Evaluating Population Management Scenarios: Crunching the Numbers before Going to the Field

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ABSTRACT: Efforts to mitigate wildlife-human conflicts typically involve management of unacceptably abundant populations. Increasingly, however, reduction of dense or increasing populations of certain wild species evokes both support and contention from the public. Management decisions involving population reduction, particularly those directed at highly visible species, should therefore be based on quantitative evaluation of potential outcomes prior to implementation. The purpose of this paper is to revisit a call for use of population modeling in management decisions by reviewing basic aspects of population analysis and the use of publicly available long-term data sets in environmental assessments and impact statements. Our objectives are to discuss 1) the relationship of population parameters to population growth, 2) methods of population projection, 3) use of data for model calibration and validation, and 4) the evaluation of management scenarios. Justification and defense of lethal or reproductive control programs to solve vertebrate pest problems requires a sound understanding of population status and the dynamics of the problem species.

KEY WORDS: model, population dynamics, wildlife damage management

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INTRODUCTION

Agricultural and urban expansion, associated misuse of natural resources, over-hunting, and trade hunting world-wide has resulted in habitat degradation, species extinction, fragmentation of habitat and wild populations, and loss or inhibition of natural population regulatory mechanisms. Consequently, wildlife biologists, particularly in Western Europe and the Americas, have over the last century focused management in the areas of habitat and species conservation.

In North America, society has subsequently witnessed dramatic recoveries and population increases in species such as the white-tailed deer (*Odocoileus virginianus*), Canada goose (*Branta canadensis*), double-crested cormorant (*Phalacrocorax auritus*), and wild turkey (*Meleagris gallopavo*) (Price and Weseloh 1986, Vangilder and Kurzejeski 1995, Ankney 1996) due to effective management and environmental programs. Species such as the raccoon (*Procyon lotor*), red-winged blackbird (*Agelaius phoeniceus*), common raven (*Corvus corax*), Canada goose, and gulls (*Larus* spp.) have also exhibited marked population increases over the last three decades (Carey and McLean 1983, Belant and Dolbeer 1993, Ankney 1996, Beletsky 1996, Kristan and Boarman 2003), primarily due to their adaptability to human presence in the landscape. Still other species, like the mountain lion (*Puma concolor*), experience progressive loss of habitat, but expand their ranges around human population centers and supplement natural prey with domestic animals (Mansfield and Charlton 1998).

Both superabundant species and those forced into progressively fragmented habitats spur debate over whether and how to manage populations. In fact, there are only three problems in population management: 1) the treatment of reduced or declining populations to increase density, 2) the exploitation of a population as a renewable resource, and 3) the treatment of a population considered as too abundant, or increasing at an unacceptable rate, so as to reduce or stabilize density (Caughley 1977). Further, management intended to reduce a species' population often serves the dual role of species conservation. For example, Bédard et al. (1995, 1999) modelled the effects of lethal removal of nesting double-crested cormorants (*Phalacrocorax auritus*) along the St. Lawrence River, in Quebec, Canada, then implemented the program to protect indigenous vegetation and dependent species from the damages associated with guano accumulation. Increasingly, however, reduction of dense or increasing populations of certain wild species evokes both support and contention from the public (e.g., double-crested cormorants, Blackwell et al. 2002).

The justification and defense of programs that involve some form of lethal or reproductive control to solve problems involving wildlife requires a sound understanding of population status and the dynamics of the problem species (Dolbeer 1998). Management decisions involving population reduction, particularly those directed at highly visible species, should therefore be based on quantitative evaluation of potential outcomes prior to implementation. The purpose of this paper is to revisit a call for use of population modeling in management decisions (Dolbeer 1998) by reviewing basic concepts of population analysis and the use of publicly available long-term data sets in environmental assessments and impact statements. In this effort, we make frequent reference to Graeme Caughley's (1977) in-depth review of the subject, *Analysis of Vertebrate Populations*, and strive to cite other works where helpful reviews are provided. Our objectives are to discuss 1) the relationship of population parameters to population

growth, 2) methods of population projection, 3) use of data for model calibration and validation, and 4) the evaluation of management scenarios.

MEASURING POPULATION CHANGE

Basic Models

Population analysis involves the numerical attributes of a population (e.g., number, sex ratio, age distribution, age-specific survival, rate of increase) together with the properties of the species and its habitat that determine these values (Caughley 1977).

Factors such as predation, hunting pressure, reproductive success, habitat loss, and resource availability and abundance directly affect individuals within the population. Subsequently, the dynamics of the population are reported as the sum of the demographic reactions of each individual (Caughley 1977). For example, the passenger pigeon (*Ectopistes migratorious*), a species whose flocks once were of such numbers that they passed observers over a series of hours, was driven to extinction by a combination of persecution and clearing of mast-producing forests in mid-western and eastern North America (Schorger 1955). Thus, decreased annual survival (i.e., the probability that an individual survives a particular year) combined with decreasing individual reproductive success due to changes in the age and sex structure of pigeon populations, as well as habitat-related factors, precipitated an unrecoverable population decline.

Given that a myriad of factors affect individuals and, subsequently, contribute to the dynamics of a population, what basic species demographic information is necessary to implement population management? The simplest measure of a population's rate of increase or decrease is the ratio of the population sizes at times 0 and t. This approach assumes that the number of animals in the population increases or decreases by a constant ratio, λ (also referred to as the finite rate), with each unit of time t as

$$N_t = N_0 \lambda^t$$

Consequently, the above model projects discrete population growth. However, Lotka (1907a,b; 1939) assumed that population growth would eventually become exponential. Thus, the relationship between population sizes at time 0 and t can be further simplified by replacing λ with e^r, as

$$N_t = N_0 e^{rt}$$

where e, the base of natural (Naperian) logarithms, is constant and r is the variable of exponential rate of increase (see also Caswell 1989, Caughley 1977, Johnson 1994, Gotelli 1995). The intrinsic rate r is related to the population size N at times 0 and t by the equation

$$r = \ln (N_t / N_0) / t$$

Here, r represents the exponential rate at which a population with a stable age distribution grows given unlimited resources (Caughley 1977). In addition, the contribution of different ages to the number of females born at birth pulse zero can then be modeled as

$$1 = \sum_{t=0}^{k} e^{-rt} l_t m_t$$

where l_t and m_t represent age-specific survival and fecundity, respectively (Lotka 1907a,b; 1939; see also reviews by Caughley 1977, Caswell 1989, Gotelli 1995).

Caughley (1977) explains the logic of Lotka's equation through a hypothetical example, as follows. We assume a population whose reproduction is via birth pulses (e.g., within a breeding season), as opposed to a birth-flow population (e.g., humans; Caughley 1977, Caswell 1989). At the birth pulse occurring at time 0 (our assumed starting time), a single female is born. The population is increasing at rate r and, again, we assume that rates of fecundity and survival remain constant. Thus, the number of females born in the previous birth pulse will have been e^{-r} and $l_1 e^{-r}$ will have survived their first year of life to be present in the population at $t = 0$. This same calculation can be extended to each age class; for example, at $t = -3$, e^{-r3} females were born and $l_3 e^{-r3}$ of these individuals survived to be present as 3-year-olds at time 0. Essentially, then, based on constant fecundity and survival rates we are calculating the fractions of individuals from previous birth pulses through the birth pulse at $t = 0$ that are born and survive to contribute to the measure of total births at $t = 0$ of 1 female.

Although Lotka's model incorporates a continuous function, it remains a discrete model. However, if time is viewed in infinitely small steps (a necessity in some analyses), the model can be expressed as an integral equation (i.e., a continuous model; see Gotelli 1995, Caswell 1989):

$$1 = \int_{t=0}^{k} e^{-rt} l_t m_t$$

Thus, this basic modelling approach of incorporating the exponential function can be used to project populations over time and to assess the contribution of each population parameter to r. Further, the exponential model is useful calibrating demographic parameters against an observed rate of increase (e.g., Figure 1, Blackwell et al. 2002).

Model Parameters

Given a projection of population growth, what aspects of a population's dynamics contribute to our measures of increase or decrease? Cleary, the proportion of the population that survives to each age or stage and the corresponding survival rate are primary factors in a population's longevity and increase. A stage-classified population model differs from an age-classified model in that a stage may comprise individuals differing in age, but sharing factors (e.g., foraging experience) known to affect vital rates (Caswell 1989, McDonald and Caswell 1993). Survival and, thus, mortality, for either an age- or stage-classified model can be arranged in table format and presented graphically as a means of tracking components of the population (see Figure 8.1 in Caughley 1977).

Fertility also contributes to a population's increase or decrease. Age- or stage-specific fertility F_s can comprise, for example, the proportion of females that breed PB_s, a measure of the female young fledged per female Fl_s (i.e., fecundity), and a period-specific survival rate (e.g., from fledging through just before age 1) for those young S_0, represented as

$$F_s = PB_s\, Fl_s\, S_0$$

Further, fertility is an elaboration of Lotka's (1907a, b) equation (see above) relating schedules of fecundity and schedules of survival to r. Here, we assume that rates of fecundity and survival may differ by age or stage, but over time they are fixed.

For example, if we assume that our population analysis is based on age of the individuals within the population, the relationship between age-specific fertility and survival at time t and age distribution within the population at time $t + 1$ can be expressed in simultaneous algebraic equations as

$$n_{1(t)}F_1 + n_{2(t)}F_2 + n_{3(t)}F_3 = n_{1(t+1)}$$

$$n_{1(t)}S_1 = n_{2(t+1)}$$

$$n_{2(t)}S_2 + n_{3(t)}S_3 = n_{3(t+1)}$$

Here, n_1, n_2, and n_3 equal the number of individuals in age classes 1 through 3 and F_1, F_2, and F_3, represent age-specific fertility. These equations form the basis for a population model comprising 3 age classes.

To allow more detailed analysis in solving the above simultaneous equations (e.g., the inclusion of stochastic variation and density-dependent relationships, as well as sensitivity analysis; see Leslie 1945, Caswell 1989, McDonald and Caswell 1993), the equations can be represented as a series of matrices

$$\begin{bmatrix} F_1 & F_2 & F_3 \\ S_1 & 0 & 0 \\ 0 & S_2 & S_3 \end{bmatrix} \begin{bmatrix} n_1 \\ n_2 \\ n_3 \end{bmatrix}_t = \begin{bmatrix} n_1 \\ n_2 \\ n_3 \end{bmatrix}_{t+1}$$

Here, the population projection matrix comprises age-specific fertility on row 1 and age-specific survival on subsequent rows. To estimate stage-specific population size at time $t + 1$, the projection matrix is postmultiplied by a population vector representing the number of individuals of each age class at time t.

However, rather than simply projecting population estimates into the future, the goal (as per Caswell 1989) is to obtain complete dynamic information from the solution to this set of static, algebraic equations (i.e., λ, the finite rate of increase, stable age distribution, age- or stage-specific reproductive values, and the sensitivity of λ to each parameter of the model). Because Caswell (1989) and McDonald and Caswell (1993) provide excellent reviews of the theory underlying matrix population models and applications of these models in demographic analyses, we will forego an in-depth discussion of this topic (however, see also Crouse et al. 1987; Johnson and Williams 1999; Kareiva et al. 2000; Blackwell et al. 2002, 2003).

MODEL CALIBRATION AND VALIDATION

Important to the accuracy of any population model (i.e., the projected versus actual growth or decline), is the biological relevance and accuracy of the parameter values. Model selection proceeds from the fitting of a set of predefined biologically realistic models to the observed data (Burnham and Anderson 1998). However, when demographic data are few, even basic population models (e.g., the exponential model) can be used to provide an initial foundation for comparison of management scenarios that might affect vital rates relative to "current" conditions, as well as guide data collection to improve understanding of the dynamics of the species in question (Beissinger and Westphal 1998, Reed et al. 1998). Situations involving few demographic data and endangered species management have set the stage for the use of basic deterministic models to evaluate management scenarios for decisions in the short term (see Crouse et al. 1987, Crowder et al. 1994, Siddeek and Baldwin 1996, Kareiva et al. 2000). Recently, this same modeling approach has been used to evaluate management options as related to wildlife damage management (e.g., Bosch et al. 2000; Francis 2000; Blackwell et al. 2002, 2003).

In many instances where wildlife population management is necessary and population-specific demographic data are few or unavailable, long-term regional or national data sets might provide, at minimum, estimates of population trends over time. These data sets are useful, as noted above, in calibrating a basic model against an observed rate of increase, or as independent data for model validation. For example, to evaluate potential population effects on an avian species identified on depredation permits and reported killed at aquaculture facilities in the northeast USA, Blackwell et al. (2000) examined long-term systematic survey data for the states and period. Data for species' population trends were obtained from the North American Breeding Bird Survey (BBS) (Sauer et al. 2003) and National Audubon Society (NAS) Christmas Bird Count (CBC) (NAS 2002a) databases.

The BBS comprises approximately 3,700 randomly-located survey routes (39.4 km each) throughout the continental USA, Canada, and Alaska that are surveyed annually in June (Peterjohn and Sauer 1993). Each route has 50 stops (at 0.8-km intervals) at which all birds seen within 0.4 km or heard at any distance are tallied during a 3-min point count (Robbins et al. 1986). The trend for a breeding population (i.e., the increase or decrease expressed as the mean percent change/year in birds per route) is reported for each state or BBS survey area, as are the associated population indices (deviations from the breeding population trend; Sauer et al. 2003).

In addition, Blackwell et al. (2000) noted that some avian species posed depredation problems in states outside their breeding range, such that the BBS data were not applicable in all cases. To examine trends for concentrations of piscivorous birds on wintering grounds, the authors used the CBC. The CBC is an annual, early-winter, 1-d survey of birds on approximately 1,700 non-

overlapping circles (24.1 km diameter) located (in a non-random procedure) throughout the USA and Canada, and in parts of Mexico, Central America, and the Caribbean islands (Butcher and McCulloch 1990). The authors also referenced Breeding Bird Atlases as indices of species' breeding distributions within a state over a 5- to 10-year period (Robbins 1990). Each state atlas represented species' breeding distributions mapped relative to a grid of blocks (with the total number variable among states), representing approximately 25 km^2 each. These atlas data provided a spatial index of species' population status.

Finally, when neither the BBS, CBC, or Breeding Bird Atlas provide information as to the status of an avian species of interest, published regional population estimates and state natural resource agency records can be accessed. These resources might also provide important long-term data for mammal populations where national survey data sets are not available.

EVALUATING MANAGEMENT SCENARIOS

Management actions to reduce or alleviate human-wildlife conflicts are often focused toward specific local populations of animals that are directly (e.g., gulls frequenting landfills) or indirectly (e.g., high densities of small mammals attracting raptors to airfields) causing the conflict situation. In many situations, lethal or reproductive control efforts are utilized as part of an integrated wildlife damage management program. Integrating population modelling efforts with local and regional datasets of animal abundance provides excellent opportunities to explore predicted outcomes of proposed management scenarios and to monitor and evaluate the effects of implemented actions upon local and regional animal populations during and after the management activities. To further illustrate the potential usefulness of population modelling in evaluating management options, we present two specific management scenarios involving direct population management of local bird populations that are hazardous to aviation at two airports.

As part of an integrated wildlife damage management plan, USDA Wildlife Services (WS) and the Port Authorities of New York and New Jersey implemented a gull reduction program to reduce gull-aircraft collisions at John F. Kennedy International Airport from 1991 through 2003 (Dolbeer 1999, Dolbeer and Bucknall 1994, Washburn et al. 2004). Wildlife Services' biologists shot laughing gulls (*Larus atricilla*) attempting to fly over the airport from a nearby nesting colony to reduce the number of gull-aircraft collisions; from 1991 through 2003, 68,717 laughing gulls were shot. In addition, laughing gulls collected during control efforts provided demographic information about the local laughing gull population and its ecology (Dolbeer and Belant 1994, Belant and Dolbeer 1996, Dolbeer and Bernhardt 2003).

During the same 13-year period, the laughing gull nesting colony was censused (Dolbeer et al. 1997) and the regional laughing gull population was modelled (Dolbeer 1998) to determine the potential influence of the management activities on the local and regional laughing gull populations. Although the nearby colony has declined by 50 to 70% during this period, the colony remained viable and productive (Washburn et al. 2003). In addition, BBS survey data and population census data for the states along the eastern seaboard (e.g., Maine to Virginia) show that regionally, laughing gull populations have increased from 1991 through 2003 (see Sauer et al. 2003, Washburn et al. 2004). Population information at local and regional scales demonstrates that this very successful management program (gull-aircraft collisions were reduced by 76 - 99% annually) corroborated prior modelling results (Dolbeer 1998) and was not detrimental to local and regional laughing gull populations.

In a second management effort, a standard wildlife hazard assessment (USDA 1998) was conducted by USDA Wildlife Services at Marine Corps Air Station (MCAS) Cherry Point, located near Havelock, NC, during February 2000 through February 2001. Canada geese were observed on or near the airfield throughout the year (Begier 2002). Peaks in Canada goose abundance occurred during April and October, corresponding to spring and autumn migration along the Atlantic Bird Migration Corridor; however, populations of resident Canada geese utilizing areas within 8 km (5 miles) of the air station likely contributed to most of the daily observations. Following attempts to use non-lethal means to deter Canada geese from using the air station, direct control activities were initiated at the facility and surrounding areas during the summer of 2001. Wildlife monitoring efforts at MCAS Cherry Point during 2002 revealed an overall decrease of 97% in Canada goose abundance. Although these findings were tangible, it was very important to examine the effects of the management actions on Canada goose populations at a local scale.

Toward this effort, local CBC and regional BBS data were examined to determine the potential impacts of the management efforts on local and regional Canada goose populations. These data sets were selected for a comparison, given the similarity in methods and the ability to examine abundance. The analysis of raw data from regional BBS routes (i.e., routes within approx. 80 km [50 miles] of the airport) revealed little data pertaining to Canada geese. However, the state-wide BBS population curve for the species indicates a positive population trend (mean change/year = 27.9%, $P < 0.08$, N = 29, 1980-2002; Sauer et al. 2003). In addition, CBC data from 4 count locations (i.e., New Bern, Pamilco, Morehead City, and New River) provided information related to local population levels. Overall, trends in abundance from these count locations were elevated and averaged over 200 birds per year (NAS 2000, 2001, 2002b). We derived the 97% decrease in observed Canada goose abundance at MCAS Cherry Point from examining point count data at the airport collected during the standard CBC data collection time period. Similar to the experiences previously mentioned, the comparisons of local and regional data to monitoring data from the installation demonstrated the efficacy of management actions at the air station.

SUMMARY

We have reviewed the basic relationship of rates of population change (i.e., the finite rate and the intrinsic rate) to population size and the incorporation of the exponential model as a simple model for evaluating rate

of change and the contribution of life-history parameters to that change. Further, we have discussed the use of long-term data sets (e.g., the BBS and CBC) in calibrating and validating population models, and applied these methods via two examples involving wildlife management at airports. Clearly, wildlife populations, humans, and the environment do not exist independently of each other. Investigations into the relationship of demographic parameters and their individual and combined effects on rate of population growth can provide the scientific foundation necessary for assessing potential effects on resources, evaluating management options, and defending management decisions before the public.

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