POPULATION DYNAMICS: THE FOUNDATION OF WILDLIFE DAMAGE MANAGEMENT FOR THE 21ST CENTURY

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ABSTRACT: To justify and defend lethal or reproductive control programs to solve vertebrate pest problems, wildlife biologists must have a sound understanding of the population status and dynamics of the problem species. Models are essential to project how populations will respond to proposed management actions, providing a scientific foundation to counter the emotional debates that often arise. Four population models (PM1 to PM4) for predicting population responses are described. PM1 and PM2 explore the relative efficacy of reproductive and lethal control for vertebrate species over 10-year intervals. PM3 simulates population responses to actual management actions through 10-year intervals. PM4 simulates population changes for a species at weekly intervals over an annual cycle, exploring the immediate (≤ 1 year) impact of population management actions. Population simulations using PM1 and PM2 demonstrated that for most vertebrate pest species considered, lethal control will be more efficient than reproductive control in reducing population levels. Reproductive control is more efficient than lethal control only for some rodent and small bird species with high reproductive rates and low survival rates. A simulation (PM3) of the removal of 47,000 laughing gulls (*Larus atricilla*) from the Long Island-New Jersey population accurately predicted the 33% decline of the population over five years. A simulation (PM4) of the annual cycle of the common grackle (*Quiscalus quiscula*) population in the eastern United States demonstrated why removing 4.2 million birds in one winter had no discernible impact on subsequent breeding populations. Understanding the population dynamics of wildlife species is the cornerstone to successful management, and population models will be essential for this task in the years to come.

KEY WORDS: black rat, fruit bat, grackle, gull, lethal control, model, population dynamics, reproductive control, vertebrate pest

INTRODUCTION

The world human population is increasing at an unprecedented rate of 90 million people/year (about 4 million/year in North America). In parallel, dramatic increases in populations of many wildlife species such as Canada geese (*Branta canadensis*), gulls (*Larus* spp.), white-tailed deer (*Odocoileus virginianus*), double-crested cormorants (*Phalacrocorax auritus*) and beaver (*Castor canadensis*) have occurred in North America over the past 30 years due to land-use changes and effective management programs by public and private agencies (e.g., Ankney 1996; Hatch 1995; Belant and Dolbeer 1993). These simultaneous population expansions inevitably lead to conflicts between wildlife and humans in an increasingly crowded world. Managing these conflicts is an intricate, difficult process because of four factors:

1) The science of wildlife management is complex, particularly understanding and predicting the behavior, population dynamics and economic/health impacts of wildlife species.

2) Wildlife biologists study and manage sentient, adaptable and secretive organisms, requiring the development of many complex, labor-intensive tools and techniques to census, monitor, and measure.

3) The sociological aspects of wildlife management are diverse and emotional, particularly the oftentimes polarized views of society regarding the killing and management of wildlife species.

4) The regulatory aspects of wildlife management can be almost overwhelming, particularly regarding the legal status of wildlife, National Environmental Policy Act (NEPA) processes, and the registration of chemicals as management tools.

The author believes that as a profession of research and management biologists, we have become so involved in techniques development, sociological issues and regulatory aspects related to wildlife management that we have lost focus on our most important mission: the science of wildlife management. Furthermore, the author contends that the foundation of wildlife management is understanding the population dynamics of the species in question. Any management action recommended should be based and clearly communicated on this foundation of population dynamics. Unfortunately, this is often not the case either because we fail to communicate our knowledge and understanding, or because we do not have the level of understanding needed.

There are many situations where lethal control has been implemented to resolve human conflicts with wildlife (e.g., Dolbeer 1986; Dolbeer et al. 1993, 1997; Bedard et al. 1995). However, our urbanized public generally advocates nonlethal means of managing problem populations of wildlife (Stout et al. 1997). To this end, there has been increased interest in the development of reproductive control strategies for wildlife species (Kirkpatrick and Turner 1985). To justify lethal or reproductive control programs to state and federal regulatory agencies and the public, wildlife biologists must have a sound understanding of the population status and dynamics of the problem species. Population models are essential to document the immediate impact that lethal or reproductive control programs will have on local, regional and continental populations and to project how

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populations will respond to these management actions. Such models provide a scientific foundation for management actions to counter the emotional debates that often arise.

The author's objective is to focus on this foundation of population dynamics from which, in his opinion, our profession has drifted. Four population models for vertebrate species developed on Excel spreadsheets are described. Second, these models are used to demonstrate fundamental principles of population dynamics for several species that often conflict with human activities. Finally, two examples are given of how these models and the underlying principles demonstrated have provided guidance and justification for management actions to reduce conflicts.

METHODS
Population Models 1 (PM1) and 2 (PM2)

PM1 explores the relative efficacy of reproductive and lethal control for vertebrate species that produce ≤1 generation per year (i.e., offspring do not reproduce until ≥1 year old). PM1 also determines reproductive and survival parameter values needed to produce a stable population and provides an estimate of the age composition. PM1 has six age classes (0 [year of birth], 1, 2, 3, 4, and 5+ year-old animals). Population parameters that must be entered are initial estimates of the age distribution and survival and reproductive rates by age class (Table 1, Figure 1). PM1 is designed to simulate population levels by age class for 20 years, the first 10 in a stabilizing or "baseline" mode and the next 10 in a "treatment" mode that shows population response to various management actions. No compensatory factors (e.g., increased annual survival rates during a period of management-induced population decline) are included in PM1. PM1 simply is designed to determine parameter values for species that result in stable populations and to compare the relative efficacy of control strategies within and among species.

To simulate population responses of a species, the best available mean values from the literature or other sources are input for the population parameters. An initial age structure is also entered, arbitrarily using 200 to 400 individuals for age-class 0 and then reasonable approximations for the remaining age classes (e.g., 90 for age-class 1, if the mean annual survival rate of 200 age-class 0 animals is estimated to be about 0.45). If these initial parameter estimates cause the population to increase (decrease), the reproductive and/or survival rates are adjusted downward (upward) until the population stabilizes by year 10 (Table 2). Parameter values that result in a stable population should represent realistic values for a typical population of the species. In year 11 (Baseline 1,000), the stable age structure from year 10 is adjusted to sum to 1,000 individuals for age classes 0 to 5+ (Figure 1). This simply provides a convenient baseline number for the stable population (1,000) to compare with population levels during the 10-year treatment period.

In treatment years 1 to 10, parameter values are adjusted to reflect the simulated management action. For example, one may want to compare the relative response of the population over 10 years to a 50% decrease in the survival rate of adult animals versus a 50% decrease in

the reproductive rate. The model is first run with the survival rate reduced and then with the reproductive rate reduced (Figure 1). These simulations provide simple but fundamental insights into the sensitivity of a species, given its population characteristics, to reproductive versus lethal control.

PM2 is a derivation of PM1 for simulating populations of rodents that produce more than one generation per year (e.g., commensals). PM2 has two age classes (immature and mature) and allows three generations per year.

Population Model 3 (PM3)

PM3 has the same basic structure as PM1 with the addition that the stable population in baseline year 0 can be adjusted to an actual population level (e.g., 131,000 nesting laughing gulls in New Jersey-Long Island in 1989 [see below]) so that a real-world population can be simulated in treatment years 1 to 10. Then, actual numbers of animals or eggs removed by management actions are entered for each of the 10 treatment years. Finally, compensatory factors can be added to adjust reproductive and survival rates upward when populations decline below baseline (stable) levels as a result of management actions (Table 1). Thus, whereas PM1 and PM2 provide a generic comparison of population responses among species and management actions, PM3 allows simulation of a real-world situation. An added bonus is that PM3 provides an estimate of the total population (non-breeding and breeding animals) when census data are available for only the breeding population (e.g., as in most colonial waterbird populations; Belant and Dolbeer 1993).

Population Model 4 (PM4)

Whereas PM1-3 simulate changes in populations at yearly intervals, PM4 simulates population changes at weekly intervals over an annual cycle. PM4 explores the immediate (≤1 year) impact of population management actions. The population is initialized (week 0 = April 23) using actual population estimates for the species to be simulated and stable age composition, reproductive and survival estimates determined from PM1. Also, the start and end weeks for fledging/weaning are entered so that young (age 0) enter the population during appropriate weeks. The population is then simulated for 52 weeks (May 1 to May 1) and parameters adjusted if needed to produce a population that is stable. For the treatment simulation, start and end weeks for removal are entered as well as the number of animals to be removed. As with PM3, a compensatory factor for survival can be added to adjust weekly survival rates upward (downward) as the population declines below (exceeds) the baseline population for a given week.

RESULTS
Population Responses to Lethal and Reproductive Control (PM1, PM2)

The Republic of Maldives, an archipelago nation in the Indian Ocean, has two mammals species, the endemic giant fruit bat (*Pteropus giganteus*) and introduced black rat (*Rattus rattus*) that damage agricultural crops (Dolbeer et al. 1988). These two species have dramatically

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Table 1. Population parameters used in Models 1 to 4.

Population Parameter	Definition
JSR[a]	Juvenile (age 0 [weaning/fledging] to age 1) survival rate.
ASR[a]	Adult ($\geq$ age 1) survival rate (annual).
ESR[a]	Egg survival rate (egg laying to fledging/weaning).
EPRA[a]	Eggs per reproducing adult/per.
FFR1...5[a]	Fraction of females reproducing in age classes 1...5.
MCF[b]	Maximum compensation factor to adjust ASR, JSR, and ESR; = 1/ASR.
CF[b]	Compensation factor for ASR, JSR, and ESR; = MCF-((MCF-1)*FIPR).
FIPR[b]	Fraction of initial (baseline) population remaining.

[a]Used in Population Models 1 to 4.
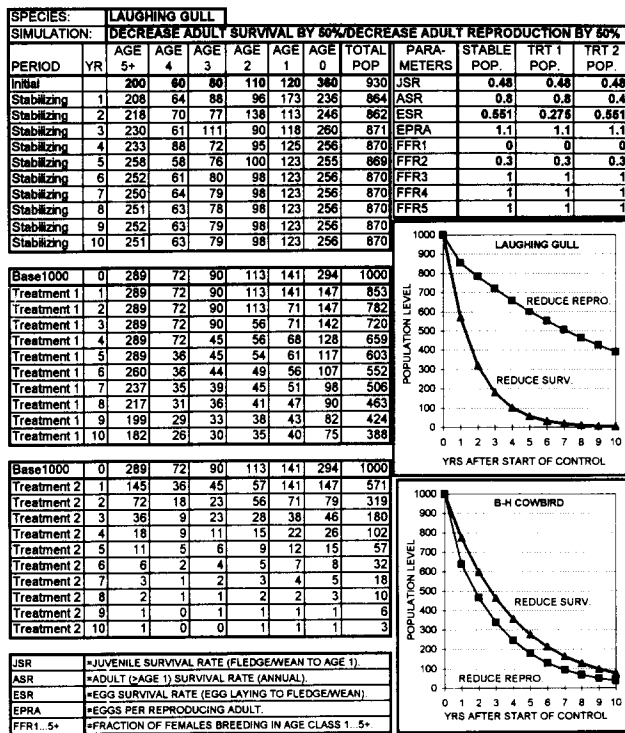[b]Used in Population Models 3 and 4.

Figure 1. Example of tabular and graphic output from Model 1 in which: 1) parameters values were determined for laughing gulls to produce stable population (stabilizing years 1 to 10); and 2) population responses to 50% reductions in survival or reproduction were simulated for 10 years (Treatments 1 and 2). In addition, graphic output for same simulations with cowbirds (see Table 2 for parameter values) is presented.

different life histories (Table 2) which provide an informative comparison of population response to control strategies (Figure 2). Fruit bat populations, with low reproductive rates and high survival rates, can be reduced four to six times more efficiently by lethal compared to reproductive control applied for three years (Table 3). In contrast, rat populations, with high reproductive rates, can be reduced two to three times more efficiently by reproductive compared to lethal control. The validity of these simulated responses was supported by management actions in the Maldives. Lethal control suppressed populations of fruit bats by 46 to 70% one year later, whereas rat populations recovered fully (Dolbeer et al. 1988).

Brown-headed cowbirds (*Molothrus ater*) and laughing gulls are bird species with contrasting life histories (Table 2) that demonstrate these same differences in population response to control strategies (Figure 1). Laughing gull populations, with relatively low reproductive rates, can be reduced four to six times more efficiently over a three-year period by lethal compared to reproductive control (Table 3). Cowbird populations, with high reproductive rates, are more efficiently reduced by reproductive control when control is directed only at adult ($\geq$ 1 year old) animals. When control can be directed at all age classes, lethal control is three times more efficient than reproductive control. Red-billed quelea (*Quelea quelea*) populations respond in a manner similar to cowbirds.

The predicted relative efficiencies of lethal and reproductive control for various vertebrate species (Table 3) can be generalized based on adult survival rate (ASR) and age at which animals reproduce (Figure 3). For species in which females first reproduce at one and two years, lethal control will be more efficient than reproductive control in reducing populations when the ASR is greater than about 0.56 and 0.23, respectively. For species in which females first reproduce at three years, lethal control always will be more efficient than reproductive control in reducing populations.

Table 2. Parameter values used in Population Models 1 to 4 that result in stable annual population levels for 11 vertebrate species that are sometimes pests.

Species[b]	Population Parameter Values[a]									
	JSR	ASR	ESR	EPRA	FFR1	FFR2	FFR3	FFR4	FFR5	MCF
GFBT	0.635	0.798	0.80	0.5	0	1	1	1	1	1.25
BRAT[c]	0.670	0.773	0.80	3.0	1	1	1	1	1	1.29
WTDR	0.570	0.700	0.89	0.9	0	0.8	1	1	1	1.43
COYT	0.250	0.603	0.88	2.5	0.3	1	1	1	1	1.67
BEAV	0.500	0.669	0.85	1.8	0	0.2	0.6	1	1	1.49
CAGO	0.300	0.699	0.60	3.0	0	0.3	1	1	1	1.43
DCCO	0.353	0.771	0.50	2.0	0	0.3	1	1	1	1.30
LAGU	0.480	0.800	0.55	1.1	0	0.3	1	1	1	1.25
BHCO	0.210	0.454	0.13	20.0	1	1	1	1	1	2.20
COGR	0.400	0.562	0.50	2.4	0.8	1	1	1	1	1.78
RBQU	0.223	0.500	0.80	2.8	1	1	1	1	1	2.00

[a]Estimates for parameters derived from literature (see below), or, when not available, by applying reasonable approximations that resulted in stable population.

[b]GFBT = giant fruit bat, BRAT = black rat (Dolbeer et al. 1988); WTDR = white-tailed deer (Hayne 1984); COYT = coyote (*Canis latrans*), Bekoff 1982); BEAV = Beaver (Hill 1982); CAGO = Canada goose (Bellrose 1976); DCCO = double-crested cormorant (Bedard et al. 1995); LAGU = laughing gull (Burger 1996); BHCO = brown-headed cowbird (Lowther 1993); COGR = common grackle (Peer and Bollinger 1997); RBQU = red-billed quelea (Jones 1989).

[c]JSR and ASR are monthly rates; EPRA/4 months; females reproduce at four months.

Table 3. Estimated relative efficiency of reproductive and lethal control based on numbers remaining after three years from an initially stable population of 1,000 individuals in which reproductive or survival rate is reduced annually by 50% (using Population Model 2 [rats] and Model 1 [all other species]).

| Species | Number Remaining After Three Years | | | Relative Efficiency[a] of Lethal to Reproductive Control (RC/LC) After Three Years | |
| | Reproductive Control (RC) | Lethal Control (LC) | | | |
		$\geq$ Age 0[b]	$\geq$ Age 1[c]	$\geq$ Age 0[b]	$\geq$ Age 1[c]
Fruit bat	731	125	191	5.8	3.8
Laughing gull	720	125	180	5.8	4.0
D.C. cormorant	673	125	183	5.4	3.7
White-tailed deer	639	125	212	5.1	3.0
Beaver	624	125	199	5.0	3.1
Canada goose	607	125	193	4.9	3.1
Coyote	486	125	264	3.9	1.8
Common grackle	460	125	349	3.7	1.7
Brown-headed cowbird	338	125	462	2.7	1.3
Red-billed quelea	368	125	421	2.9	0.7
Black rat	97[d](406)[e]	307[c]	675[d]	0.3[c]	0.6[d]

[a]Efficiency ratios presented are specific to population status after three years and will increase during additional years of treatment.

[b]Survival reduced 50% for age classes $\geq$ 0.

[c]Survival reduced 50% for age classes $\geq$ 1.

[d]Survival and reproduction of adults ($\geq$ 3 months old) reduced three times/year.

[e]Survival and reproduction of adults ($\geq$ 3 months old) reduced one time/year.

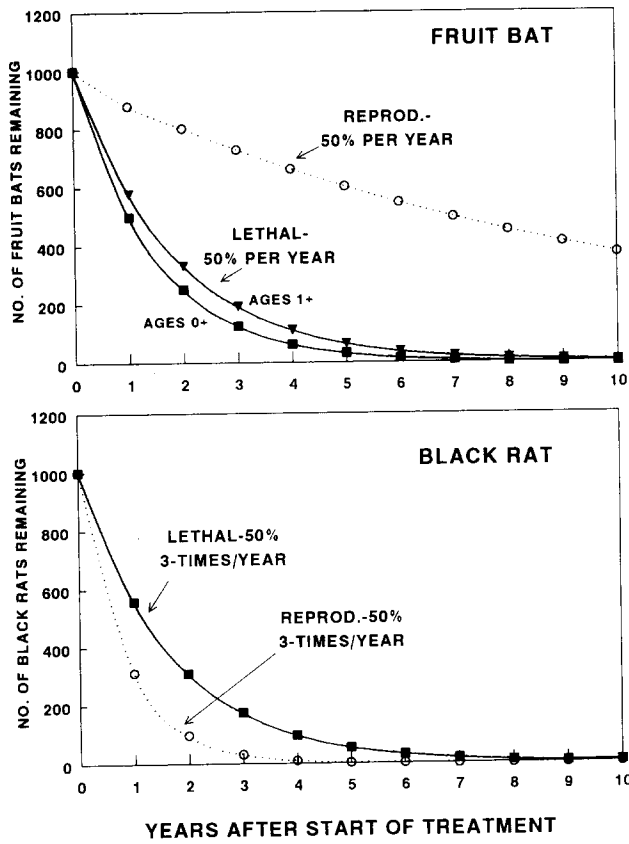**This paper has been peer reviewed.**   6

Figure 2. Relative efficiency of reproductive and lethal control (yearly 50% reduction in reproductive or survival rate from values that produce stable population) for giant fruit bats (Population Model 1) and black rats (Population Model 2).
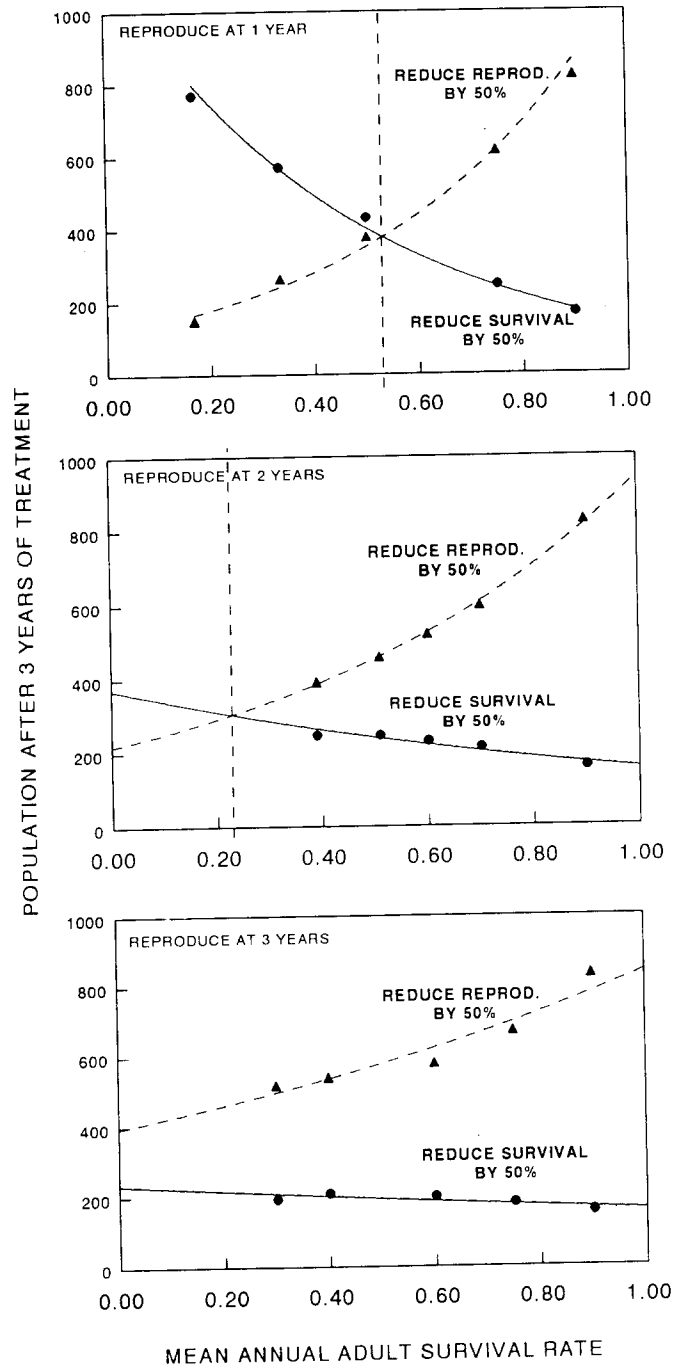
Figure 3. Relative efficiency of reproductive and lethal control (yearly 50% reduction in reproductive or survival rate from values that produce stable population) in relation to mean adult annual survival rate for hypothetical vertebrate species that first reproduce at one, two, or three years of age.

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Response of Laughing Gulls to Control (PM3)

A colony of laughing gulls on Jamaica Bay Wildlife Refuge, New York immediately adjacent to John F. Kennedy International Airport (JFKIA) increased from 15 to 7,600 nests, 1979 to 1990. During this period, there was an increase of the entire coastal New Jersey-Long Island (NJLI) population from about 31,000 nests in 1977 to 61,500 nests in 1989 to 1990 (Belant and Dolbeer 1993).

The large nesting colony next to JFKIA created a hazard for aircraft during summer because gulls frequently overflew the airport on daily foraging trips (Dolbeer et al. 1993). Because the colony was on protected National Park Service land, management options to reduce aircraft collisions with gulls (bird strikes) were limited. From 1991 to 1997, biologists shot 47,600 laughing gulls flying over the airport during May to August, reducing gull strikes by 66 to 89% (Dolbeer and Bucknall 1998).

This management action, involving the removal of a relatively large number of gulls within a major metropolitan area, received intense media and public scrutiny (USDA 1994). Therefore, it was imperative to document the impact of killing on the regional population to assure the public that responsible management actions were being implemented (Belant and Dolbeer 1993). PM3 provided an objective means of predicting the impact of this shooting program on the NJLI population and putting the level of kill into perspective with regard to the total population.

First, PM3 estimated that in addition to the 131,000 nesting birds censused in 1989 to 1990, the population contained about 60,000 non-nesting adults (≥ 1 year old, Table 4). Second, PM3 predicted a 26% decline in the NJLI nesting population from 1989 to 1995, whereas actual surveys estimated about a 33% decline. Finally, if an egg-oiling program had been conducted in which the number of nests oiled was equivalent to the number of gulls killed, PM3 predicted a decline of about 8% from 1989 to 1995. Neither the national nor northeast regional (Virginia to Maine) population of laughing gulls has declined during the years (1991 to 1997) of the shooting program, based on North American Breeding Bird Survey results, 1966 to 1996 (Burger 1996; Sauer et al. 1997).

Response of Blackbirds to Control (PM4)

From 1974 to 1992, an estimated 38.2 million blackbirds (*Icterinae*) and starlings (*Sturnus vulgaris*) were killed in the southern United States by surfactant applications to winter roosts (Dolbeer et al. 1997). These management operations had no detectable impact on subsequent nesting population levels in the northern United States (Dolbeer et al. 1997), a finding that had been predicted (U.S. Dept. Inter. 1976) based on simulations from an earlier version of PM4 (Dolbeer et al. 1976). The greatest number of birds removed during a single winter was 4.2 million common grackles in 1977. A simulation with PM4 of the annual population cycle of common grackles in the eastern United States demonstrated the minimal impact of removing 4.2 million birds during January (Figure 4).
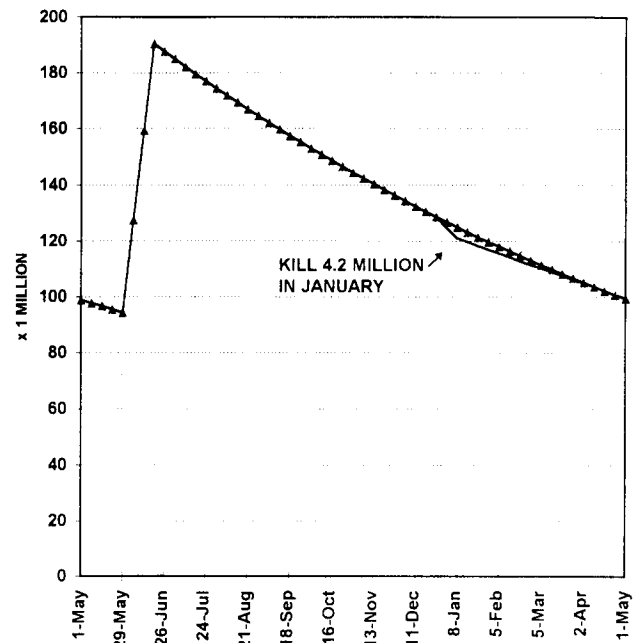

Figure 4. Simulated annual cycle of population of common grackles in eastern North America (Population Model 4) showing no control and the removal of 4.2 million birds in winter 1978 (Dolbeer et al. 1997).

DISCUSSION

Population models provide an essential framework for understanding the population dynamics of wildlife species to guide the development, evaluation and defense of management decisions. First, such models provide predictions of parameter values needed to produce a stable or changing (e.g., 10% mean annual increase) population level for a species. Second, models provide estimates of population responses to various control strategies, either hypothetically (PM1, PM2) or for actual situations (PM3, PM4). As demonstrated in this paper, these models can provide critical perspective into the impact, or lack thereof, that a given level of reproductive or lethal control has on a population in an actual or proposed management action.

Two criticisms of population modeling as a management tool are that data on parameter values often are inadequate and that models cannot account for all variables influencing populations. The author contends that these criticisms are not valid. First, there are adequate population data for many situations with species such as gulls, deer, waterfowl and blackbirds. Furthermore, for those situations or species with meager data, the author contends these criticisms provide even greater justification for modeling. Obviously, models cannot account for all variables influencing populations, and model output always should be viewed cautiously in light of the assumptions, model constraints and quality of data. However, management decisions are made whether or not models are used. Models provide an objective

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Table 4. Predicted response (Population Model 3) of laughing gull population on Long Island, New York and New Jersey to killing (actual) and egg oiling (hypothetical) in relation to field-based estimates of nesting population, 1977 to 1997 (numbers x 1,000).

| | | | Predicted Nesting and Total Population | | | |
| | | | After Killing[c] | | After Egg Oiling[d] | |
Year	Estimated Nesting Population[a]	Number of Gulls Killed[b]	Nesting	Total[e]	Nesting	Total[e]
1977	61					
1985	122					
1989	131		131	190	131	190
1990			131	190	131	190
1991		14.2	121	177	131	190
1992		11.8	113	161	131	182
1993		6.5	107	151	129	176
1994		3.7	103	147	124	174
1995	88	6.2	97	140	121	173
1996		2.0	95	137	120	170
1997		3.2	93	133	118	170

[a]Based on actual nest censuses summarized by Belant and Dolbeer (1993) and Dolbeer et al. (1998).

[b]Birds shot at John F. Kennedy International Airport (93%, Dolbeer et al. 1998) and Atlantic City International Airport (7%, J. Floyd, U.S. Dept. Agric., unpubl. data).

[c]In addition to the number of birds actually killed, it is assumed 50% of short birds resulted in nest failure.

[d]Hypothetical simulation: number of nests oiled (100% effective) equal to the number of birds killed.

[e]Total population includes nesting birds plus non-breeders (age 1 to 5) determined from age composition and estimated fraction of population breeding in each age class (Table 2).

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framework whereby assumptions and parameter estimates are explicitly stated in numerical values and mathematical relationships. Subsequent simulations produce testable hypotheses that can be challenged via experimentation. Models simply make those decisions more objective and provide professional wildlife managers and the public with an improved means of arriving at, justifying, debating and evaluating decisions (Starfield 1997).

Modeling also clearly identifies parameters for which improved data are needed for a species or situation, thereby focusing research efforts so that more reliable predictions can be made and defended. For example, data for key parameters such as the fraction of females breeding in younger age classes (e.g., age classes 2 to 3 for double-crested cormorants; Bedard et al. 1995) are often meager, making estimates of reproductive rate uncertain. Also, estimates of the total population being managed are often lacking (e.g., Torres et al. 1996), making evaluation of management impacts difficult even if good data were available on population parameters such as survival and reproductive rates. By requiring estimates for each of the population parameters, a manager quickly prioritizes critical data gaps.

Population simulations using PM1 and PM2 demonstrated that for most of the vertebrate pest species considered in this paper, lethal control will be more efficient than reproductive control in reducing population levels. This finding conflicts with the growing public desire for nonlethal methods of solving wildlife damage problems of which reproductive control is currently fashionable, at least conceptually (Kirkpatrick and Turner 1985). Professional biologists should not allow these outside pressures to cause them to stray from the fundamental principles of wildlife management, of which population dynamics is the cornerstone.

Reproductive control may have a place in wildlife management. But the author contends that efforts for reproductive control should focus on those species for which the concept is most likely to be successful, such as rodents and small birds. Furthermore, if reproductive control strategies are developed and used on long-lived species such as deer and geese, biologists need to be honest with the public about the length of time required for such strategies to reduce populations relative to lethal control.

In conclusion, as professional biologists practicing wildlife damage management, we have an obligation to be leaders in taking appropriate management actions based on the principles of wildlife science, and we betray our profession when we become followers of vacillating public opinion. We should not be afraid to recommend and implement lethal control to manage legitimate damage situations when: 1) such actions are justified based on the population status and dynamics of the species; 2) alternative control methods are impractical or less efficient; and 3) outcomes can be monitored to evaluate the impact of killing on target populations and in solving problems. Understanding the population dynamics of wildlife species is the cornerstone to successful management, and population models such as described in this paper will be essential for this task in our increasingly crowded world in the years to come.

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