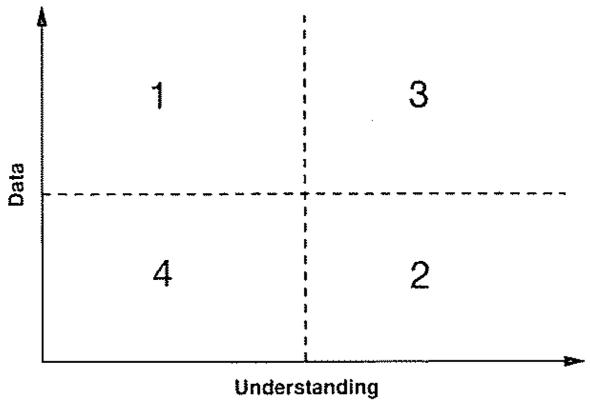

Figure 1. Holling's (1978) classification of modelling problems. Area 1 is the region for statistical analyses, area 3 covers the physical sciences, and areas 2 and 4 cover the majority of biological problems.

common misconception that modelling in biology cannot proceed with only limited data, and modelling is often put off until much data have been collected. In general, many required parameters can be derived or estimated, and a model constructed. Parsimonious model construction can be used to determine exactly what data are required, and sensitivity analysis to determine what accuracy is necessary for these parameters. Deliberate or accidental introduction of a species outside its natural range is an area where often limited data are available since survival rates and breeding success may vary significantly from those found at the site of origin.

For any population to colonise new habitats successfully it must become established, it must have a positive growth rate and be able to spread, and must avoid extinction. Establishment and extinction of a small population are so dependent on the variation in natural mortality and fecundity of a few individuals, that we should only model them stochastically, which will result in defining the probabilities of establishment or extinction. For example, modelling could be used to produce a probability of which of the 530 known exotic bird introductions (Long 1981) would become established, but could never have exactly predicted which 127 species would have succeeded.

Simple population models can also be used to cross-check demographic parameters (fecundity, mortality and dispersal) with population censuses, and determine to which parameters the population is most sensitive. This is now being commonly performed in many population management studies (e.g. foxes, Harris & Smith 1987; rabbits, Smith & Trout 1994) and conservation studies (e.g. black duck, Blandin 1992).

Prediction of population trends

The annual rate of population growth can be estimated indirectly from known population parameters, or directly from a minimum of two censuses; ideally either two exact population counts or two exact geographical distributions. The former assumes that geographical spread has not occurred and the latter that breeding density has not changed. Table 1 gives estimated rates of population growth, r, for a number of species in Britain. These have been derived from different censuses during different years and are therefore only examples. For comparison, estimated population growth rates are also given for some species which are not introduced. These figures are derived from the equation

$$r = \log_e (N_t / N_0) / t,$$

where t is the time in years between population estimates N_0 and N_t. A species with $r = 0.1$, will be growing at 10% per annum, while a result of $r = -0.1$ will result in a 10% decline per annum. From Table 1 it can be seen that the ruddy duck *Oxyura jamaicensis* and the rose-ringed parakeet *Psittacula*

Table 1. Estimated rates of population growth, r, for some example bird species in Britain over the period given, where $r = log_e (N_t/N_0)/t$ and t is the time in years between population estimates N_o and N_t. Group I concerns naturalised populations, and group II native ones. Population census data derived from Sharrock (1976), Lack (1986), Kear (1990), Marchant *et al.* (1990) and Gibbons, Reid & Chapman (1993).

Species	*r*	*Period*
Group I		
Ruddy duck *Oxyura jamaicensis*	0.140	1963-1989
Rose-ringed parakeet *Psittacula krameri*	0.131	1970-1990
Canada goose *Branta canadensis*	0.093	1972-1991
Naturalised Greylag goose *Anser anser*	0.089	1970-1986
Mandarin duck *Aix galericulata*	0.066	1972-1991
Egyptian goose *Alopochen aegyptiacus*	0.030	1963-1991
Group II		
Goldeneye *Bucephala clangula*	0.139	1982-1990
Collared dove *Streptopelia decaocto*	0.125	1964-1970
Ringed plover *Charadrius hiaticula*	0.034	1974-1984
Chaffinch *Fringilla coelebs*	0.018	1969-1988
Goldcrest *Regulus regulus*	0.003	1970-1988
Teal *Anas crecca*	-0.032	1972-1991

krameri are the introduced species with the most rapidly growing populations, growing at 14% and 13% per annum respectively. This is about as fast as the goldeneye *Bucephala clangula*, or the collared dove *Streptopelia decaocto* during the late 1960s. Such an approach, even in the absence of comprehensive data, may indicate whether a species is likely to become widespread, and thus permit targeting resources toward monitoring. However, care must always be taken when producing results based on only two censuses. The goldcrest *Regulus regulus* example shows a stable population that hides fluctuations in the intervening years.

The speed of spread of an established population may be calculated from simple equations (Taylor 1980; Murray 1988):

$$V = 2\,(rD)^{1/2},$$

where the speed of advance, V (km yr^{-1}), is derived from the net birth rate, r, and a diffusion coefficient, D (km^2yr^{-1}), the annual increase in area of a population. This technique would be best suited to non-migratory birds. Indeed the more sedentary and localised the species, the better the calculation. However, the derivation of the net birth rate for localised exotic species would be hard to estimate with accuracy.

Management implications

Models to aid in the control of pest species can be easily produced using a classic logistic growth equation, plus a term to represent control. Figure 2 is derived from data on coypu *Myocastor coypus* population expansion and control (Gosling & Baker 1991). The coypu was declared eradicated within nine years of the start of organised control. The solid line in Figure 2, representing the annual level of control actually achieved, shows that the *a priori* requirement of a number of hard winters to further reduce survival was necessary to achieve control within the ten year period. If the level of control had been just 10% less (dashed line in Figure 2) this model shows that it is unlikely that control would have been successful. In addition, this model can be used to estimate the relative level of economic damage caused by a pest while undergoing different levels of control. If the level of damage is directly proportional to the number of individuals, and the number of years for which they are present, then the relative levels of damage can be estimated by the integral (area under the curve) of the graph under different control regimes. This simple approach can

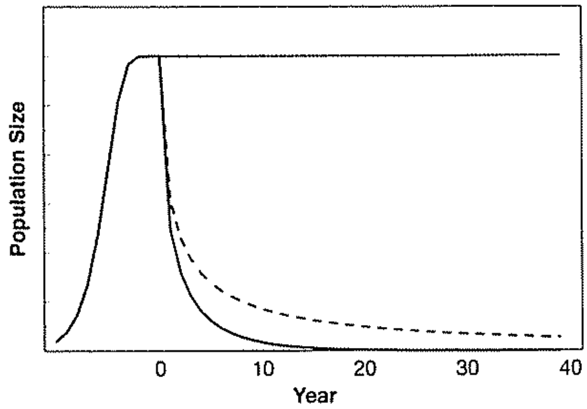

Figure 2. Graph showing the population size of a pest following three levels of control: dotted line, no control (assuming no further population growth); dashed line, 41% control per annum; solid line, 51% control per annum. The graph is based on the logistic equation using population parameters relevant to the coypu.

be used as a crude estimate of potential damage caused by populations subject to different levels of control. When the cost of such control is included, the cost-benefit of all options can be evaluated by policy makers and landowners alike. This approach is currently in use by MAFF to predict damage caused by different pest species.

Another approach to modelling the options for control is computer simulation modelling generally written in BASIC or FORTRAN, although a number of computer packages are now available (e.g. RAMAS, Ferson (1990); VORTEX, Lacy (1993); Model Maker by SB Technology; Matchcad by Mathsoft Inc.). Using this approach spatial details can be included. Figure 3 shows the spatial

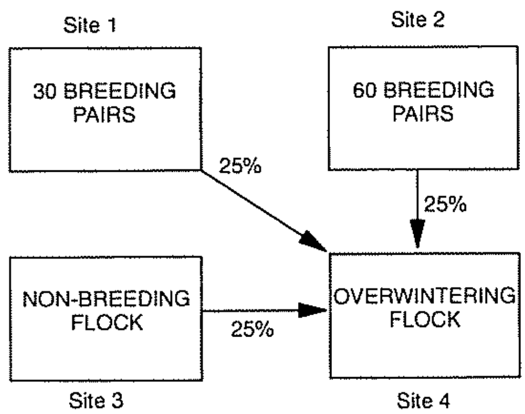

Figure 3. The spatial organisation of four simulated flocks of geese showing the over-wintering transfer of birds between sites.

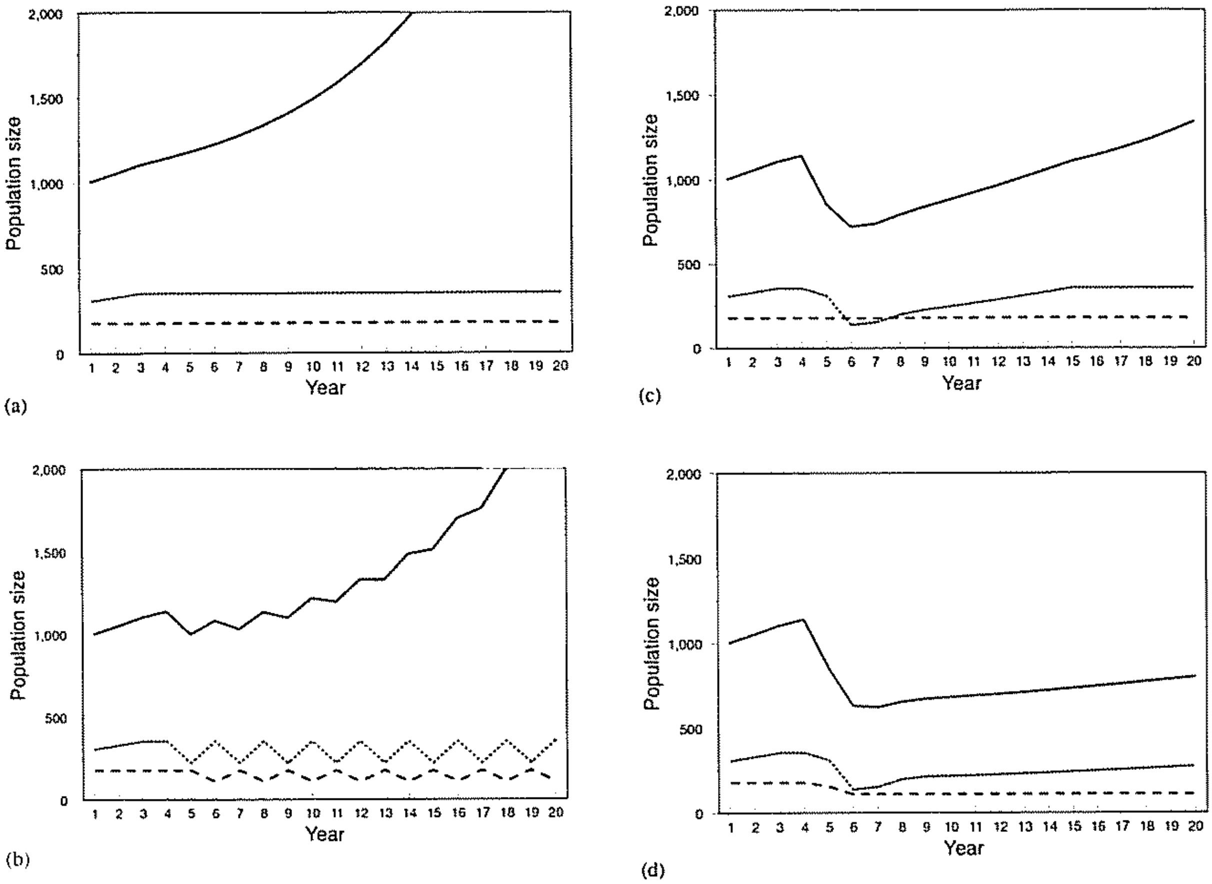

Figure 4. The population size of Canada geese at the simulated sites in Figure 3. The total population size (solid line), population of site 1 (dashed line) and site 2 (dotted line) are shown. These graphs represent no control (a), continuing 50% egg control (b), a single 50% cull (c), and combined cull and egg control (d).

arrangement and interaction of four simulated flocks of Canada geese *Branta canadensis*. Site 1 is the preferred location for breeding geese and site 3 accepts the overflow of geese unable to find a breeding space at sites 1 or 2. 25% of the geese from each of the sites 1, 2 and 3 move to site 4 to overwinter.

Figure 4 shows the results of population growth following four control strategies: no control (Figure 4a), 50% egg control at sites 1 and 2 in alternate years (Figure 4b), 50% cull at all sites in year 4 (Figure 4c), and 50% cull at all sites in year 4 followed by 50% egg control at site 1 in each of the following years (Figure 4d). The solid line shows the total population size and the broken lines the population sizes at the two breeding sites. From this it can be seen that egg control alone is unlikely to markedly affect population growth, and that a cull approximately every ten years, or a cull followed by constant egg control is necessary to maintain a low population size. This simplified model was based on age specific survival rates, and has not yet been tested in the wild. Models with such specific assumptions are of immense benefit in regional population control, where it is important to integrate control policies in different locations.

Conclusion

Simple mathematical models are available to estimate many of the requirements of population researchers, from estimating population parameters, to growth rates and level of control required to constrain or eradicate pest species. The simplest of such models require only population estimates, but population control models benefit from age- and possible sex-specific parameter estimates. The theory of such models is now well understood, but although many approaches to modelling populations are available, and despite the advances in speed of modern computers, such models are commonly under-utilised.

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