J. Great Lakes Res. 34:122–133
Internat. Assoc. Great Lakes Res., 2008

Bioenergetics and Prey Consumption of Breeding Double-crested Cormorants in the Beaver Archipelago, Northern Lake Michigan

Nancy E. Seefelt* **and James C. Gillingham**

Department of Biology
Central Michigan University
Mount Pleasant, Michigan 48859

ABSTRACT. *Colonial waterbirds are an important component of Great Lakes ecosystems. In order to investigate the role these birds play in an aquatic food web, bioenergetics models, using allometric equations, were applied to breeding double-crested cormorants* (Phalacrocorax auritus) *and their offspring in the Beaver Archipelago, northern Lake Michigan. These models were parameterized using detailed information collected during the 2000 and 2001 breeding seasons, as well as literature values. Each breeding season was divided into stages in the models to reflect changes in cormorant diet and population size documented in the study area. The models estimated the total prey biomass consumed as 1,445 metric tonnes (mt) of prey in 2000, and 1,585 mt of prey in 2001. Each year, the majority of the prey biomass was alewife* (Alosa pseudoharengus)*, with these fish comprising a greater percentage of prey biomass consumed in 2001. An increase in cormorant reproductive success in 2001 may be linked to this increase in alewife biomass consumed; the breeding bird population size, however, declined in 2001 as compared to 2000. The other prey items, which are not considered to be species of commercial or sport value, were also important contributors to bird diet and consumption of these species did tend to vary from year-to-year. Overall, the application of bioenergetics models allows for greater understanding of the role of cormorants as predators and as energy links in the system.*

INDEX WORDS: *Cormorant, bioenergetics,* Phalacrocorax auritus*, Great Lakes, alewife, allometric equations.*

INTRODUCTION

The double-crested cormorant (*Phalacrocorax auritus*) (hereafter: DCCO) breeding population has increased substantially throughout the Great Lakes basin over the last several decades (Ludwig 1984, Cuthbert *et al*. 1997, Ludwig and Summer 1997, Wires *et al*. 2001). In the Beaver Archipelago of northern Lake Michigan, the breeding population size peaked in 1997 at 11,709 pairs (Cuthbert *et al*. 1997), and remained relatively large in 2000 and 2001, with 10,125 and 9,705 breeding pairs, respectively (Seefelt and Gillingham 2005).

As opportunistic fish predators, DCCOs often feed in shallow waters on forage fish (Lewis 1929, Birt *et al*. 1987, Seefelt 2005, Seefelt and Gillingham 2006a), however sportfish can comprise a significant portion of their diet in some systems (Johnson *et* al. 2002, Rudstam *et al*. 2004). Depending on the system of interest, migrating cormorants can have either localized effects on fisheries (Kirsch 1995) or much more significant impacts on some prey species (Rudstam *et at*. 2004, Dobeisz *et al*. 2005). During the breeding season, cormorants can deplete some prey species around their colonies (Birt *et al*. 1987). Cormorants in Lake Erie, however, do not preferentially forage in areas of historically high fish concentrations, but in areas close to their colonies (Stapanian *et al*. 2002). Although the effects on forage fish populations can be limited and may only occur in localized areas (Madenjian and Gabrey 1995), research indicates that cumulative effects on forage species can also be large scale (Ridgeway *et al*. 2006). The impact of foraging cormorants on fisheries of interest varies by location; regardless, bird predation on forage fish can impact aquatic community structure because of the role these fish play in community trophic dynamics (Craven and Lev 1987).

Waterbird bioenergetics can assess the importance of avian predators in energy transfer and nu-

*Corresponding author. E-mail: seefe1ne@cmich.edu

trient cycling in aquatic systems (Wiens and Scott 1975). Models are used to calculate the food requirements necessary for a bird's daily energy expenditure and thus, can estimate total prey consumption (Cairns *et al.* 1991). By this quantification, the demands avian predators place on aquatic communities can be determined (Madenjian and Gabrey 1995). Because cormorants can be wide-ranging generalists, it is difficult to measure their energy demands directly. However, many modeling approaches have been developed to estimate the energetics of metabolism and adjust for other factors that may influence energy requirements (Wiens 1984).

The primary variables incorporated into bioenergetic models include calculated daily energy demands, food type, daily consumption, and population estimates (Fowle 1997). Direct measurements of wild bird metabolism have been be used to develop allometric equations that predict avian metabolic rates based on body mass (Kendeigh *et al.* 1977). Techniques such as doubly-labeled water and time-budget analysis can measure metabolism of free ranging birds (Nagy 1989, Birt-Friesen *et al.* 1989). In addition, many indirect modeling approaches have been developed to extrapolate individual metabolic estimates to whole populations (Wiens 1984, Cairns *et al.* 1991, Glahn and Brugger 1995, Madenjian and Gabrey 1995, Fowle 1997). In all models, energy consumption is based on metabolism. Furthermore, these models have applied specific caloric requirements to daily energy expenditure to estimate food consumption, and have been useful in estimating total prey consumption by avian populations.

Several studies have investigated the influence of fish-eating birds on fisheries both in Europe (Suter 1995, Warke and Day 1995) and in the Laurentian Great Lakes (Madenjian and Gabrey 1995, Maruca 1997, Neuman *et al.* 1997, Lantry *et al.* 1999, Schiavone 2001, Schiavone 2003, Hebert and Morrison 2003, Dobeisz *et al.* 2005). Research suggests that waterbirds play central roles in marine food webs (Cairns 1992), and this probably holds true in Great Lakes community dynamics. To get a realistic picture of the impact avian predators have on fish populations, it is necessary to incorporate quantitative data on the diets, population size, and energy requirements of the bird species. In addition, reliable data on the size of the fish populations, with the appropriate spatial and temporal scales, is necessary to more fully understand the potential impacts (Draulans 1988). Yet even with the latter lacking, bioenergetics approaches can still aid in determining the energy demands placed on aquatic systems by avian predators. Understanding energy demands can then allow for further investigation of the relationship these predators may have with their prey, and to compare the prey consumption by birds to other sources of mortality.

In this study, we used a bioenergetics approach based on allometric equations to investigate the energy demands and estimate annual prey consumption of breeding DCCOs and their chicks in the Beaver Archipelago, northern Lake Michigan during 2000 and 2001. In addition, we estimated the biomass of individual prey species consumed by birds each year. Quantifying waterbird predation on fish and other species is important in understanding the northern Lake Michigan food web. In addition, this work can be directly compared to work in other systems, such as Lake Erie (Madenjian and Gabrey 1995, Hebert and Morrison 2003), in an effort to understand the role of cormorants in Great Lakes ecosystems.

METHODS

Study Area

The Beaver Archipelago of northern Lake Michigan consists of about ten main islands and numerous small islands (Fig. 1). The number of smaller islands depends on fluctuating lake levels. Gull Island (1.0 km^2), Hat Island (0.05 km^2), Pismire Island (0.02 km^2), and Hog Island (8 km^2) contained nesting colonies of DCCOs in 2000 and 2001 (Fig. 1). The Hog Island colonies were located on two peninsulas known as Grape Spit, on the west side of the island, and Timms Spit, on the east side of the island (Fig. 1). Population data collected in the Main Archipelago (including colonies on Hat, Hog, and Pismire islands) in 2000 (8,316 pairs) and 2001 (8,096 pairs) were used in the construction of the bioenergetics models (Table 1). Gull Island (including two colonies, North and South) is separated from the main island group by almost 18 km (11 miles) of open water to the west of Beaver Island. From bi-weekly aerial surveys (unpublished data) it was concluded that the cormorants breeding at Gull Island remained relatively close to these colonies and did not regularly travel to the Main Archipelago. This assumption was strengthened by a radiotelemetry study of cormorants breeding in the Main Archipelago that found that typical foraging distances of 2.5 km (1.55 miles) from the breeding colonies (Seefelt and Gillingham 2006b). Further-

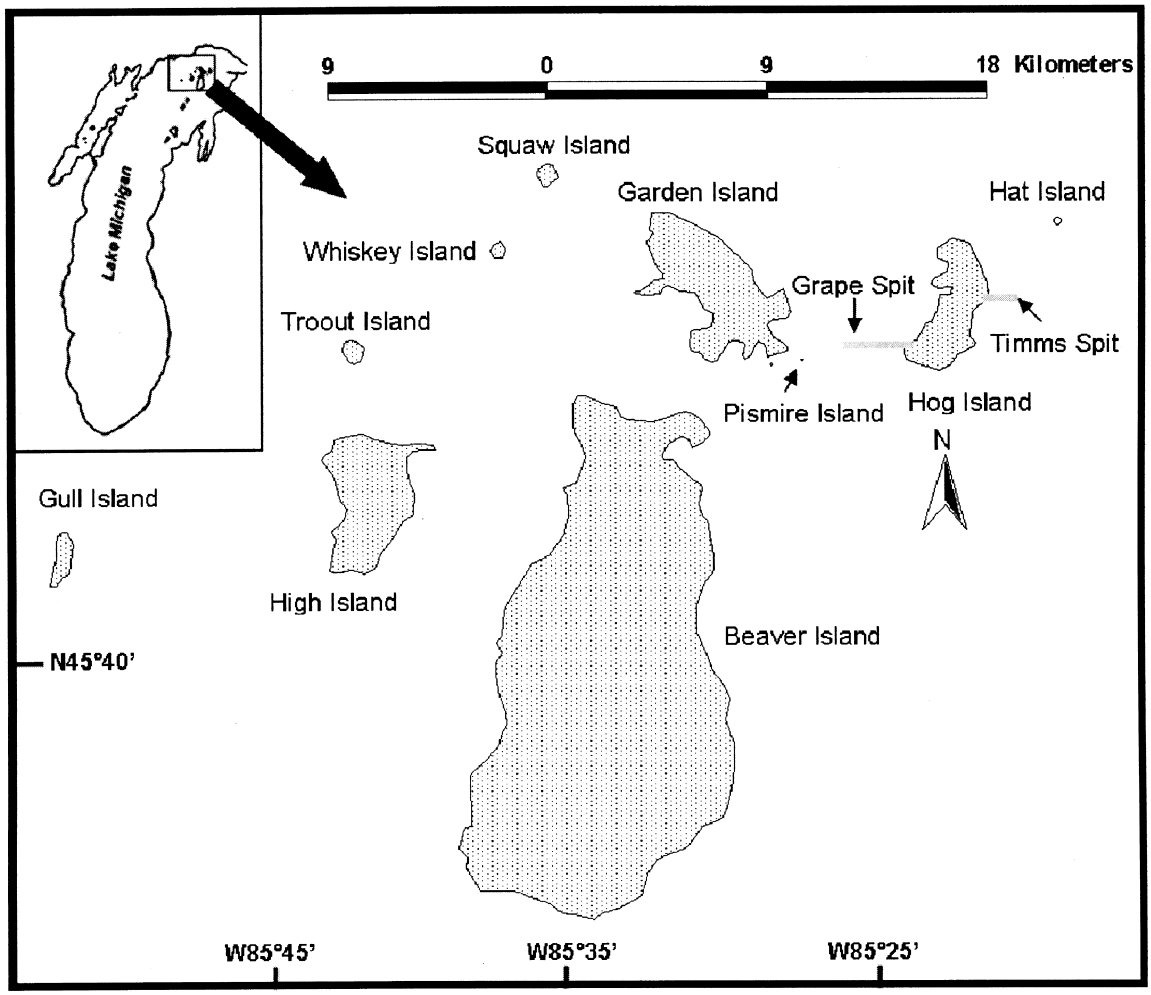

FIG. 1. The Beaver Archipelago of northern Lake Michigan.

more, dietary analysis indicated that Gull Island birds fed primarily on alewife (*Alosa pseudoharengus*) throughout the breeding season and lacked near-shore prey species in their diet, including crayfish (*Orconectes* sp.), brook stickleback (*Culaea inconstans*), and johnny darter (*Etheostoma nigrum*). These same near-shore species were present in the diet of birds breeding in the Main Archipelago (Seefelt 2005). Similar dietary differences were reported by Ludgwig *et al.* (1989). Therefore, the models were limited to the Main Archipelago colonies because of their close proximity to important near-shore sport fish habitats, including a smallmouth bass (*Micropterus dolomieui*) fishery.

Model Construction

The major model parameters include (1) seasonal arrival/departure dates of cormorants, (2) population estimates of adult birds and chicks, (3) food habit data, and (4) estimates of avian daily energy expenditure (DEE). Population estimates and diet data were collected in the study area (Seefelt 2005) and, whenever possible, model inputs were measured in the field each year. Three ground counts spread over the breeding season were conducted during 2000, and again in 2001, to document the peak population size, as well as changes in population size and clutch size, over the breeding season (Seefelt 2005). To assess the diet of cormorants, regurgitate samples (collected during colony visits) and stomach contents of harvested birds (collected throughout the breeding season) were used to estimate diet composition (Seefelt 2005). A third method, pellet analysis, was determined to be less reliable for DCCO diet quantification in the study area (Seefelt and Gillingham 2006a). Other model

TABLE 1. Life history characteristics of double-crested cormorants used to model prey consumption by breeding adult and young birds in the Beaver Archipelago, 2000 and 2001.

Characteristic	2000	2001
Number of Nests (seasonal high)	8316	8096
kJ (calories) per egg[a]	0.315(75.4)	0.315(75.4)
Clutch Size—Early Season	2.60	2.89
Clutch Size—Mid Season	1.50	2.38
Number of Incubation Days[b]	28	28
Hatch Rate (% of eggs laid)[c]	62	62
Fledge (days)[b]	50	50
Fledged Rate (% of chicks hatched)	29	49
Hatch-year Mortality (% year)[d]	42	42
Breeder Mortality (% year)[e]	20	20
Mass at Hatch (g)[b]	34	34
Adult Mass (kg)	2.0	2.0

[a] Kendeigh *et al.* 1977
[b] Hatch and Weseloh 1999
[c] Blomme 1981
[d] Madenjian and Gabrey 1995
[e] Cairns *et al.* 1991
All other inputs were measured in the field by the authors

inputs were taken from the literature. A complete list of model parameters for each year is shown in Table 1. Because these bioenergetic models provide descriptive estimates of daily and seasonal prey consumption, no formal statistical comparisons or confidence limits were calculated.

To provide better accuracy in the model, the breeding season was divided into three categories: pre-nesting stage/incubation stage (20 April–12 June), nestling stage (13 June–31 July), and post-nesting stage (01 August–10 September). Dietary data were categorized by date to reflect the changes in DCCO diet and population size as the breeding season progressed. These proportions were used to determine the biomass of individual prey species consumed by cormorants over the breeding season (Table 2, from Seefelt 2005). Models were applied to each year's data separately.

The bioenergetic models typically follow a procedure outlined by Madenjian and Gabrey (1995) and are then modified to include individual prey species by Hebert and Morrison (2003). However, in this study, models were developed using a spreadsheet (Microsoft Office Excel®). Our mode1s used allometric equations dependent on body mass to determine DEE for breeding adult DCCOs and their chicks. These equations were successfully used in the past (Birt-Friesan *et al*. 1989, Cairns *et al*. 1991, Madenjian and Gabrey 1995, Hebert and Morrison 2003). Details of the equations used can be found in Appendix 1 of Madenjian and Gabrey (1995) and in Seefelt (2005).

To maintain consistency with earlier models (Madenjian and Gabrey 1995, Hebert and Morrison 2003), the body mass for adult cormorants was determined by averaging the 150 birds harvested for the dietary study during 2000 and 2001. For adult birds, the daily energy intake (DEI) is determined by dividing DEE by the assimilation efficiency (given as 0.80 by Furness 1978). In addition, the bioenergetics of egg production was included in the model following the work of Kendeigh *et al*. (1977). The greatest number of nests counted each year was used to best estimate the maximum energy

TABLE 2. The proportion of individual prey item biomass consumed by breeding adult and young double-crested cormorants for the pre-breeding/incubation (20 April–12 June), nestling (13 June–31 July), and post-breeding (01 August–10 September) periods in the Beaver Archipelago, 2000 and 2001. Sample sizes reflect the number of regurgitates and stomachs combined. (from Seefelt 2005)

	2000			2001		
Prey Item	Pre-nesting/ Incubation (n = 31)	Nestling (n = 208)	Post-breeding (n = 21)	Pre-nesting/ Incubation (n = 130)	Nestling (n = 600)	Post-breeding (n = 50)
Alewife (*Alosa pseudoharengus*)	0.49	0.54	0.22	0.22	0.81	0.70
Crayfish (*Orconectes* spp.)	0	0.24	0.36	0	0.02	0.05
Sculpin (*Cottus* spp.)	0	0.06	0.08	0.30	0.05	0.07
9-spine Stickleback (*Pungitius pungitius*)	0.01	0.01	0.01	0.38	0.01	0
Sucker (*Catostomus* spp.)	0.11	0.11	0.19	0.03	0.10	0.16
Spottail Shiner (*Notropis hudsonius*)	0.29	0	0	0.01	0	0
Other*	0.01	0.04	0.14	0.06	0.01	0.02

* This category may contain species that have proportions listed as "0" during that same time period

TABLE 3. The energy density in kJ/kg (kcal/kg) for some prey species that are consumed by double-crested cormorants in the Beaver Archipelago, 2000 and 2001.

Prey Species	Energy Density kJ/kg (kcal/kg)
Alewife (*Alosa pseudoharengus*)[a]	8.272(1.977)
Crayfish (*Orconectes spp.*)[a]	4.506 (1.077)
Sculpin (*Cottus spp.*)[a]	6.247 (1.493)
9-spine Stickleback (*Pungitius pungitius*)[a]	6.247 (1.493)
Sucker (*Catostomus spp.*)[b]	3.699 (0.884)
Spottail Shiner (*Notropis hudsonius*)[b]	4.992 (1.193)

[a] From Cummins and Wuycheck (1971)
[b] From Bryan *et al.* (1996)

input needed for egg production. Daily food consumption (DFC) was found by dividing DEI by the average energy density (AED) of bird diet for each stage of the breeding season. In addition, the total DEI for all adult birds was summed throughout each segment of the breeding season. The DEI of individual prey types was then determined by multiplying total cormorant DEI by the proportion that a particular prey species appeared in the diet by mass during each stage of the breeding season. Then prey DEI was multiplied by energy content conversion factors for each prey type (Table 3, Cummins and Wuycheck 1971, Bryan *et al.* 1996) to determine the biomass of each prey type consumed. These values were calculated for each time period of the breeding season (pre-nest/incubation, nestling and post-breeding stages) and then combined to determine the total biomass (units: metric tonnes or mt) of prey consumed for each year by adult birds.

The breeding season for cormorant chick models was divided into two segments, pre-fledging and post-fledging, which corresponded to the nestling and post-breeding time segments, respectively, for adult birds. To simplify the model, all eggs hatched simultaneously and all young fledged on the same date. An allometric equation (from Kendeigh *et al.* 1977) was used to determine the daily energy expenditure of a pre-fledged bird (nestling) (DEEN), and then daily food consumption by a pre-fledged bird (DFCN) was determined. Since pre-fledged birds grow throughout the season, this equation included a daily growth increment (DG), which was equal to the food needed to increase the mass of the bird. Growth rate was assumed to be a linear relationship and modeled as described in Madenjian and Gabrey (1995). Since young birds continue to grow and gain mass after fledging, a similar equation was used to determine post-fledged birds' DFC. However, growth was modeled at 25% of that of nestlings to reflect the increased energy requirements of flight. When fledglings attained adult body mass, the allometric equation was further modified to mimic the adult equation (Madenjian and Gabrey 1995). The total consumption of prey biomass by chicks was determined using the same method used in adult populations. These biomass values were added to adult values to determine total biomass of each prey type consumed for each time period of the breeding season and also yearly totals. In addition, the total biomass of prey consumed by a single chick that survived the entire simulation for each year was calculated by summing the AED for one chick during both the pre-fledging and post-fledging time periods.

Sensitivity Analysis

Sensitivity analysis was performed to determine which model parameters were most influential in calculating total DEI and, therefore prey consumption, by breeding cormorants and their chicks. An individual parameter perturbation method was used (Bartell *et al.* 1986, Madenjian and Gabrey 1995). Thirteen model inputs were examined for a total of 26 simulations. For each sensitivity analysis simulation, only one model input was changed while all other parameters were left at their original values. A simulation was conducted for an individual model input by raising it from its original value by 10%; a second simulation was performed for that same model input by lowering its value 10% from its original value. The outputs from these simulations were compared to the original model's output to determine percent change.

RESULTS

The models calculated the DFC per adult breeding bird in 2000 based on the ACD of the diet to be the same during the pre-nesting/incubation and nestling periods, but estimated to increase during the post-breeding period (Table 4). The DFC values per adult bird for 2001 were similar to 2000 levels during the pre-nesting/incubation period, but estimated to be lower for the nestling and post-breeding periods (Table 4). These lower values during 2001 are due to the consumption of prey having more energy per kg. In 2000, the DFC per chick based on ACD of the diet ranged from 0.02 kg to

TABLE 4. Total daily food consumption (kg) for breeding double-crested cormorants during each period of the breeding season in the Beaver Archipelago, 2000 and 2001.

	Daily Food Consumption (kg)	
	2000	2001
Pre-nesting/Incubation Stage	0.55	0.55
Nestling Stage	0.55	0.48
Post-breeding Stage	0.65	0.51

TABLE 5. Total seasonal food consumption (kg) per pre-fledged (nestling) and post-fledged (fledgling) double-crested cormorant chicks in the Beaver Archipelago, 2000 and 2001.

	Seasonal Food Consumption (kg)	
	2000	2001
Pre-fledged Chick	9.0	7.9
Post-fledged Chick	26.0	20.4
Seasonal Totals	35.0	28.3

0.32 kg from hatching to the end of the pre-fledging period (Fig. 2). For the post-fledging period in 2000, DFC per chick ranged from 0.60 kg at fledging to 0.65 kg, when chicks attained adult size. In 2001, the DFC per chick ranged from 0.01 kg to 0.28 kg from hatching to the end of the pre-fledging period. For the post-fledging period in 2001, DFC per chick ranged from 0.47 kg at fledging to 0.51 kg, when chicks attained adult size. The sharp increase in energy requirements between nestling and fledging birds is due to the energy input needed for flight. Models indicate that chicks in 2001 consumed less prey per chick than chicks in 2000 due to a more energy-dense diet in 2001; in 2001, a cormorant chick consumed approximately 78% of prey biomass consumed by a chick in 2000 before leaving the study area (Table 5).

According to modeling results, breeding DCCOs and their young consumed an estimated total of 1,445 mt of prey in 2000. Of this, almost 30% of the prey biomass consumed by DCCOs were alewife, and 24.5% were crayfish. Other prey, including sculpin (*Cottus* spp.), nine-spine stickleback (*Pungitius pungitius*), sucker (*Catostomus* spp.), and spottail shiner (*Notropis hudsonius*), together made up most of the remainder of the diet (37.5%) (Table 6). In 2001, adult and young birds consumed a combined estimated total of 1,585 mt of prey. Alewife comprised almost 40% of the diet, with the second most important prey being sculpin (22%). Other prey, including crayfish, nine-spine stickleback, sucker, and spottail shiner collectively comprised almost a third of the diet (32%) (Table 6). In addition, the "other" category contributed 8%

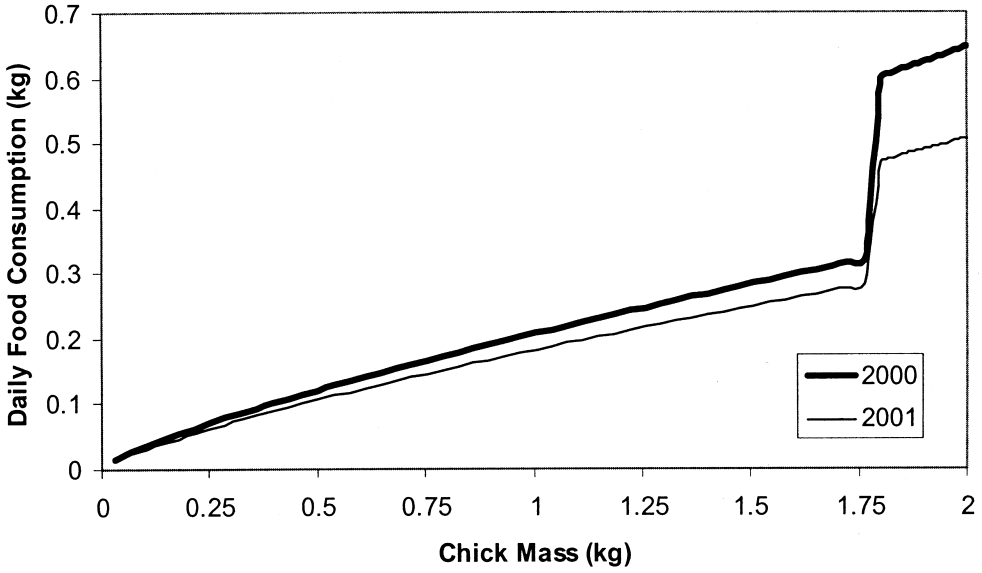

FIG. 2. Daily food consumption (kg) of double-crested cormorant chicks in the Beaver Archipelago in Lake Michigan, 2000 and 2001. The sharp increase in daily food consumption (chick mass = 1.75 kg) is due to the energy consumption necessary for flight in fledglings.

TABLE 6. Biomass (mt) of prey consumed by both breeding double-crested cormorants and their offspring in the Beaver Archipelago, 2000 and 2001.

	Biomass Consumed (mt)	
	2000	2001
Alewife (*Alosa pseudoharengus*)	427	696
Crayfish (*Orconectes spp.*)	354	55
Sculpin (*Cottus spp.*)	60	369
9-spine Stickleback (*Pungitius pungitius*)	13	172
Sucker (*Catostomus spp.*)	301	271
Spottail Shiner (*Notropis hudsonius*)	168	5
Other	122	17
Seasonal Totals	1,445	1,585

and 6% to the cormorant diet in 2000 and 2001, respectively. This category included primarily johnny darter, brook stickleback, and trout-perch (*Percopsis osmiscomaycus*). Some prey items, such as spottail shiner, were common in the pre-nesting/incubation diet samples but uncommon during the other breeding season stages. Because of this rarity, spottail shiners were included in the "other" category when they were found in the nestling period or post-breeding season diet.

Sensitivity analysis revealed that adult and young bird assimilation efficiency, the number of nests, and adult mass were most influential in determining model output, as determined by comparing absolute values to those produced by perturbing the model by increasing and decreasing individual parameters by 10 % (Table 7). For both the number of nests and adult mass, if input values were increased, model output values also increased (as indicated by the positive numbers in the +10% column). However, an increase to assimilation efficiency (both adult and young birds) resulted in a decrease in model output (as indicated by the negative number in the -10%) because birds would receive more usable energy from each prey item. In contrast, when assimilation energy was decreased, birds were required to consume more food (as indicated by the positive number in the +10%). Most other model inputs changed the output between 0% and 2.5%; calories per egg and mass at hatching changed the model output by less than 1%. Overall, the models were fairly robust in regard to any uncertainty in model inputs.

TABLE 7. Sensitivity analysis results for change in input parameters on daily energy intake of double-crested cormorants as determined by bioenergetics models.

	Input Perturbation Error	
Model Output	+10%	–10%
Number of Nests	+10.0	–10.0
Adult Mass	+7.2	–7.4
Hatch Rate	+2.5	–2.5
Fledge Rate	+1.1	–1.1
Hatch–year Mortality	–0.8	+0.8
Breeder Mortality	–0.6	+0.6
kJ (calories) per Egg	0.0	0.0
Adult Assimilation Efficiency	–9.1	+11.1
Young Assimilation Efficiency	–9.1	+11.1
Energy Density of Prey (kcal/kg)	–0.1	+0.1
Mass at Hatching	0.0	0.0
Incubation Length (days)	–0.5	+0.5
Fledgling Length (days)	–0.3	+0.3

DISCUSSION

According to the bioenergetics models, breeding DCCOs and their young consumed an estimated 1,445 mt and 1,585 mt of prey during 2000 and 2001, respectively. During both years, alewife contributed the greatest biomass to these totals, relative to other prey species. However, in 2001, alewife comprised more than one and a half times the biomass of the birds' diet as compared to 2000. Alewife is a major planktivorous species in the Lake Michigan community and an important energy link to upper consumer levels (Madenjian *et al.* 2004). Alewife is an important link between inshore and deep lake communities (Eck and Brown 1987, Madenjian *et al.* 2004). Because of its life history and abundance, alewife is considered to be a key species in Lake Michigan and its population trends appear to be a driving force in fish community dynamics (Eck and Brown 1987, Madenjian *et al.* 2002, Madenjian *et al.* 2004). Although alewife biomass in Lake Michigan has remained relatively stable between the early 1980s and 2003 (Madenjian *et al.* 2002, Madenjian *et al.* 2004), local availability of the species may have fluctuated between 2000 and 2001. Further, warm spring temperatures in 1998 led to moderately high numbers of age-3 alewives in 2001 in Lake Michigan (Madenjian *et al.* 2004) and these fish are an attractive prey size for DCCOs. Still further, alewife has a higher energy density as compared to other available prey

(Cummins and Wuycheck 1971, Bryan *et al.* 1996). This, as well as their schooling habits and general availability in the system, may make these fish a desirable prey for cormorants and explain why birds rely on alewife as a major energy source.

Several other prey taxa showed year-to-year variability in terms to their importance to cormorant diet. Crayfish and spottail shiner were both prominent in terms of biomass consumed in 2000. However, in 2001, the biomass contributed to the diet of DCCOs sharply declined for both taxa. The other category, which included only fish, also showed a sharp decline in 2001. This result emphasized the importance of each prominent prey type in 2001, and the importance of alternative prey in 2000 in contributing to the overall energy demands of the breeding DCCO population and their offspring. In contrast, the biomass of both nine-spine stickleback and sculpin in DCCO diet increased in 2001 as compared to 2000. Only one prey type, sucker, remained relatively constant in terms of biomass when both years were compared. The energy density of fish, with the exception of suckers, is higher than crayfish (Cummins and Wuycheck 1971, Bryan *et al.* 1996). Suckers, as larger prey items, provide more energy than crayfish per prey item, averaging 0.74 kJ compared to 0.02 kJ, respectively.

The number of breeding DCCO declined from 2000 to 2001. According to the models, however, the total estimated biomass of prey consumed by DCCOs increased. This increase in prey biomass consumed may have been due to higher reproductive success reflected by both the total number of chicks produced and the number of chicks fledged per pair in 2001, as compared to 2000. Hatch and Weseloh (1999) remarked that the local densities of DCCOs may be affected by the temporal and spatial distribution of their prey. Number of young produced by each pair each year (and thus, the total number of chicks produced) could also be influenced by yearly prey availability patterns. For example, cormorant reproductive success may be intimately linked to alewife populations in some systems (Weseloh and Ewins 1994). In addition, in the North Channel of Lake Huron, DCCOs have been shown to exhibit density-dependent population growth (Ridgeway *et al.* 2006), which could also help explain the greater reproductive output in 2001 in the Beaver Archipelago.

The DFC (daily food consumption) for both adult birds and chicks was estimated as higher in 2000 than in 2001, and therefore, so was the biomass of prey necessary to raise a chick to fledging. In addition, DFC was shown to change as the breeding season progressed during both years in proportion to the energy density of the diet; yearly variations are due to the overall greater energy density of the diet in 2001 than in 2000. Fewer prey items were consumed per individual in 2001, but more chicks were successfully raised to fledging. The model estimates suggested that energy density of prey types consumed and prey availability were better predictors of the number of chicks successfully fledged per year than were the number of nests. However, the models were most sensitive to the number of nests present, adult body mass, and the assimilation efficiency. Although the number of nests and adult body mass were measured directly each year, assimilation efficiency used in the models was a standard value (80%) used in previous models (Madenjian and Gabrey 1995, Hebert and Morrison 2003). However, the digestive efficiency of free-living chicks has been measured at 85% (Dunn 1975), and digestive efficiency can vary depending on prey type (Brugger 1993). Therefore, there could be considerable differences in the DEE in the field and values predicted by the model. Direct measurements of DEE in free-living birds are still needed to better calibrate bioenergetic models in many systems (Carss *et al.* 1997).

Unlike previous studies (Madenjian and Gabrey 1995, Hebert and Morrison 2003), we did not attempt to model the importance of non-breeding cormorants in the system or the migratory seasons. In the Beaver Archipelago, it was difficult to ascertain the population size of non-breeders during the breeding season. When plumage patterns and gonad development (harvested birds only) were used to determine maturity, very few non-adults were documented in flocks and harvested birds (unpublished data). An exception to this was the post-breeding season, when some birds collected were fledglings. Better estimation of the number of non-breeding birds during the breeding season and the inclusion of migration would enhance this study. Further work is necessary to fully estimate the biomass of prey consumed by all DCCOs in the system, including during migration.

As with the work of Madenjian and Gabrey (1995), better estimates of prey fish populations are necessary to fully understand the impact the breeding DCCOs and their young may have on these prey populations in the study area. Smallmouth bass is one species that has been recently censused in the Beaver Archipelago (Seider 2003) Although this

species has not been recently documented as an important prey item in cormorant diet in the Beaver Archipelago (Seefelt 2005), Ludwig *et al*. (1989) documented smallmouth bass in the diet of DCCOs in northern Lake Michigan. Their methods involved counting food items regurgitated during the handling of birds and estimating prey mass, with few prey actually collected and/or measured. However, in parts of northern Lake Michigan, it was estimated that smallmouth bass could possibly represent up to 3% of the biomass of prey items collected in 1989 (based on a few bass collected out of 286 food items). Regardless, by estimated biomass, alewife, sucker, and common shiner were all more prominent in the samples collected (Ludwig *et al*. 1989). To date, there is little information regarding the availability of many of these other species in the Beaver Archipelago, which continue to be important in the DCCO diet in the study area. Our study was an attempt to better quantify the role of cormorants as predators on a local scale and how their impact may vary from year-to year; however, without better estimates of prey availability, understanding whether cormorants are exhibiting prey selectivity and/or competing with desired species, as well as their ecological role in the system, remains unclear.

Overall, the extent of impacts DCCOs have on fisheries seems to be site-dependent and to vary by the scale of the investigation. Several studies in the Great Lakes have attempted to determine if cormorants have a secondary impact on predaceous fish. In Lake Ontario, cormorants were estimated to consume < 1% of the available forage fish, compared to 13.3% taken by salmonids in the early 1990s (Madenjian and Gabrey 1995). Similarly, in the early 1990s in Lake Erie, cormorants were estimated to take < 2% of the biomass of forage fish consumed by walleye (*Stizostedian vitreum*). Other predators (including mergansers and gulls) ate more fish than cormorants (Weseloh and Casselman 1992). These studies emphasize that cormorants have a minor impact on fisheries over a lake-wide scale. However, cormorants may still impact local forage fish and contribute to local changes in prey availability, thus influencing local populations of sport/commercial species. In Oneida Lake, for example, cormorant predation on yellow perch (*Perca flavescens*) and juvenile walleye is a leading factor in the decline of the fisheries (Rudstam *et al*. 2004). In Lake Ontario, DCCOs annually consume more biomass of smallmouth bass and yellow perch compared to anglers and commercial fishers (Johnson *et al*. 2002).

The Lake Michigan food web has profoundly changed over the last several decades, yet in 2003, alewife were still the most abundant prey fish (Madenjian *et al*. 2004). This exotic species and many others, as well as other anthropogenic impacts, have profoundly changed the Lake Michigan ecosystem since pre-settlement. Currently, cormorants, in conjunction with predatory fish, are probably functioning as important predators of alewife and other prey fish on a local scale within the Beaver Archipelago. Long-term trends in alewife biomass suggest that salmonids have been effective in reducing lake-wide alewife biomass from historical highs, and have also been effective in maintaining relatively low lake-wide alewife biomass over the last several decades (Madenjian *et al.* 2002). The combined impacts of cormorants and other predators, as well as many ecological factors, contribute to the community dynamics and overall functioning of the northern Lake Michigan ecosystem.

ACKNOWLEDGMENTS

The authors acknowledge Dr. Don Hall of Michigan State University for his financial and intellectual assistance. We would also like to thank Jory Jonas and other members of the Michigan Department of Natural Resources—Fisheries Division for their support and technical assistance. We also acknowledge the U.S. Fish and Wildlife Service, in particular Seney National Wildlife Refuge personnel, for the permit (Permit Number MB022886) to conduct this work. In addition, the Michigan Department of Natural Resources—Wildlife Division, Central Michigan University Research Excellence Funds, and Michigan State University Department of Zoology and Ecology, Evolutionary Biology and Behavior Program, for providing funding for this study. We are indebted to the Central Michigan University Biological Station and a NSF Grant (#DBI 0224795) for logistical support. We are grateful to all members of our field and lab crew, especially Dr. Beth Leuck of Centenary College, Shreveport, Louisiana. Lastly, we would like to thank Dr. Martin Stapanian and two anonymous reviewers for their comments and suggestions on how to improve this manuscript.

REFERENCES

Bartell, S.M., Breck, J.E., Gardener, R.H., and Brenhert, A. L. 1986. Individual parameter perturbation and error analysis of fish bioenergetics models. *Can. J. Fish. Sci.* 43:160–168.

Birt, V.L., Birt, T.P., Goulet, D., Cairns, D.K., and Montevecchi, W.A. 1987. Ashmole's halo: direct evidence for prey depletion by a seabird. *Mar. Ecol. Prog. Ser.* 40:205–208.

Birt-Friesen, V.L, Montevecchi, W.A., Cairns, D.K., and Mackes, S.A. 1989. Activity-specific metabolic rates of free-living northern gannets and other seabirds. *Ecology* 70:357–367.

Blomme, C. 1981. Status and breeding success of double-crested cormorants in two North Channel (Lake Huron) colonies in 1979. *Ont. Field Biol.* 35:70–78.

Brugger, K.E. 1993. Digestibility of three fish species by double-crested cormorants. *Condor* 95:25–32.

Bryan, S.D., Soupir, C.A., Duffy, W.G., and Freiburger, C.E. 1996. Caloric densities of three predatory fishes and their prey in Lake Oahe, South Dakota. *J. Freshwat. Ecol.* 11:153–161.

Cairns, D.K. 1992. Bridging the gap between ornithology and fisheries science: use of seabird data in stock assessment models. *Condor* 94:811–824.

Cairns, D.K., Chapdelaine, G., and Montevecchi, W.A. 1991. Prey exploitation by seabirds in the Gulf of St. Lawrence. In *The Gulf of St. Lawrence: Small Ocean or Big Estuary?* J.-C. Therriault, ed., *Can. Spec. Publ. Fish. Aquat. Sci*. 113:277–291.

Carss, D.N., and the Diet Assessment and Food Intake Working Group. 1997. Techniques for assessing cormorant diet and food intake: towards a consensus view. *Suppl. Ric. Biol. Selvaggina* 26:197–230.

Craven, S.R., and Lev, E. 1987. Double-crested cormorants in the Apostle Islands, Wisconsin, USA: population trends, foods habits and fishery depredations. *Colon. Waterbirds* 10:64–71.

Cummins, K.W., and Wuycheck, J.C. 1971. Caloric equivalents for investigations in ecological energetics. *Mitt. Int. Theor. Agnew. Limnol.* 18:1–51.

Cuthbert, F.J., McKearnan, J. and Wemmer, L. 1997. *U.S. Great Lakes tern and cormorant survey: 1997 progress report*. Department of Fisheries and Wildlife, University of Minnesota, St. Paul.

Dobiesz, N.E., McLeish, D.A., Eshenroder, R.L., Bence, J.R., Mohr, L.C., Henderson, B.A., Ebener, Nelepa, T.F., Woldt, A.P., Johnson, J.E., Argyle, R.L., and Makarewicz, J.C. 2005. Ecology of the Lake Huron fish community 1970–1999. *Can. J. Fish. Aquat. Sci.* 62:1432–1451.

Draulans, D. 1988. Effects of fish-eating birds on freshwater fish stocks: an evaluation. *Biol. Conserv.* 44:251–263.

Dunn, E.H. 1975. Caloric intake of nestling double-crested cormorants. *Auk* 92:553–565.

Eck, G.W., and Brown, E.H. 1987. Recent changes in Lake Michigan's fish community and their probable causes, with emphasis on the role of the alewife (*Alosa pseudoharengus*). *Can. J. Fish. Aquat. Sci.* 44:53–60.

Fowle, M.R. 1997. Population dynamics, food habits, and bioenergetics of Double-crested Cormorants in Lake Champlain. M.S. thesis, University of Vermont, Burlington.

Furness, R.W. 1978. Energy requirements of seabird communities: a bioenergetics model. *J. Anim. Ecol.* 47:39–53.

Glahn, J.F., and Brugger, K.E. 1995. The impact of double-crested cormorants on the Mississippi Delta catfish industry: a bioenergetics model. *Colon. Waterbirds* 18 (Spec. Publ. 1):168–175.

Hatch, J.J., and Weseloh, D.V.C. 1999. Double-crested cormorant (*Phalacrocorax auritus*). In *The Birds of North America*, No. 441, A. Poole, and F. Gill, eds., pp. 1–36. Philadelphia, Pennsylvania: The Birds of North America, Inc.

Hebert, C.E., and Morrison, H.A. 2003. Consumption of fish and other prey items by Lake Erie waterbirds. *J. Great Lakes Res.* 29:213–227.

Johnson, J.H., Ross, R.M., and McCullough, R.D. 2002. Little Galloo Island, Lake Ontario: a review of nine years of double-crested cormorant diet and fish consumption information. *J. Great Lakes Res.* 28:182–192.

Kendeigh, S.C., Dol'nik, V.R. and Gavrilov, V.M. 1977. Avian energetics. In *Granivorous Birds in Ecosystems*, J. Pinowski and S.C. Kendeigh, eds., pp. 127–205. London, England: Cambridge University Press.

Kirsch, E.M. 1995. Double-crested cormorants along the upper Mississippi River. *Colon.l Waterbirds* 18 (Special Issue 1):131–136.

Lantry, B.F., Eckert, T.H., and Schneider, C.P. 1999. The relationship between the abundance of smallmouth bass and Double-crested Cormorants in the Eastern Basin of Lake Ontario. In *Final Report: To Assess the Impact of Double-crested Cormorant Predation on the Smallmouth Bass and Other Fisheries of the Eastern Basin of Lake Ontario.* NYSDEC Special Report, February, 1999. Section 12, pp. 1–10.

Lewis, H.G. 1929. *The Natural History of the Double-crested Cormorant*. Ottawa, Ontario: Ru-Mi-Loo Books.

Ludwig, J.P. 1984. Decline, resurgence and population dynamics of Michigan and Great Lakes double-crested cormorants. *Jack Pine Warbler* 62:91–102

_____, and Summer, C.L. 1997. Population status and diet of cormorants in Les Cheneaux Islands area. In *History, Status, and Trends in Populations of Yellow Perch and Double-crested Cormorants in Les Cheneaux Islands, Michigan*. J.S. Diana, G.Y. Belyea, and R.D. Clark, Jr., eds., pp. 5–25. Michigan Depart-

ment of Natural Resources – Fisheries Division, Lansing, Michigan, #17.

_____, Hull, C.N., Ludwig, M.E., and Auman, H.J. 1989. Food habits and feeding ecology of nesting double-crested cormorants in the upper Great Lakes, 1986–1989. *Jack-Pine Warbler* 67:115–126.

Madenjian, C.P., and Gabrey, S.W. 1995. Waterbird predation of fish in western Lake Erie: a bioenergenics model application. *Condor* 97:141–153.

_____, Fahnenstiel, G.L., Johengen, T.H., Nalepa, T.F., Vanderploeg, H.A., Fleisher, G.W., Schneeberger, P.J., Benjamin, D.M., Smith, E.B., Bence, J.R., Rutherfor, E.S., Lavis, D.S., Robertson, D.M., Jude, D.J., and Ebner, M.P. 2002. Dynamics of the Lake Michigan food web, 1970–2000. *Can. J. Fish. Aquat. Sci.* 59:736–753.

_____, Desorcie, T.J., and Holuszko, J.D. 2004. Status and trends of prey populations in Lake Michigan, 2003. Report, Great Lakes Fishery Commission, Lake Michigan Committee Meeting, Ypsilanti, Michigan.

Maruca, S.L. 1997. The impact of cormorant predation on yellow perch in Les Cheneaux Islands, Lake Huron. In *History, Status, and Trends in Populations of Yellow Perch and Double-crested Cormorants in Les Cheneaux Islands, Michigan*. J.S. Diana, G.Y. Belyea, and R.D. Clark, Jr., eds., pp. 47–70. Michigan Department of Natural Resources—Fisheries Division, Lansing, Michigan, Special Report, #17.

Nagy, K.A. 1989. Field bioenergetics: accuracy of models and methods. *Physiol. Zool*. 62:237–252.

Neuman, J., Pearl, D.L., Ewins, P.J., Black, R., Weseloh, D.V.C., Pike, M., and Karwowski, K. 1997. Spatial and temporal variation in the diet of double-crested cormorants (*Phalacrocorax auritus*) breeding in the lower Great Lakes in the early 1990s. *Can. J. Fish. Aquat. Sci.* 54:1569–1584.

Ridgeway, M.S., Pollard, J.B., and Weseloh, D.V.C. 2006. Density dependent growth of double-crested cormorant colonies on Lake Huron. *Can. J. Zool.* 84:1409–1420.

Rudstam, L.G., VanDeValk, A.J., Adams, C.M., Coleman, J.T.H., Forney, J.L., and Richmond, M.E. 2004. Cormorant predation and population dynamics of walleye and yellow perch in Oneida Lake. *Ecol. Appl.* 14:149–163.

Schiavone, A. 2001. Double-crested Cormorant predation on smallmouth bass and other fishes of the eastern basin of Lake Ontario: summary of 2000 studies. In *Final Report: To Assess the Impact of Double-crested Cormorants Predation on the Smallmouth Bass and Other Fisheries of the Eastern Basin of Lake Ontario.* NYSDEC Special Report, February, 2001. Section 1, pgs. 1–5.

_____. 2003. Double-crested Cormorant predation on smallmouth bass and other fishes of the eastern basin of Lake Ontario: summary of 2002 studies. In *Final Report: To Assess the Impact of Double-crested Cormorants Predation on the Smallmouth Bass and Other Fishers of the Eastern Basin of Lake Ontario.* NYSDEC Special Report, February, 2003. Section 1, pp. 1–4.

Seefelt, N.E. 2005. Foraging ecology, bioenergetics and predatory impact of breeding Double-crested Cormorants (*Phalacrocorax* auritus) in the Beaver Archipelago, northern Lake Michigan. Doctoral dissertation, Michigan State University, East Lansing.

_____, and Gillingham, J.C. 2005. The double-crested cormorant in Lake Michigan: a review of population trends, ecology and current management. In *State of Lake Michigan: Ecology, Health and Management*, T. Edsall and M. Munawar, eds., pp 351–363. New Delhi: Ecovision World Monograph Series.

_____, and Gillingham, J.C. 2006a. A comparison of three methods to investigate the diet of breeding double-crested cormorants (*Phalacrocorax auritus*) in the Beaver Archipelago, northern Lake Michigan. *Hydrobiologia* (Spec. Publ.) 567:57–67.

_____, and Gillingham, J.C. 2006b. Foraging locations of double-crested cormorants in the Beaver Archipelago of northern Lake Michigan: implications for smallmouth bass declines. *Waterbirds* 29:473–480.

Seider, M.J. 2003. Population dynamics of smallmouth bass in the Beaver Archipelago, northern Lake Michigan, 1999–2002. M.S. thesis, University of Georgia, Athens, Georgia.

Stapanian, M.A., Bur, M.T., Tyson, J.T., Seamans, T.M., and Blackwell, B.F. 2002. Foraging locations of double-crested cormorants on western Lake Erie: site characteristics and spatial associations with prey fish densities. *J. Great Lakes Res.* 28:155–171.

Suter, W. 1995. The effect of predation by wintering cormorants *Phalacrocorax carbon* Grayling *Thymallus thymallus* and trout (Salmonidae) populations: two case studies from Swiss rivers. *J. Appl. Ecol.* 32:29–46.

Warke, G.M.A., and Day, K.R. 1995. Changes in the abundance of cyprinid and percid prey affect the rate of predation by cormorants *Phalacrocorax carbo carbo* on salmon *Salmo salar* smolt in northern Ireland. *Ardea* 83:157–166.

Weseloh, D.V.C., and Casselman, J. 1992. Calculated fish consumption of Double-crested Cormorants in eastern Lake Ontario. Abstracts of Scientific Papers Presented at the 1992 Annual Meeting of the Colonial Waterbird Society: 76, and *Colonial Waterbird Society Bulletin* 16(2):63–64.

_____, and Ewins, P.J. 1994. Characteristics of a rapidly increasing colony of double-crested cormorants (*Phalacrocorax auritus*) in Lake Ontario: population size reproductive parameters and band recoveries. *J. Great Lakes Res.* 20:443–456.

Wiens, J.A. 1984. Modeling the energy requirements of

seabird populations. In *Seabird Energetics*, G.C. Whittow and H. Rahn, eds., pp. 255–285. New York, New York: Plenium Press.

_____, and Scott, J.M. 1975. Model estimation of energy flow in Oregon coastal seabird populations. *Condor* 77:439–452.

Wires, L.R., Cuthbert, F.J., Trexel. D.R., and Joshi, A.R. 2001. *Status of the Double-crested Cormorant* (Phalacrocorax auritus) *in North America.* Final Report to U.S. Fish and Wildlife Service, Arlington, V.A.

Submitted: 9 April 2007
Accepted: 2 October 2007
Editorial handling: Martin A. Stapanian