

# Dynamics of the double-crested cormorant population on Lake Ontario

*Bradley F. Blackwell, Martin A. Stapanian, and D. V. Chip Weseloh*

**Abstract** After nearly 30 years of recolonization and expansion across North America, the double-crested cormorant (*Phalacrocorax auritus*) occupies the role of a perceived and, in some situations, realized threat to fish stocks and other resources. However, population data necessary to plan, defend, and implement management of this species are few. Our purpose was to gain insight into the relative contribution of various population parameters to the overall rate of population growth and identify data needs critical to improving our understanding of the dynamics of double-crested cormorant populations. We demonstrated the construction of a biologically reasonable representation of cormorant population growth on Lake Ontario (1979–2000) by referencing literature values for fertility, age at first breeding, and survival. These parameters were incorporated into a deterministic stage-classified matrix model. By calculating the elasticity of matrix elements (i.e., stage-specific fertility and survival), we found that cormorant population growth on Lake Ontario was most sensitive to survival of birds about to turn age 3 and older. Finally, we demonstrated how this information could be used to evaluate management scenarios and direct future research by simulating potential environmental effects on fertility and survival, as well as a 5-year egg-oiling program. We also demonstrated that survival of older birds exerts more effective population control than changes in fertility.

**Key words** double-crested cormorant, Lake Ontario, *Phalacrocorax auritus*, population dynamics, population management, stage-classified matrix model

The double-crested cormorant (*Phalacrocorax auritus*) is a North American foot-propelled diver that is primarily piscivorous and distributed from Alaska and Newfoundland south to northern Mexico and the western Caribbean (Hatch and Weseloh 1999). *P. auritus* (hereafter referred to as cormorant) has long been the target of speculation concerning its potential negative effects on fish stocks in North America, with persecution commonplace during the nineteenth and early twentieth centuries (Taverner 1915, Mendall 1936, Hatch 1995, Krohn et al. 1995). Environmental contamination (e.g., organochlorines such as DDE) as well as persecution contributed to the decline of cormorant populations, particularly in

the interior region of North America through approximately the early 1970s (Weseloh et al. 1983, Hatch 1995, Ludwig et al. 1995). However, environmental efforts in the United States and Canada, combined with international protection by the inclusion of the cormorant in the USA-Mexican Convention of 1972 (Trapp et al. 1995), effected a dramatic recovery and subsequent recolonization and expansion of the species across North America, particularly within the region of the Laurentian Great Lakes (Price and Weseloh 1986, Weseloh and Ewins 1994, Krohn et al. 1995, Weseloh et al. 1995, Tyson et al. 1999). In addition, Glahn et al. (1999) suggested that the expansion of the channel catfish (*Ictalurus punctatus*) industry

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Address for Bradley F. Blackwell: United States Department of Agriculture, Animal and Plant Health Inspection Service, Wildlife Services, National Wildlife Research Center, Ohio Field Station, 6100 Columbus Avenue, Sandusky, OH 44870, USA; e-mail: bradley.f.blackwell@aphis.usda.gov. Address for Martin A. Stapanian: United States Geological Survey, Lake Erie Biological Station, 6100 Columbus Avenue, Sandusky, OH 44870, USA. Address for D. V. Chip Weseloh, Canadian Wildlife Service, Environment Canada, Ontario Region, 4905 Dufferin Street, Downsview, Ontario M3H 5T4, Canada.

in the Delta region of Mississippi after 1985 contributed to increased survival of wintering cormorants.

With the cormorant's resurgence in North America, some people again view the bird as being in conflict with human interests (Nettleship and Duffy 1995). The effects, perceived or real, appear to be largely related to scale. There is evidence that the cormorant has a deleterious effect on aquaculture in part of its winter range (Glahn and Stickley 1995, Glahn et al. 2000), on local populations of anadromous fishes in obstructed rivers (Krohn et al. 1995, Blackwell and Krohn 1997, Blackwell et al. 1997), and, though evidence is primarily qualitative, on the vegetation immediately surrounding cormorant breeding colonies (Bédard et al. 1995, 1999; Weseloh et al. 2002). However, in most quantitative studies, the cormorant has been described as an opportunistic forager posing no threat to the maintenance of healthy fish stocks (Mendall 1936, Campo et al. 1993, Madenjian and Gabrey 1995, Milton et al. 1995, Bur et al. 1999, Trapp et al. 1999). The debate is further confused in situations of suspected but scientifically unsupported conflicts. For example, perceived conflicts have driven unlawful efforts to reduce cormorant populations, such as the poaching of cormorants on Pigeon and Little Galloo Islands, Lake Ontario in 1993 and 1998, respectively (Ewins and Weseloh 1994; New York Department of Environmental Conservation, unpublished data), and on Little Charity Island, Lake Huron, Michigan in 2000 (United States Fish and Wildlife Service, unpublished data).

A crucial factor facing managers of the various habitats used by cormorants is the paucity of demographic data by which to evaluate population changes, assess damage, and predict future population trends (Weseloh and Ewins 1994, Hatch and Weseloh 1999, Glahn et al. 2000). Further, there is little use of dynamic tools that rigorously evaluate management alternatives prior to their implementation and identify data needed to refine management procedures. Dolbeer (1998) suggested that situations characterized by meager population data provide a sound justification for developing preliminary population models.

Ideally, model selection proceeds from the fitting of a set of predefined biologically realistic models to the observed data (Burnham and Anderson 1998, see also Frederiksen and Bregnballe 2000a). However, when demographic data are few, crude population models can be used to provide an initial

basis for comparison of management scenarios that might affect vital rates relative to "current" conditions and guide data collection to improve understanding of the dynamics of the species in question (Beissinger and Westphal 1998, Reed et al. 1998). Both Beissinger and Westphal (1998) and Reed et al. (1998), however, cautioned against construction of complex models and interpretation of model output as absolute when input data were limited or speculative.

Because management of the cormorant in North America involves opposing views from conservationists, sport fishing concerns, and the aquaculture industry, with the often conflicting responsibilities of species conservation and damage management resting on governments (Acord 1995, Keith 1995, Trapp et al. 1995), an approach is necessary by which local or regional management scenarios can be evaluated and future research directed. Our objectives were to 1) construct a simple deterministic population model for cormorants on Lake Ontario, 2) evaluate the contribution of model parameters to the observed growth in the cormorant population, and 3) identify population parameter data needs critical for improving understanding of the dynamics of the cormorant population on Lake Ontario relative to potential management scenarios.

## Methods

### *Model construction and calibration*

We used total annual counts of "apparently occupied nests" (Ewins et al. 1995: 180) conducted during the nestling phase of reproduction on the 20 known cormorant colonies on Lake Ontario (Price and Weseloh 1986; Weseloh et al. 2002; D. V. C. Weseloh, unpublished data) to estimate the intrinsic rate of increase for the cormorant population from 1979 through 2000 (Figure 1). The intrinsic rate of increase  $r$  is related to the population size  $N$  at times 0 and  $t$  by the equation

$$r = \frac{\ln\left(\frac{N_t}{N_0}\right)}{t}$$

The rate  $r$  represents the exponential rate at which a population with a stable age distribution (see below) grows given unlimited resources (Caughley 1977). We then constructed a stage-classified matrix population model (Caswell 1989,

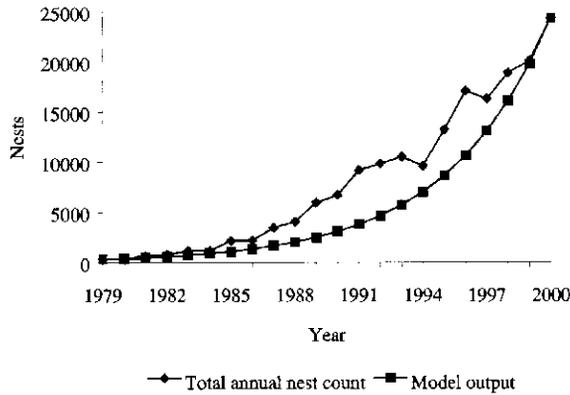


Figure 1. Total annual counts of “apparently occupied nests” (Ewins et al. 1995:180) conducted during the nestling phase of reproduction on the 20 known double-crested cormorant colonies on Lake Ontario, 1979 to 2000, versus model output calibrated to the observed intrinsic rate of increase ( $r = 0.207$ ).

McDonald and Caswell 1993) projected over the annual cycle of the cormorant and based on a pre-breeding census (i.e., tracking the first age class from being almost age 1 until they are almost age 2). In this manner, the effects of first-year mortality are incorporated into the fertility coefficients (Caswell 1989).

A stage-classified model differs from an age-classified model in that a stage may comprise individuals differing in age, but sharing factors (e.g., foraging experience in cormorants) known to affect vital rates (Caswell 1989, McDonald and Caswell 1993). We grouped birds into 3 stages, with the first 2 stages age-specific (e.g., Hitchcock and Gratto-Trevor 1997). We defined the third stage as comprising individuals of age 3 and older because the cormorant 1) likely exhibits age-specific survival up to age 3 (Palmer 1962), 2) generally begins breeding at age 3 (Palmer 1962, Ludwig 1984), 3) is considered long-lived (Hatch and Weseloh 1999), and 4) has an age-structure at local and regional levels that is unclear (Dolbeer 1991; D. T. King, United States Department of Agriculture, National Wildlife Research Center, Mississippi Field Station, unpublished data). The resulting stage-classified projection matrix,

$$\mathbf{A} = \begin{bmatrix} F_1 & F_2 & F_3 \\ S_1 & 0 & 0 \\ 0 & S_2 & S_3 \end{bmatrix},$$

comprised fertility elements for birds about to turn age 1 ( $F_1$ ), age 2 ( $F_2$ ), and age 3+ ( $F_3$ ) on the first row. Fertility was related to the stage-specific pro-

portion of females breeding ( $PB_S$ ), mean number of female young fledged per female ( $FI_S$ ), and survival of young from fledging to just before age 1 ( $S_0$ ) as

$$F_S = PB_S FI_S S_0.$$

Subsequent rows of the projection matrix included survival of birds from just before age 1 to just before age 2 ( $S_1$ ), from just before age 2 to just before age 3 ( $S_2$ ), and from just before age 3 on ( $S_3$ ).

To estimate stage-specific population size at time  $t+1$ , the projection matrix was postmultiplied by a population vector as

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

where  $n_1$ ,  $n_2$ , and  $n_3$  equaled the number of individuals in stages 1 through 3. Further, if a population projection matrix  $\mathbf{A}$  is positive, or non-negative and primitive (i.e., all matrix elements are  $\geq 0$  and the matrix becomes positive when raised to sufficiently high powers), there exists a real eigenvalue  $\lambda_A > 0$  (i.e., the dominant eigenvalue of the projection matrix) that is equal to  $e^r$  (i.e., the finite rate of increase; Caswell 1989, McDonald and Caswell 1993), where

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

The right eigenvector of  $\mathbf{A}$ ,  $\mathbf{W}_A$ , represents the stable age distribution such that

$$\mathbf{A} \mathbf{W}_A = \lambda_A \mathbf{W}_A.$$

Regardless of the initial population size, if  $\mathbf{A}$  meets the conditions noted above, the population will grow at a rate given by  $\lambda_A$  with a structure proportional to  $\mathbf{W}_A$ . Also,  $\mathbf{A}$  will have a left eigenvector  $\mathbf{V}_A$  comprising stage-specific reproductive values and related to  $\lambda_A$  as

$$\mathbf{V}'_A \mathbf{A} = \lambda_A \mathbf{V}'_A.$$

Reproductive value is a composite of the extent of future reproduction of a female of stage  $x$ , the probability of surviving to realize that reproductive contribution, and the time required for the offspring to be produced (Caswell 1989). Both  $\mathbf{W}_A$  and  $\mathbf{V}_A$  are necessary in evaluating the sensitivity of  $\lambda_A$  to

Table 1. Population parameters referenced to construct a stage-classified projection matrix of double-crested cormorant population growth on Lake Ontario (1979–2000).

Parameter	Estimate	Source
Annual survival of birds from fledging to just before age 1	30–35%	Hickey 1952, Palmer 1962, van de Veen 1973, Ludwig 1984
Annual adult survival <sup>a</sup>	85%	Hickey 1952, Palmer 1962, van de Veen 1973, Ludwig 1984
Percentage age-2 individuals that breed	≥17%	Palmer 1962, van de Veen 1973, Weseloh and Ewins 1994
Percentage age-3+ individuals that breed	98.4%	van de Veen 1973
Mean annual productivity	1.7–2.5 young/nest	Weseloh et al. 1995, Fowle et al. 1999

<sup>a</sup> Product of survival values for individuals about to turn age 2 and individuals about to turn age 3 and older.

effects on fertility and survival (see below).

We calibrated stage-specific matrix parameters based on literature values for cormorants (which included data from Lake Ontario populations; Table 1) and relative to the intrinsic rate of increase ( $r = 0.207$ ) for the population (Price and Weseloh 1986; D.V.C. Weseloh, unpublished data). The data for the Lake Ontario cormorant colonies were pooled to produce a general model. Thus, while our approach was robust to various situations affecting vital rates within a population, the specific model was less useful in depicting the dynamics of individual colonies. We assumed that a proportion of cormorants about to turn age 2 would breed (van de Veen 1973, Price and Weseloh 1986, Weseloh and Ewins 1994, Weseloh et al. 1995) and the population would exhibit a 1:1 sex ratio. To calculate the dominant eigenvalue and corresponding eigenvectors, we used MATLAB (The Math Works, Inc., Natick, Mass. USA).

### Sensitivity analysis

We calculated the proportional change in  $\lambda_A$  relative to proportional changes in the elements  $a_{ij}$  of the projection matrix  $\mathbf{A}$  (i.e., the elasticity). Elasticity measures the effect of a change in the transition element  $a_{ij}$  on the population growth rate  $\lambda_A$ , relative to the effects of equal and absolute changes in other elements (Caswell et al. 1984, de Kroon et al. 1986). Further, elasticity measures of matrix elements provide useful information for managing populations of interest. For example, they can be used to identify potential management strategies that may either lead to the fastest rate of population

recovery (Beissinger and Westphal 1998) or to efficient reduction in population growth of “nuisance” species. The elasticity of  $\lambda_A$  is represented as

$$\frac{a_{ij}}{\lambda_A} \left( \frac{\mathbf{v}_i \mathbf{w}_j}{\langle \mathbf{V}_A, \mathbf{W}_A \rangle} \right),$$

where  $\mathbf{v}_i$  is the  $i$ th element of  $\mathbf{V}_A$ ,  $\mathbf{w}_j$  is the  $j$ th element of  $\mathbf{W}_A$ , and  $\langle \rangle$  indicates the scalar product of the vectors  $\mathbf{V}_A$  and  $\mathbf{W}_A$ . We contrasted effects on rate of increase due to separate 10% decreases

in parameter values for fertility and survival.

To build upon information gained from this sensitivity analysis, we then simulated effects on population parameters that could be caused by environmental conditions or population management. Over a simulated 5-year interval involving 1000 permutations per year, both stage-2 and -3 fertility values and stage-2 and -3 survival values (i.e., breeding females) were varied randomly from 50% below to 10% above the calibrated value. The same factor of change was used for the 2 fertility and survival parameters, but specific to each permutation within a year. We calculated the dominant eigenvalue  $\lambda_A$  separately for median changes (over the 1,000 permutations/year) in fertility versus survival (i.e., while holding either fertility or survival parameters to their calibrated values).

We then used the same approach to simulate an egg-oiling program that would decrease only fertility parameters by 50 to 80% annually over a 5-year simulation. The range of reduction in fertility was intended to reflect logistic difficulties in treating every nest successfully (e.g., tree versus ground nesters, timing of oiling relative to egg-laying, and possible re-nesting; see Bédard et al. 1995, Blackwell et al. 2000). We made no assumptions regarding area, number of colonies, immigration, or emigration.

## Results

Our calibrated model comprised 50% survival from fledging to just before age 1, a mean adult survival rate of 88%, and a mean annual productivity of 1 female fledgling per breeding female (i.e., the

Table 2. Stage-classified<sup>a</sup> projection matrix of double-crested cormorant population growth on Lake Ontario (1979–2000). Fertility estimates (row 1) comprise the product of stage-specific proportion of females breeding (0.50 stage 2, 0.99 stage 3), mean number of female young per female breeder (0.8 stage 2, 1.2 stage 3), and survival from fledging to just before age 1 (0.5).

$F_1 = 0.0000$	$F_2 = 0.2000$	$F_3 = 0.5940$
$S_1 = 0.8700$	0.0000	0.0000
0.0000	$S_2 = 0.881$	$S_3 = 0.8900$

<sup>a</sup>  $F_{\text{stage}}$  values represent fertility of birds about to turn age 1 ( $F_1$ ), age 2 ( $F_2$ ), and age 3+ ( $F_3$ ), while  $S_{\text{stage}}$  values represent survival of birds from just before age 1 to just before age 2 ( $S_1$ ), just before age 2 to just before age 3 ( $S_2$ ), and from just before age 3 on ( $S_3$ ).

average of the 2 stage-specific mean annual productivities; Table 2). The stable age distribution (i.e., the proportion of the population at each stage) comprised over 50% stage-3 individuals, and stage-3 individuals also exhibited the highest reproductive value (Table 3). Post-multiplying the projection matrix by a population vector corresponding to nest-count data for 1979 (apportioned relative to the stage-specific proportion of females breeding and the stable age distribution) produced an exponential growth curve that approximately mirrored the observed population through 1984, but underestimated the number of nests by as much as 59% of the observed value through 1999 ( $\bar{x}$  % difference in nest number = 39.7, SD = 17.3, Figure 1).

Sensitivity analysis revealed that the rate of population increase was most sensitive to survival of adult birds from just before age 3 and older, followed by survival of birds from just before age 1 to just before age 2 (Figure 2). Comparable and separate decreases in stage-specific fertility and survival elements further emphasized the contribution of survival to regulating population growth ( $\bar{x}$  [SD]  $r$  due to effects on stage-specific survival: 0.180 [0.015]; fertility: 0.197 [0.011]). Similarly, simula-

Table 3. Right (stable age distribution  $\mathbf{W}$ ) and left eigenvectors (reproductive values  $\mathbf{V}$ ) of the stage-classified projection matrix of double-crested cormorant population growth on Lake Ontario (1979–2000).

Stage	Stable age distribution	Reproductive value (female fledglings/female of stage x)
1	0.2825	1.0
2	0.1998	1.4
3+	0.5177	1.7

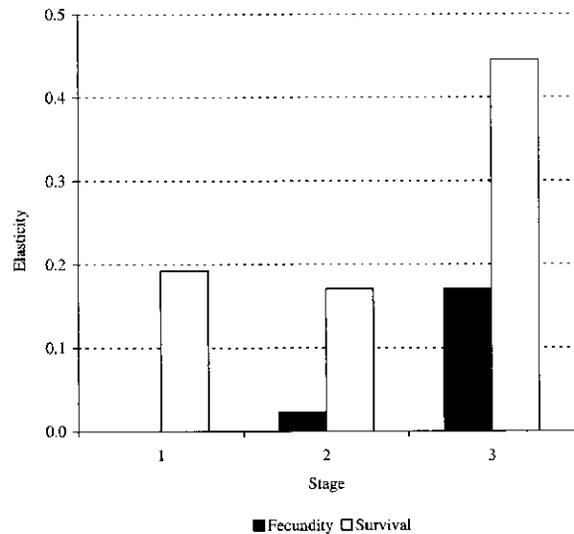


Figure 2. Measures of stage-specific elasticity for fertility and survival values in a matrix model of double-crested cormorant population growth on Lake Ontario, 1979–2000, calibrated to the intrinsic rate of increase ( $r = 0.207$ ).

tions reflecting environmental or population control affecting fertility and survival separately over a 5-year period produced on average a 2-fold difference in the annual rate of increase, with the greatest decrease in  $r$  resulting from effects on survival ( $\bar{x}$  [SD]  $r$ : 0.081 [0.007];  $r$  due to effects on fertility: 0.167 [0.002]). Further, based on median values from 1000 permutations per year, simulated egg-oiling over 5 years reduced fertility values on average (SD) by 65% (0.5) and produced a mean (SD) annual  $r$  of 0.0447 (0.002), approximately 22% of the observed rate of increase.

## Discussion

Our model of cormorant population growth for Lake Ontario provided a biologically reasonable representation of Lake Ontario cormorant population dynamics and a method by which managers may evaluate potential effects of no action, population reduction, or other management options. Specifically, the model structure was conservative relative to population age structure and the complications associated with quantifying the effects of immigration and emigration (Price and Weseloh 1986; Frederiksen and Bregnballe 2000a, b) on the annual rate of increase. The model reflected lake-wide versus colony-specific changes in nest numbers. Values for population parameters were similar to those reported in prior research and comparable

with rates found for great cormorants (*P. carbo sinensis*; e.g.,  $\bar{x}$  first year survival=0.58,  $\bar{x}$  annual adult survival=0.88; Frederiksen and Bregnballe 2000a, b).

The model, however, was simple relative to variability associated with climatic and resource effects on population growth. In particular, the model did not include density-dependent effects, such as the potential changes in the percentage of younger individuals breeding with loss of older breeders (e.g., Coulson et al. 1982). Further, because of few demographic data, model validation was impossible. However, our incorporation of biologically reasonable data into a projection matrix provided a dynamic method for comparison of potential relative effects of population parameters within local or regional cormorant populations. Similar approaches have been taken in situations involving few demographic data and endangered species management (Crouse et al. 1987, Crowder et al. 1994, Doak et al. 1994, Siddeek and Baldwin 1996, Kareiva et al. 2000), in cases of wildlife damage management (Bregnballe et al. 1997, Fowle et al. 1999, Bosch et al. 2000, Francis 2000), and in waterfowl management (Williams 1989, Williams and Nichols 1990, Johnson et al. 1993, Nichols et al. 1995, Johnson and Williams 1999).

As structured, model output indicated that survival parameters, particularly survival of birds from just before age 3 on, outweighed effects of fertility on the annual rate of increase. Bédard et al. (1999) noted that because cormorants exhibited deferred maturity, small clutch size, and low recruitment of birds into the breeding population, changes in adult survival could produce marked changes in the annual rate of increase. Further, because the cormorant is long-lived (Palmer 1962, Hatch and Weseloh 1999) and the percentage of individuals breeding by age 2 is generally low, survival of stage-1 and -2 individuals had less of an effect on  $r$ . Results of simulated effects on fertility and survival due, for example, to decreased availability of food or breeding habitat, or the deterministic effects of population reduction measures, also indicated the annual rate of population increase was most sensitive to changes in adult survival.

Simulation of a 5-year egg-oiling program, by modifying fertility values only, resulted in a mean 78.4% decrease in the value of  $r$ , with annual population growth maintained at approximately 4.5%. A decrease in fertility values by approximately 77% would be required to reduce population growth to

zero (assuming no immigration the following year). Cormorants in the Great Lakes region, however, often nest in trees, with some nests >10 m above the ground. For example, 5,202 cormorant nests were recorded in trees (none on the ground) on Middle Island, Ontario in Lake Erie during 2000 (Weseloh et al. 2002). The effort and time required annually to access nests in trees, coupled with the results from our simulation, suggest that egg-oiling alone would be an inefficient management alternative for controlling cormorant population growth on Lake Ontario. However, given the model assumptions and simulation results, management scenarios that include lethal control of adults would likely effect a more rapid (negative) change in the annual rate of increase of the cormorant population.

The need for scientific inquiry into problems associated with cormorants and screening of cormorant population management alternatives, such as presented here in the context of Lake Ontario, was recently voiced by the United States Fish and Wildlife Service (USFWS; Federal Register Volume 64, No. 215, 1999). Further, the USFWS prepared a draft Environmental Impact Statement (EIS; USFWS 2001) to address the various management options for reducing conflicts associated with burgeoning cormorant populations. Since 1972, the USFWS has issued depredation permits for damage by migratory birds, allowed egg-oiling to control cormorant population growth on Little Galloo Island, New York, and more recently implemented a depredation order (March 1998; 50 Code of Federal Regulations 21.47) allowing aquaculture facilities in 13 states to take unlimited numbers of cormorants when they are found committing or about to commit depredations to aquaculture stocks. The EIS, however, included management alternatives of "no action" to "large-scale population control" on breeding and wintering grounds and migration areas, but listed as the proposed action the establishment of a new depredation order.

In addition, the Ontario government is considering management alternatives for cormorants, primarily to protect rare ecosystems found on islands within the Canadian Great Lakes and address the questions of cormorant predation on fish populations (K. Loftus, Ontario Ministry of Natural Resources, personal communication). We suggest that investigations into the relationship of demographic parameters and their individual and combined effects on rate of cormorant population

growth will provide the scientific foundation necessary for assessing potential effects on resources and evaluating management options.

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