



Energetic considerations for managing double-crested cormorants on Lake Champlain

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ABSTRACT

We studied foraging distribution, activity budgets, fish consumption, and energetics of double-crested cormorants (*Phalacrocorax auritus*) at two breeding colonies on Lake Champlain. Our objective was to determine if fish consumption and distribution of predation changed with movements of cormorants associated with efforts to reduce numbers of cormorants on one of the colonies. Wildlife managers reduced populations of cormorants on Young Island, Vermont by oiling their eggs, which resulted in dispersal of breeding cormorants 35 km south to Four Brothers Islands, New York. We found that as cormorants shifted from Young Island to the colony on Four Brothers Islands, energy demands, foraging distribution, and total fish consumption increased. Birds on Four Brothers Islands foraged a greater distance from the colony compared to birds on Young Island. Additionally, consumption of yellow perch (*Perca flavescens*) shifted to rainbow smelt (*Osmerus mordax*) when more birds bred on Four Brothers Islands. The dispersal of cormorants from Young Island to Four Brothers Islands reduced predation on yellow perch but increased overall fish consumption. Our estimates of fish consumption ranged from 322,000–425,000 kg of fish per year at Young Island to 899,000–1,086,000 kg of fish per year at Four Brothers Islands. Results from this study demonstrate secondary impacts of management on Young Island to unmanaged areas.

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Introduction

When managing wildlife, it is important to understand ecological relationships of managed species to determine direct and indirect consequences of management activities. Wildlife managers base decisions on anticipated outcomes, but unanticipated consequences of management can alter outcomes. Such is the case with double-crested cormorants on Lake Champlain, a colonial species that began breeding in 1981 on Young Island, Vermont, and expanded in 1984 to Four Brothers Islands, New York. The population grew rapidly (Fowle et al., 1999) and reached a peak of 4459 nesting pairs in 1999, at which time wildlife managers began spraying cormorant eggs with corn oil to reduce productivity on Young Island. They began oiling eggs to curb population growth and limit associated destruction of vegetation and displacement of other colonial species on this island (Garland et al., 1998). Management activities on Young Island led to

increased breeding dispersal from Young Island south 35 km to Four Brothers Islands, where cormorant numbers were not controlled (Duerr et al., 2007). Diets of cormorants from these colonies differ (DeBruyne et al., 2012). Cormorants nesting on Young Island consumed mostly yellow perch. The dominant prey of cormorants from Four Brothers Islands was rainbow smelt but has shifted to include alewife (*Alosa pseudoharengus*) after alewife became established in Lake Champlain. Thus, differences in population dynamics between the two colonies may result in differences in foraging ecology. Therefore, a secondary effect of population management on Young Island may be a reduction in predation of yellow perch and an increase in consumption of rainbow smelt and alewife.

Understanding fish consumption by cormorant populations is important because cormorants have been implicated in the decline of some sport fish populations. For example, cormorant predation was linked to shrinking populations of yellow perch and walleye (*Sander vitreus*) in Oneida Lake, NY (VanDeValk et al., 2002; Rudstam et al., 2004) and declines of smallmouth bass (*Micropterus dolomieu*) and yellow perch populations in Lake Ontario, NY (Burnett et al., 2002; Lantry et al., 2002). In contrast, other studies have concluded that cormorants are opportunistic foragers that mostly consume fish with little sport value (see reviews by Trapp et al., 1999 and Wires et al., 2001:181–207). On Oneida Lake, cormorant predation peaked during post-breeding periods when large numbers of migrants arrived

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(VanDeValk et al., 2002), which illustrates why it is important to know predation throughout the time when cormorants are present.

To assess differences in energy demands and fish consumption by double-crested cormorants between colonies on Lake Champlain, we modified an energetics model based on activity budgets for great cormorants (Grémillet et al., 1995). Other techniques used to estimate energy expenditure and food intake rates of waterbirds, such as use of doubly-labeled water (DLW; Feltham, 1995) or allometric equations based on body mass (Lasiewski and Dawson, 1967; Kendeigh et al., 1977) would not allow us to achieve our objectives. Allometric equations are global estimates (Feltham and Davies, 1997) and would not elucidate differences in energy requirements within Lake Champlain because cormorant mass does not differ between colonies (Duerr, A.E. and Capen, D. E. unpublished data). Methods incorporating DLW do not distinguish among activities and will not allow us to infer sources of differences between sites.

The purpose of our research was to assess whether management that shifted cormorants from one colony to another has the potential to affect fish populations. Our specific objectives were to 1) describe foraging distribution, 2) document activity budgets, and 3) estimate energy requirements and fish consumption by cormorants throughout the year from colonies on Young Island and Four Brothers Islands on Lake Champlain.

Methods

Study site

Our study took place at two cormorant colonies in Lake Champlain (Fig. 1). One colony was on Young Island, Vermont, which is owned and managed by the Vermont Department of Fish and Wildlife. The

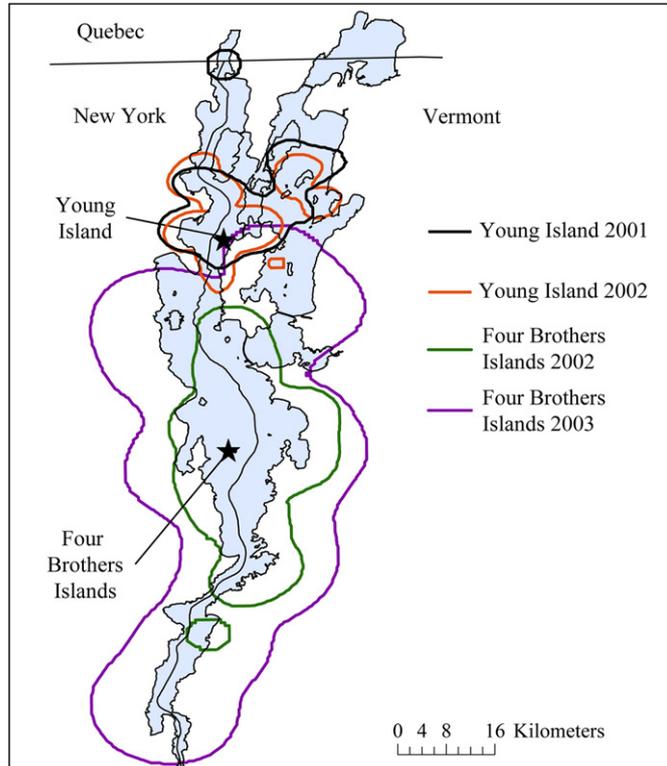


Fig. 1. Foraging distribution for double-crested cormorants breeding on Young Island, Vermont and Four Brothers Islands, New York on Lake Champlain depicted by 95% kernel home ranges. Young Island home ranges are given for 2001 (dark gray line; 2570 ha) and 2002 (light gray line; 2180 ha). Home ranges for Four Brothers Islands are given for 2002 (black and gray line; 6580 ha) and 2003 (black dashed line; 18,950 ha).

second colony was Four Brothers Islands, New York, owned by The Nature Conservancy and managed by its Adirondack Chapter. The two study sites are 35 km apart; further descriptions are given in Duerr et al. (2007).

Experimental framework

We studied cormorant activities on Young Island in 2001 and 2002 and on Four Brothers Islands in 2002 and 2003. Throughout this time, Young Island was managed experimentally such that about half of nests were treated with corn oil to prevent hatching (Duerr et al., 2007). Cormorants on Four Brothers Islands were not managed during the period of our study.

We divided each year of the study into five reproductive stages. The pre-breeding stage ran from when cormorants first arrived on Lake Champlain in mid-March until they began incubating eggs. Incubation and nestling stages were when most cormorants incubated eggs (25–28 days) or cared for nestlings (about 7 weeks) (Lewis, 1929; Mendall, 1936; Hatch and Weseloh, 1999). The fledging stage was after nestlings fledged and accompanied adults on foraging trips, and ended at the start of the post-breeding stage when young were independent of parents (10 weeks after hatching; Mendall, 1936). The post-breeding stage lasted until all cormorants migrated away from Lake Champlain by mid-October.

Cormorants were captured and radio-tagged (King et al., 2000) from Young Island in 2001–2002 and Four Brothers Islands in 2002–2003 (Table 1). We captured adults on the nesting colony after they had incubated eggs for at least 2 weeks (i.e., during the second half of the incubation stage), some with modified leg hold traps (King et al., 1994) and others with hand nets at night. At the end of the nestling stage, fully-grown nestlings were captured by hand and radio-transmitters were attached. Radio tags transmitted signals for 6 to 9 months and lasted throughout nesting stages within a year, but not from one year to year. All radio-transmitters and harnesses attached to cormorants weighed less than 40 g.

Foraging distribution

We followed cormorants as they left nesting colonies and mapped locations of foraging flocks while recording activities of radio-tagged cormorants (61.3%) and while shooting cormorants for diet analysis (38.7%; see DeBruyne et al., 2012). Cormorants were shot after foraging and they began to return to their colony. Cormorants generally flew over water and avoided flying over land when moving between foraging locations and nesting colonies. We used the function for weighted-cost distance in ArcGIS (ESRI, Redlands, California, USA) to measure the shortest distance between foraging locations and nesting colonies without traversing land. Foraging locations observed sequentially are spatially autocorrelated (Kernohan et al., 2001), so we included foraging locations that we recorded at least 1 h apart to minimize this effect. Repeated-measures ANOVA was used to compare travel distances among years for each colony, between colonies, and among nesting stages. For comparisons in foraging extent by colony, we combined foraging locations separated by 1 h and calculated the 95% fixed-kernel home ranges for each colony and year (Beyer, 2004).

Table 1

Number and age of double-crested cormorants captured and radio-tagged on Lake Champlain from 2001 to 2003.

Colony	Year	Adults	Subadults	Juveniles
Young Island	2001	21	1	11
	2002	26	0	6
Four Brothers Islands	2002	4	0	3
	2003	30	0	0

Activity budgets

Cormorant activity budgets were recorded by following individual birds that were radio-tagged. We documented the amount of time individuals were on their nesting colony and used a motorboat to follow a focal cormorant to record time spent flying, swimming, perching, and foraging while away from the colony. We continued recording activities of the focal bird from the time it left a colony until it returned to the colony or until a field shift ended after spending 8 h in the field for a given day. Attempts were made to record the same number of activity budgets on each radio-tagged cormorant each year. Our focal cormorant was the first radio-tagged bird to leave an island, provided a budget had not been recorded recently for that bird.

To determine the proportion of time cormorants spent on their nesting colony, we recorded whether each radio-tagged cormorant was present every 15 min. Colony presence was recorded manually during daytime hours in 2001 near Young Island and in 2002 on Four Brothers Islands. We used a datalogging computer attached to a scanning receiver (Advanced Telemetry Systems, Isanti, MN) to record automatically colony presence throughout each day and night in 2002 on Young Island and in 2003 on Four Brothers Islands. From colony-presence data, the proportion of time radio-tagged cormorants spent on the colony was calculated.

We were not able to record the full duration of most cormorant flights because boats used to follow cormorants were too slow or wave action was too great to safely keep up with flying birds. For most flights, flight time was calculated by measuring the distance between successive locations where a focal cormorant was observed and multiplying this by the average flight speed for cormorants, thus calculating minimum flight times. We timed 29 flights of radio-tagged cormorants and calculated flight speed for each of these flights.

Duration of foraging and swimming at the water surface was determined by reclassifying time that cormorants dove below or were at the water surface. Because the radio signal fades or disappears when a radio transmitter goes below the water surface, we recorded the duration of individual dives. Cormorants that were actively foraging spent time on the water surface recovering from one dive before initiating the next dive. This surface recovery was considered as part of the foraging activity because estimates of energetic costs of foraging include both dive and recovery (Schmid et al., 1995; Enstipp et al., 2006). Dives for double-crested cormorants averaged 1.55 times longer than surface recoveries (Enstipp et al., 2006). We reclassified time when a cormorant was at the surface longer than dive recovery as surface swimming. Cormorant activities were recorded as foraging when we could not record individual dives because transmitter signals did not completely fade during shallow dives, but knew a cormorant was foraging based on observations of the flock.

We described cormorant activities as proportion of daytime that they spent on their nesting colony and proportion of time away from their nesting colony. Time away from the colony was separated into time spent flying, swimming, foraging, and perching. Proportion of time that cormorants spent in activities while away from the colony and proportion of time spent on nesting colonies were compared between years for each colony, between colonies, among nesting stages, between ages of cormorants, and between treatments on Young Island. Because these measures were obtained repeatedly for individual birds, we used repeated-measures ANOVA when making comparisons. We used the arcsine-square root transformation when comparing proportion of time spent for activities. Activities of adult cormorants from the egg-oiling experiment on Young Island were compared in a separate analysis.

Energetics modeling

We constructed an energetics model for cormorants based on activity data collected on Lake Champlain coupled with energetic costs

for activities (Schartz and Zimmerman, 1971; Grémillet et al., 1995; Grémillet et al., 2000). The model consisted of a series of calculations to estimate total energy requirements (illustrated in a flow chart; Fig. 2). These calculations included three basic steps: 1) estimating energy requirements from activity budgets, 2) estimating size of the cormorant population, and 3) estimating fish consumption based upon assimilation efficiency and energy density of prey items. We estimated energy requirements and fish consumption for three age groups: adults or breeding cormorants, subadults or non-breeding cormorants, and juveniles or hatch-year cormorants.

Step 1 – energy requirements

The first step of the energetics model was calculating energy requirements for each age group (Fig. 2a–d). We completed calculations for each 24-h day that cormorants were present on Lake Champlain. Daytime and nighttime activities were separated, with daytime beginning and ending at civil twilight. Energy required for each activity is the product of the duration that a cormorant participated in the activity (from activity budgets) and the rate of energy expended by cormorants for that activity (Table 2). Total energy requirements were the sum of energy expenditures for all activities.

The portion of daytime that cormorants spent on nesting colonies was recorded, but not their activities while there. We assumed that double-crested cormorants behaved similarly to great cormorants (*Phalacrocorax carbo*) while on the nesting colony and included average durations of time spent for nest building, preening, being alert, resting, and other activities from Grémillet et al. (2000). Energy requirements for other on-colony activities were estimated by Storch et al. (1999) for great cormorants; however, resting metabolic rates for double-crested cormorants (4.59 W/kg; Enstipp et al., 2006) are known to be lower than for great cormorants (5.08 W/kg; Storch et al., 1999). Therefore, we reduced energy expenditures for on-colony activities in proportion to differences in metabolic rates between these species.

We did not obtain activity data for all nesting stages in some years or for subadults, and had to make assumptions in the model. Activity budgets for cormorants could not be recorded before attaching radio-transmitters during the incubation stage; therefore, we assumed that prebreeding activities were the same as for the incubation stage. This assumption matches our observations of general activity levels at colonies, including rates that cormorants left and returned to colonies. Activity budgets for cormorants during the post-breeding stage on Young Island in 2001 and Four Brothers Islands in 2002 were not recorded, and we assumed that these activities were the same as during 2002 for Young Island and 2003 for Four Brothers Islands, respectively. Activity budgets for subadults were assumed to be the same as for breeding adults from each colony excluding breeding activities. We estimated energy requirements for activities based upon an average mass of all cormorants (1820 g) that were collected for diet analysis in 2001–2002 (DeBruyne et al., 2012).

Activity specific metabolic rates were adjusted to account for costs of thermoregulation (Fig. 2b), when ambient temperatures fell below the lower thermoneutral limit for cormorants (21 °C day, 17.5 °C night) and included the difference between body temperature (41.2 °C day, 40.2 °C night) and air or water temperatures (Hennemann, 1983). We used daily or nightly averaged air temperatures recorded on Lake Champlain for each year (Vermont Monitoring Cooperative, 2006). For swimming and foraging activities, we used average daily water temperatures taken 2–3 m below the water surface in 2000–2001 and 2004–2005 in Shelburne Bay on Lake Champlain for all years (T. Manley, Middlebury College; unpublished data). Enstipp et al. (2006) estimated energetic costs of foraging in water temperatures below the thermoneutral limit for cormorants. We calculated the portion of these costs attributable to thermoregulation and removed it when we estimated energy required for cormorants that foraged in warmer water.

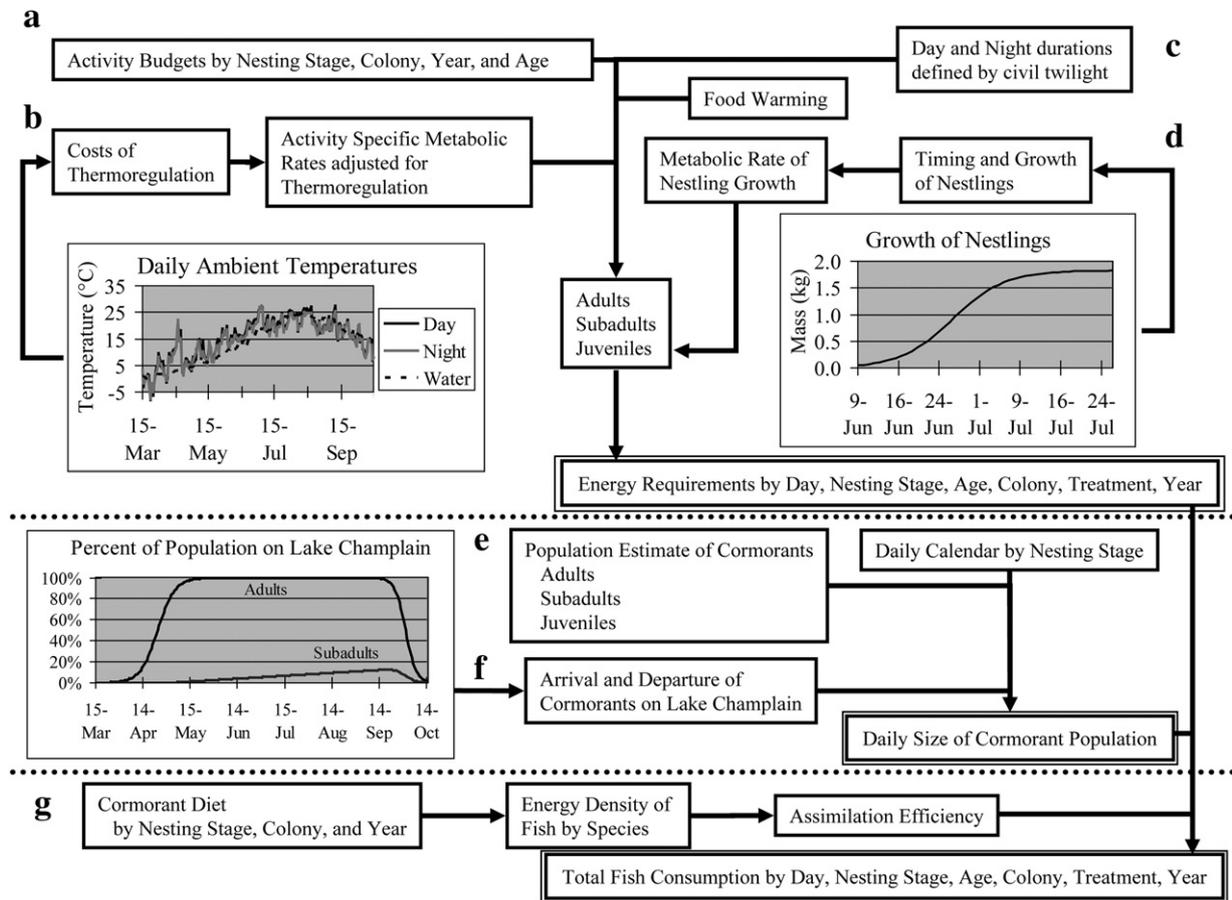


Fig. 2. Flow chart of energetics model used to estimate energy requirements and total fish consumption of double-crested cormorants on Lake Champlain from 2001 to 2003. Energy requirements are calculated from a) activity budgets, b) costs of thermoregulation, c) durations of day and night times and costs of warming food items, and d) growth of nestlings. Daily estimates of population size are determined from e) population estimates by age and f) arrival and departure of cormorants from Lake Champlain. Total fish consumption is calculated by g) estimating energy gained from cormorant diets to fulfill energy requirements for the estimated size of the population.

Additional energy requirements for cormorants included resting at night and warming food items (Fig. 2c). Energy costs to warm ectothermic prey items from water to the body temperature of cormorants were calculated as the product of mass of food (g), specific heat of water (4.17 J/g/°C), and the difference between water and body temperature (Wilson and Culik, 1991).

In addition to energy requirements for activities of juveniles during the fledgling and post-breeding stages, we included energy requirements for growth of nestlings (Fig. 2d). Nestling growth follows a logistic pattern from mass at hatching (27.6–34.7 g) to an asymptotic mass equal to 93–98% of adult mass (Dunn, 1975b; DesGranges, 1982; Leger and McNeil, 1987). When modeling growth, we used the average of those reported (logistic constant = 0.20, inflection point = 18.5 days, and asymptotic mass = 1828 g). Energy requirements for nestling growth was modeled as $0.1 \times M^{0.7427}$, where M = mass in g (Dunn, 1975a).

Step 2 – population estimates

For each day included in the model, we estimated the number of cormorants present at each colony (Fig. 2e–f). The peak number of adult cormorants on each colony was estimated by doubling a count of active nests taken late in the incubation stage. Arrival of cormorants onto Lake Champlain was modeled by fitting a logistic curve to counts of cormorants observed on Young Island from mid-March to mid-May following Ricklefs (1967): $k = -0.18$, inflection point = 24 April. We modeled departure of cormorants using a logistic curve in which cormorants departed Lake Champlain from 15 September to 15 October ($k = 0.30$, inflection point = 1 October). Numbers of subadult cormorants present on each colony were based upon ratios

of adults to subadults recorded by counting adults and subadults in foraging flocks with greater than ten birds throughout each year. We used regression to relate adult-to-subadult ratio to the Julian date for all years combined to obtain daily estimates of this ratio; subadults had lighter plumage than adults. The number of subadults was the product of the daily ratio and the daily estimate of the number of adults present at each colony.

We estimated the number of juveniles at each colony as the average number of nestlings per nest that reached an age of 14 days (Young Island = 2.54/nest (Fowle et al., 1999); Four Brothers Islands = 1.35 [D.E. Capen, unpublished data]). Daily estimates of the number of juveniles in the population were calculated as the product of the number of juveniles per nest, the number of nests per colony that was not oiled, and the daily portion of the population present (as calculated for adults).

Step 3 – fish consumption

Daily energy requirements for cormorants were summed for each colony, nesting stage, year, and age class and converted to mass of fish consumed based on the proportion of a cormorant's diet by species consumed (DeBruyne et al., 2012), energy density of prey items, and assimilation efficiency for cormorants (Fig. 2g). We assumed that unidentified prey items represented the same species, in the same proportions, as identified prey items in cormorant diets. Energy densities of prey items were 4186 J/g for yellow perch and sunfish and 4814 J/g for rainbow smelt (Hewett and Johnson, 1992). Assimilation efficiency was 77% for adults and subadults (Brugger, 1993) and 85% for nestlings (Dunn, 1975a).

Table 2

Activity specific metabolic rates, costs of thermoregulation, and other key values used in modeling energetic requirements for double-crested cormorants on Lake Champlain.

Measurement	Value from literature	Converted value used in model	Source
Daytime resting	4.59 W/kg	8.392 W	Enstipp et al. (2006)
Nighttime resting	0.74 cm ³ O ₂ /g h	7.54 W	Hennemann (1983)
Flight	Calculated as 125.15 W for 1.82 kg cormorant	125.15 W	Pennycuick (1989a)
Surface swimming ^a	17.8 W/kg average of swimming and sitting still on water	32.53 W	Ancel et al. (2000)
Foraging ^b	23.26 W/kg	36.83 W	Enstipp et al. (2006)
Thermoregulation for daytime resting	0.127 W/kg	0.232 W	Enstipp et al. (2006)
Thermoregulation for nighttime resting	87% of value for daytime resting	0.203 W	Hennemann (1983)
Thermoregulation for wing spreading	123% of value for daytime resting	0.286 W	Hennemann (1985)
Thermoregulation for swimming	0.581 W/kg	1.062 W	Enstipp et al. (2006)
Cormorant body temperature	41.2 °C day	Same	Hennemann (1983)
	40.2 °C night		
Amount of time spent with wings spread	2.6% of day	Same	Hennemann (1988)

^a Metabolic rate measured for another species in genus *Phalacrocorax*.^b Average of post-absorptive energy demand in 1.0 and 10.0 m water.

Sensitivity analysis

We determined sensitivity of our estimates of total energy requirements to model variables by increasing variable values by 10% and calculating the percentage change in the total energy requirements estimated by the model. Sensitivity of variables (metabolic rates, activity budgets, and fish consumption) to total energy requirements was checked for both colonies combined for 2002 because this was the only year that we collected data on both colonies. When checking sensitivity of activity budgets, the amount of time cormorants spent in all activities combined was allowed to exceed 100%. Therefore, we checked sensitivity of the model to each variable while holding all other variables constant.

Results

Foraging distribution

From 2001 to 2003, we identified 1148 foraging locations of which we observed 384 at least 1 h apart. Distances from nesting colonies to foraging locations varied by nesting stage ($F_{4, 378} = 8.58$, $P < 0.001$), colony ($F_{1, 378} = 3.75$, $P < 0.054$) and year ($F_{2, 378} = 24.88$, $P < 0.001$). Cormorants foraged farthest from their nesting colony during the post-breeding stage (Table 3). Cormorants from Four Brothers Islands

traveled up to 10.9 km farther in 2002 and up to 25.7 km farther in 2003 to forage than did cormorants from Young Island. For the Four Brothers Islands, cormorants traveled more than twice as far to forage in 2003 than in 2002. Differences between years and colonies are reflected in a larger foraging home range for Four Brothers Islands in 2003 than in 2002 or for Young Island in 2001–2002 (Fig. 1).

Activity budgets

We recorded activity budgets for 150 adult and 16 juvenile cormorants (Table 4). On average, activity budgets for adults were 188.9 min (SE = 33.0) and juveniles were 68.5 min (SE = 15.1). We stopped recording 26 (17%) activity budgets for adults (none for nestlings) at the end of field shifts and before radio tagged cormorants returned to their breeding colony.

The proportion of time cormorants flew (Table 4, Fig. 3) varied by nesting stage ($F_{3, 48} = 4.06$, $P = 0.012$) but not by year ($F_{2, 66} = 1.77$, $P < 0.179$), age ($F_{1, 66} = 0.25$, $P = 0.6215$), colony ($F_{1, 66} = 0.00$, $P = 0.951$), or treatment on Young Island ($F_{1, 33} = 0.5$, $P = 0.483$). Away from the nesting colony, cormorants flew 18% of the time during incubation and nestling stages, 11% during the fledgling stage, and 7% during the post-breeding stage. Average flight speed from 29 timed flights was 15.2 m/s (SE = 0.80). This is similar to flight speed of 14.7 m/s for cormorants reported by Pennycuick (1989b) but slower than 17.0 m/s (61.2 km/h) reported by Custer and Bunck (1992).

The proportion of time spent swimming (Table 4, Fig. 3) varied by year ($F_{2, 66} = 4.80$, $P = 0.011$), but not by nesting stage ($F_{3, 48} = 0.60$, $P = 0.617$), age ($F_{1, 66} = 0.13$, $P = 0.722$), colony ($F_{1, 66} = 0.35$, $P = 0.554$), or treatment on Young Island ($F_{1, 33} = 1.28$, $P = 0.265$). Cormorants swam less in 2001 (20% of time spent away from the colony on average) than in 2002 (37%) or 2003 (25%).

The proportion of time spent foraging (Table 4, Fig. 3) varied by nesting stage ($F_{3, 48} = 3.68$, $P = 0.018$) and year ($F_{2, 66} = 7.16$, $P = 0.002$), but not by age ($F_{1, 66} = 2.99$, $P = 0.095$), colony ($F_{1, 66} = 0.50$, $P = 0.482$), or treatment on Young Island ($F_{1, 33} = 0.03$, $P = 0.870$). Cormorants spent more time foraging in 2002 (40% of time away from the colony) and 2003 (40%) than 2001 (20%). Cormorants foraged most during the nestling (20–55%) and fledgling (26–67%) stages, and more during the post-breeding stage (1–56%) than incubation (1–42%).

While away from the colony, perching time (Table 4, Fig. 3) varied by nesting stage ($F_{3, 48} = 9.18$, $P < 0.001$) and year ($F_{2, 66} = 18.85$, $P < 0.001$) but not by age ($F_{1, 66} = 0.96$, $P = 0.331$), colony ($F_{1, 66} = 0.08$, $P = 0.777$) or treatment on Young Island ($F_{1, 33} = 0.69$, $P = 0.413$). On average, cormorants perched more in the post-breeding stage than other nesting stages. They perched more in 2001 (20–71% of time) than in 2002

Table 3

Mean distances (km) that double-crested cormorants traveled to foraging locations from Young Island and Four Brothers Islands on Lake Champlain, 2001–2003.

Colony	Year	Nesting stage	N	Mean	SE
Young Island	2001	Incubation	19	6.4	1.2
		Nestling	44	6.5	0.6
		Fledgling	18	11.3	2.2
		Postbreeding	21	14.4	2.2
	2002	Prebreeding	24	6.1	0.9
		Incubation	31	9.3	1.0
		Nestling	53	6.3	0.6
		Fledgling	26	7.6	1.3
Four Brothers Islands	2002	Postbreeding	28	14.0	1.2
		Prebreeding	9	12.9	2.2
		Incubation	9	17.3	1.3
		Nestling	20	7.9	1.0
	2003	Fledgling	8	10.8	3.4
		Postbreeding	10	9.1	1.6
		Incubation	6	14.8	1.7
		Nestling	38	21.6	2.4
		Fledgling	12	15.9	3.9
		Postbreeding	8	33.3	7.7

Table 4
Mean proportion of time that double-crested cormorants spent in various activities while away from Young Island and Four Brothers Islands, Lake Champlain, 2001–2003.

Colony	Year	Age ^a	Treat ^b	Stage ^c	Fly			Swim			Perch			Forage		
					N	Mean	SE	N	Mean	SE	N	Mean	SE	N	Mean	SE
Young Island	2001	A	N	Inc	1	0.06	0.000	1	0.01	0.000	1	0.93	0.000	1	0.01	0.000
				Nest	5	0.23	0.072	5	0.33	0.090	5	0.08	0.060	5	0.35	0.095
				Fled	4	0.06	0.032	4	0.18	0.109	4	0.50	0.256	4	0.19	0.114
				Post	3	0.03	0.022	3	0.14	0.096	3	0.54	0.049	3	0.14	0.098
				Inc	3	0.05	0.027	3	0.27	0.263	3	0.64	0.321	3	0.27	0.269
				Nest	8	0.15	0.036	8	0.38	0.060	8	0.27	0.111	8	0.40	0.062
	2002	A	N	Fled	2	0.02	0.006	2	0.08	0.019	2	0.59	0.037	2	0.08	0.019
				Post	1	0.03	0.000	1	0.35	0.069	1	0.78	0.000	1	0.19	0.000
				Inc	8	0.14	0.028	8	0.40	0.069	8	0.05	0.044	8	0.42	0.067
				Nest	21	0.15	0.045	21	0.46	0.056	21	0.07	0.049	21	0.32	0.048
				Fled	5	0.13	0.062	5	0.39	0.099	5	0.00	0.000	5	0.48	0.143
				Post	6	0.05	0.009	6	0.22	0.055	6	0.28	0.066	6	0.44	0.041
Four Brothers Islands	2002	A	N	Inc	10	0.21	0.045	10	0.38	0.050	10	0.05	0.053	10	0.36	0.061
				Nest	18	0.14	0.036	18	0.45	0.065	18	0.00	0.000	18	0.41	0.063
				Fled	6	0.12	0.052	6	0.38	0.121	6	0.20	0.133	6	0.29	0.095
				Post	7	0.04	0.022	7	0.27	0.125	7	0.56	0.146	7	0.13	0.019
				Fled	2	0.07	0.072	2	0.50	0.019	2	0.00	0.000	2	0.43	0.053
				Nest	3	0.08	0.001	3	0.32	0.137	3	0.05	0.051	3	0.55	0.107
	2003	A	N	Fled	1	0.04	0.000	1	0.28	0.000	1	0.00	0.000	1	0.67	0.000
				Fled	2	0.13	0.009	2	0.57	0.001	2	0.00	0.000	2	0.30	0.008
				Inc	8	0.25	0.099	8	0.17	0.064	8	0.28	0.117	8	0.30	0.115
				Nest	22	0.26	0.025	22	0.22	0.025	22	0.12	0.049	22	0.40	0.042
				Fled	5	0.22	0.047	5	0.42	0.080	5	0.02	0.017	5	0.34	0.066
				Post	4	0.21	0.051	4	0.18	0.025	4	0.05	0.047	4	0.56	0.095

^a Cormorant ages were adults (A) and juveniles (J).
^b Experimental treatments included oiled (O) and not-oiled (N).
^c Nesting stages were incubation (Inc), nestling, (Nest), fledgling (Fled), and post-breeding (Post).

(5–43%) and 2003 (2–28%). Within a year, cormorants perched most in the post-breeding stage (39–43%). Cormorants perched more in incubation and fledgling stages (5–27%) and least during the nestling stage (4–20%). Two exceptions to these patterns were for the incubation stage on Young Island in 2001 (71%) and the post-breeding stage on Four Brothers Islands in 2003 (6%).

The proportion of daytime that cormorants remained on their colonies (Table 5, Fig. 3) differed among nesting stages ($F_{3, 220} = 8.24$,

$P < 0.001$), between ages ($F_{2, 96} = 5.21$, $P = 0.007$) and among years ($F_{2, 96} = 5.59$, $P = 0.005$), but not between colonies ($F_{1, 96} = 1.75$, $P = 0.189$) or treatments on Young Island ($F_{1, 38} = 1.54$, $P = 0.222$). On average, cormorants spent less time on their nesting colony as the season progressed, but this trend varied by year. Cormorants spent the most time (43–96%) on Young Island in 2001 and the least time (16–38%) on Four Brothers Islands in 2003. Juveniles spent more time (43–96%) on colonies than did adults (16–63%).

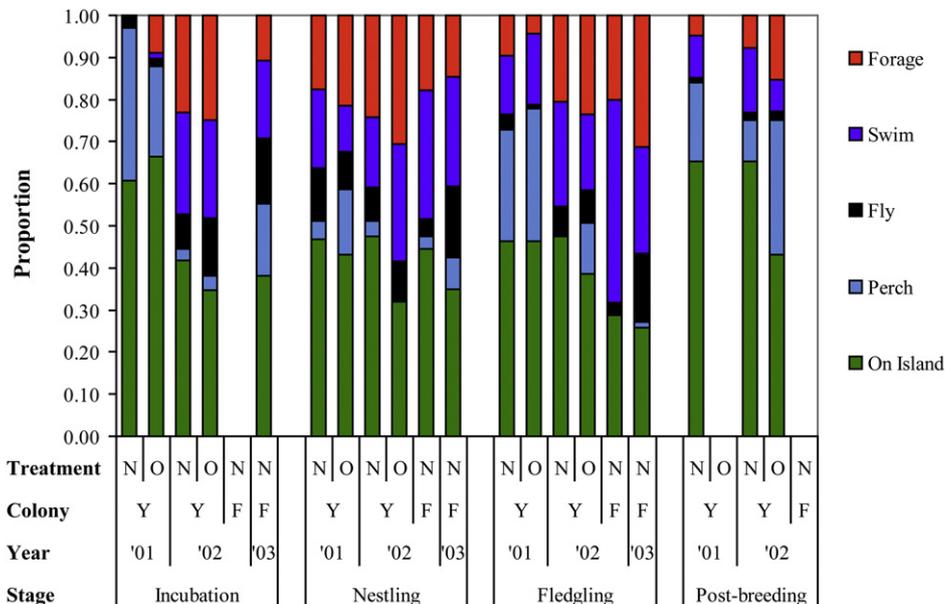


Fig. 3. Proportion of daytime that adult double-crested cormorants spent participating in various activities while on and off nesting colonies on Lake Champlain from 2001 to 2003. Treatments include not oiled (N) and oiled (O). Colonies are Young Island (Y) and Four Brothers Islands (F).

Table 5

Mean proportion of daytime that double-crested cormorants spent on Young Island and Four Brothers Islands on Lake Champlain, 2001–2003.

Colony	Year	Age ^a	Treat ^b	Stage ^c	N	Mean	SE
Young Island	2001	A	N	Inc	7	0.61	0.112
				Nest	7	0.47	0.075
				Fled	4	0.46	0.094
		O	Post	2	0.65	0.076	
			Inc	6	0.67	0.068	
			Nest	7	0.43	0.076	
	2002	A	N	Post	1	0.43	
				Nest	11	0.96	0.016
				Fled	11	0.72	0.043
		J	Post	5	0.43	0.161	
			Inc	9	0.42	0.060	
			Nest	13	0.48	0.071	
Four Brothers Islands	2002	A	N	Fled	11	0.48	0.076
				Inc	12	0.35	0.036
				Nest	13	0.32	0.072
		O	Fled	9	0.39	0.066	
			Nest	6	0.56	0.123	
			Fled	6	0.35	0.072	
	2003	A	N	Nest	2	0.45	0.203
				Fled	2	0.29	0.266
				Inc	3	0.72	0.042
		J	Nest	3	0.68	0.044	
			Fled	3	0.72	0.042	
			Inc	20	0.38	0.057	
2003	A	N	Nest	30	0.35	0.033	
			Fled	30	0.26	0.038	
			Post	22	0.16	0.031	

^a Cormorant ages were adults (A) and juveniles (J).

^b Experimental treatments included oiled (O) and not-oiled (N).

^c Nesting stages were incubation (Inc), nestling, (Nest), fledgling (Fled), and post-breeding (Post).

Energetics modeling

We estimated daily energy requirements for cormorants on Lake Champlain based upon average body mass of adults (1820 g). Estimates of energy demands varied between colonies and age classes, and ranged from 1112 to 3748 kJ/day (Table 6). Estimates were lowest for Young Island in 2001, increased in 2002, but still were less than on Four Brothers Islands in 2002. Energy demands were greatest for cormorants nesting on Four Brothers Islands in 2003. Differences in energy demands among years and nesting stages are due to variation in cormorant activities and ambient temperatures.

Table 6

Average daily (kJ) energy demands per double-crested cormorant and total (1,000,000 kJ) energy per colony for each age group and treatment for cormorants nesting on Young Island and Four Brothers Islands on Lake Champlain, 2001–2003.

Colony	Year	Age ^a	Treat ^b	Nesting stage ^c											
				Pre		Inc		Nest		Fled		Post		All Year	
				Daily	Total	Daily	Total	Daily	Total	Daily	Total	Daily	Total	Daily	Total
Young Island	2001	A	N	1603	24.8	1471	45.4	2887	144.1	1322	31.6	1356	57.7	1775	303.7
			O	1864	43.6	1744	80.1	2523	187.5	1112	39.6	1567	99.7	1834	450.5
		SA	N	1437	0.1	1471	2.4	2883	19.9	1322	6.9	1356	17.2	1410	46.5
	2002	A	N	3354	52.1	3363	96.8	2676	124.6	1887	42.1	1565	62.3	2564	377.9
			O	3692	99.9	3748	186.8	3292	265.5	1885	72.8	1582	109.4	2848	734.4
		SA	N	3402	0.3	3363	5.6	2672	18.8	1887	10.1	1565	20.4	1816	55.3
Four Brothers Islands	2002	A	N	3241	265.9	3284	497.9	2632	645.6	1927	226.5	3144	676.6	2944	2312.6
			SA	N	3295	0.5	3284	10.6	2629	35.6	1927	20.0	3144	81.0	2222
		J	N					1576	280.8	1423	112.8	1755	250.0	1629	643.5
	2003	A	N	3265	297.5	3279	553.7	3279	895.9	2662	348.5	3153	755.9	3175	2851.5
			SA	N	3322	0.6	3279	11.8	3276	49.6	2662	30.7	3153	90.5	2448
		J	N					1576	312.8	1390	122.7	1769	281.2	1630	716.7

^a Cormorant ages were adults (A), subadults (SA), and juveniles (J).

^b Experimental treatments included oiled (O) and not-oiled (N).

^c Nesting stages were pre-breeding, (Pre), incubation (Inc), nestling, (Nest), fledgling (Fled), and post-breeding (Post).

We derived estimates of total energy required by cormorants on Lake Champlain by multiplying daily population estimates by estimates of daily energy demands. Cormorant numbers built up gradually from mid-March to mid-May as adults arrived onto nesting colonies (Fig. 4). We counted adults and subadults in 94 flocks of cormorants. Subadults began to arrive onto Lake Champlain beginning on 2 May, and the proportion of subadults within flocks increased gradually (0.0015 per day, SE=0.0002) throughout each summer (linear regression $F_{1,92} = 33.13$, $P < 0.001$, $R^2 = 0.26$). The adult-to-subadult ratio peaked at 1:0.15 at the end of the season. In mid-July, eggs hatched. Birth pulses were larger on Four Brothers Islands (3286–3747) than on Young Island (1232–1322) because approximately half of the eggs on Young Island were sprayed with oil and did not hatch. Starting in mid-September, cormorant numbers declined as all age groups migrated from Lake Champlain. Our estimates of total energy consumed for each colony of cormorants on Lake Champlain varied from 1.04 to 3.75 billion kJ from 2001 to 2003 (Table 6). Finally, we estimated that cormorants consumed 312,000–425,000 kg of fish per year at Young Island and 899,000–1,086,000 kg of fish per year at Four Brothers Islands (Table 7). Cormorants from Four Brothers Islands consumed more fish than did cormorants on Young Island because the colony on Four Brothers Islands was more than twice as large and energy demand per bird was higher than on Young Island.

Our sensitivity analysis indicated that models for estimating energy requirements of cormorants on Lake Champlain in 2002 were most sensitive to energy demands of flying for metabolic variables and amount of time spent swimming for activity budget variables (Table 8). Increasing these variables by 10% resulted in an increase of energy demands of 2.1 and 2.3%, respectively. Estimates of fish consumption were most sensitive to changes in assimilation efficiency for adult cormorants. Increases in energy densities of yellow perch and rainbow smelt also showed moderate sensitivities in the model (Table 8).

Discussion

On Lake Champlain, we found that foraging dynamics of double-crested cormorants differed noticeably between two important breeding sites, Young Island and Four Brothers Islands. Energetic requirements of cormorants were greater on Four Brothers Islands than on Young Island. The unintended consequence of managing cormorant productivity on Young Island was dispersal of cormorants (Duerr et al., 2007) to a site where energy demands were greater

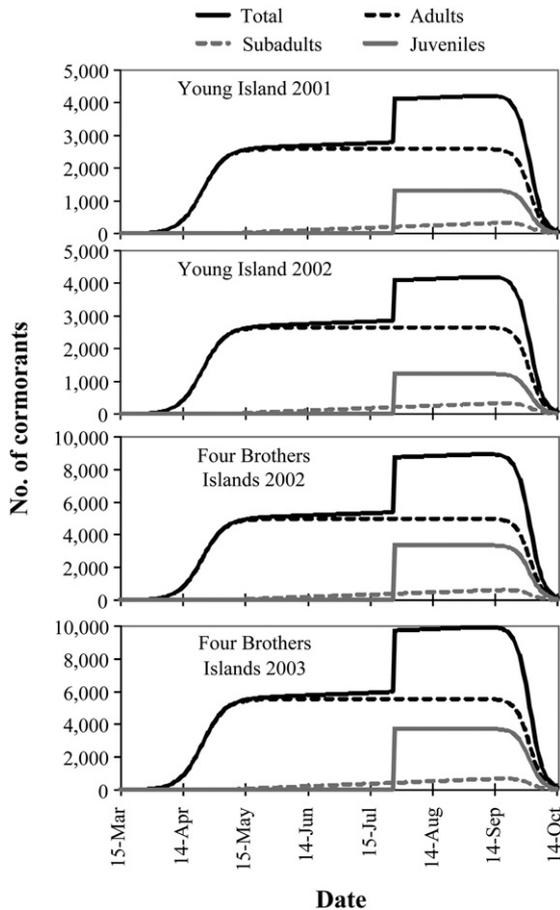


Fig. 4. Numbers of double-crested cormorants by age and date associated with colonies on Young Island and Four Brothers Islands on Lake Champlain, 2001–2003.

and, thus, total fish consumption by cormorants on Lake Champlain increased.

An expected consequence of oiling cormorant eggs is a reduction in activity levels and energy demands of adults whose eggs were oiled because they do not have to expend energy to provision nestlings. Clearly, adults raising young provide food (energy) for nestlings that is beyond the needs of adults themselves. By accounting for nestling demands separately in our energetics model, we were able to compare activities and energy demands only for adult birds

and found no differences between treatments on Young Island. Reproductive failure at a colony reduces energy demands and fish consumption only by what is required by nestlings.

Foraging distribution of cormorants on Lake Champlain varied spatially and temporally. Distances to foraging locations from Young Island tended to be consistent between years, with a general trend toward longer distances as the breeding season progressed. Distances from Four Brothers Islands to foraging locations varied widely within and between years, but were consistently greater than for Young Island. Our pattern for Young Island is consistent with the foraging distribution of two colonies in Lake Michigan, where cormorants shifted foraging locations within years (Custer and Bunck, 1992). However, the spatial extent of the area used for foraging was similar for both colonies in Lake Michigan, but differed for colonies in Lake Champlain.

As expected, cormorant activities differed among breeding stages, with energetic demands placed on breeding adults becoming more intense as nestlings grew. Of the activities tracked, we classified time spent on the colony, perching off the colony, and nighttime activities as resting activities. Generally, double-crested cormorants rested more before and after the nestling stage and were relatively more active (i.e., flying, swimming, and foraging) during the nestling stage. Cormorants were also more active on Four Brothers Islands than on Young Island. Great cormorants also were more active during nestling stages than during incubation; however, they swam and foraged less (2–8% of daytime) and flew less (1–4% of daytime) than double-crested cormorants (Grémillet et al., 1995; Grémillet, 1997). Differences between species culminated in greater, but less variable, time spent resting (87–97% of the time) during incubation and nestling stages (Grémillet et al., 1995) than for double-crested cormorants (32–97%). Great cormorants and South Georgian shags (*Phalacrocorax georgianus*) also spent considerably less time away from their breeding colonies (29 and 38%) during the nestling stage than double-crested cormorants (Wanless et al., 1995; Grémillet, 1997). Differences among species suggest double-crested cormorants are more active than other species in the genus *Phalacrocorax*, which is supported by similar flight (8% of daytime) and foraging (17% of daytime) times during winter (King et al., 1995) as we found during summer.

Cormorants had high energy demands during the pre-breeding and incubation stages. This is due to increased thermoregulation costs associated with low air and water temperatures in April and May. Our estimates of energy expenditures for cormorants during the pre-breeding and incubation stages were about equal to (2001) or greater than (2002–2003) the estimated maximum energy expenditures for cormorants wintering in Mississippi (2106 kJ/day; Glahn and Brugger, 1995), although we make this comparison with caution

Table 7

Fish consumption (1000 kg) by double-crested cormorants from Young Island and Four Brothers Islands on Lake Champlain, 2001–2003.

Colony	Year	Total energy or species	Nesting stage ^a						Total
			Pre	Inc	Nest	Fled	Post		
Young Island	2001	Yellow perch	19.6	36.6	110.3	31.2	36.8	234.5	
		Rainbow smelt	0.0	0.0	11.7	0.0	35.5	47.3	
		Sunfish	0.7	1.3	2.6	3.3	0.9	8.8	
		Other	1.0	1.8	10.7	2.9	5.1	21.6	
	2002	Yellow perch	30.2	76.9	136.3	48.9	74.9	367.2	
		Rainbow smelt	0.0	11.1	9.5	0.1	0.0	20.7	
		Sunfish	15.9	0.0	4.7	1.6	2.8	25.0	
		Other	1.2	0.0	1.2	0.7	9.6	12.7	
Four Brothers Islands	2002	Yellow perch	82.0	92.6	72.8	28.0	104.8	380.3	
		Rainbow smelt	0.6	27.7	161.4	37.6	140.6	367.8	
		Sunfish	0.0	15.2	4.4	0.0	14.7	34.3	
		Other	0.0	18.0	27.5	40.2	31.4	117.1	
	2003	Yellow perch	91.7	103.0	95.6	39.2	117.3	446.9	
		Rainbow smelt	0.6	30.8	211.9	52.5	157.3	453.2	
		Sunfish	0.0	17.0	5.8	0.0	16.4	39.1	
		Other	0.0	20.0	36.1	56.2	35.1	147.5	

^a Nesting stages were pre-breeding, (Pre), incubation (Inc), nestling, (Nest), fledging (Fled), and post-breeding (Post).

Table 8

Percentage change in energy requirements for double-crested cormorants from Young Island and Four Brothers Islands in 2002 when we increased variables for an energetics model by 10%. Absolute values of percent changes are ranked for each variable category.

Variable	Percent change	Rank for category
<i>Fish consumption</i>		
Assimilation efficiency adults	−8.68%	1
Assimilation efficiency nestlings	−0.67%	5
<i>Energy content</i>		
Yellow perch	−5.13%	2
Rainbow smelt	−2.66%	3
Sunfish	−0.41%	6
Other	−0.89%	4
<i>Metabolic rates</i>		
<i>Costs of thermoregulation</i>		
Perch	0.37%	9
Swim	0.95%	4
Spread wing	0.57%	8
Night resting	0.03%	12
<i>Metabolic rates in thermoneutral zone</i>		
Nighttime resting	0.89%	5
On island	0.66%	7
Fly	2.22%	1
Perch	0.13%	10
Swim	1.75%	2
Forage	1.30%	3
Duration of wing spreading	0.00%	13
MR of chicks	0.83%	6
Growth rate of chicks	−0.08%	11
<i>Activity budgets</i>		
<i>Adults</i>		
On island	0.74%	4
Fly	2.08%	2
Perch	0.17%	9
Swim	2.56%	1
Forage	1.68%	3
<i>Juveniles</i>		
On island	0.25%	5
Fly	0.17%	8
Perch	0.04%	10
Swim	0.19%	7
Forage	0.23%	6

because energy demands were calculated using different energetic models. Energy demands of adult cormorants are similar for incubation and nestling stages despite differences in activity levels. This is due to greater costs of thermoregulation during the colder incubation stage. Subadults avoided high thermoregulation costs during the colder pre-breeding stage by delaying arrival on Lake Champlain until mid May.

Cormorant activities and energy demands differed between years and colonies, on Lake Champlain. Birds from Young Island rested more (perched off the colony and spent more time on the colony) in 2001 compared to either colony in 2002–03. For Young Island, cormorants expended the least amount of energy per bird in 2001. Cormorants from Four Brothers Islands spent more time swimming and less time on their colony in 2003 than either colony in 2001–2002, thus expending the most energy per bird. Cormorants expended more energy on Four Brothers Islands than on Young Island in any year. These differences in energy demands between colonies provide a picture of colony quality on Lake Champlain, which is mirrored in lower productivity levels on Four Brothers Islands compared to Young Island in the absence of management (Fowle et al., 1999; D. E. Capen, unpublished data).

Secondary consequences of cormorant management stem from differences in foraging dynamics between colonies on Lake Champlain. Comparing daily energy requirements for each year (all year, Table 6), adult cormorants from Four Brothers Islands required 2944–3175 kJ/day and their counterparts on Young Island required 1775–2848 kJ/day. Cormorants that moved from Young Island to Four Brothers

Islands during our study, had 35% greater energy demands, requiring consumption of 185 g more rainbow smelt per day, but 84 g fewer yellow perch, based on average diet composition for each colony (DeBruyne et al., 2012). In 2003, alewife invaded Lake Champlain (Marsden and Hauser, 2009) and have become a dominant item in the diet of cormorants from Four Brothers Islands, further reducing consumption of yellow perch and to a lesser extent reducing consumption of rainbow smelt (DeBruyne et al., 2012). Management of cormorants on Young Island also increased since 2003, resulting in fewer than 150 pair attempting to nest. Differences in energy requirements and prey base between colonies illustrate the need to incorporate fish predation into management decisions, especially when management strategies shift cormorants from one area to another.

Our estimates of energy requirements for double-crested cormorants on Lake Champlain are consistent with other studies (see review by Ridgway, 2010). Estimates of daily energy expenditures from energetics models based on allometric equations and respirometry measurements range from 1927–2760 kJ/day (Glahn and Brugger, 1995; Derby and Lovvorn, 1997; Enstipp et al., 2006; Seefelt and Gillingham, 2008). Estimates from our energetics model are similar, although estimates from specific nesting stages fall below (1112 kJ/day) and above (3748 kJ/day) this range. Use of our activity based model allowed us to make detailed comparisons of energy expenditures among nesting stages, years, and between colonies that would not have been possible using other methods.

We made several assumptions when constructing the energetics model so we could fill data gaps and complete the model. By examining sensitivity of model outputs to changes in variable values, we can assess the potential consequences of our assumptions. Changes to variable values (10% increase) for activity budgets and metabolic rates had very little influence on total energy demands (<2.5%, Table 6). These results suggest that any bias due to assumptions should be minimal. Also, we applied assumptions equally to both colonies; therefore, biases would affect estimates of energetic demands for both colonies and would not change conclusions of comparisons between Young Island and Four Brothers Islands. Assumptions that activity budgets were equal for pre-breeding and incubation stages within colonies, and that post-breeding stages were the same between years for each colony also do not alter our conclusions. We found differences in activities and energy demands, despite holding activity budgets constant between years for these nesting stages. Violations of our assumptions may influence model estimates and increases uncertainty in model outputs; however, our estimates are similar to other estimates of daily energy expenditures for this species, including those based upon allometric equations recommended by some for consistency (Carss et al., 1997; Ridgway, 2010). Our estimates represent a starting point for incorporating energy demand and fish consumption by cormorants into management of fish populations, cormorant populations, or both in Lake Champlain.

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References

- Ancel, A., Starke, L.N., Ponganis, P.J., Van Dam, R., Kooyman, J.L., 2000. Energetics of surface swimming in Brandt's cormorants (*Phalacrocorax penicillatus* Brandt). *J. Exp. Biol.* 203, 3727–3731.
- Beyer, H.L., 2004. Hawth's Analysis Tools for ArcGIS. (URL: <http://www.spatialecology.com/htools>) (Accessed 5 October 2006).
- Brugger, K.E., 1993. Digestibility of three fish species by double-crested cormorants. *Condor* 95, 25–32.
- Burnett, J.A.D., Ringler, N.H., Lantry, B.F., Johnson, J.H., 2002. Double-crested cormorant predation on yellow perch in the eastern basin of Lake Ontario. *J. Great Lakes Res.* 28, 202–211.
- Carss, D.N., The Diet, Assessment and Food Intake Working Group, 1997. Techniques for assessing cormorant and food intake: towards a consensus view. *Suppl. Ric. Biol. Selvaggina* 26, 197–230. http://web.tiscalinet.it/sv2001/WI%20-%20CRSG/diet_foodintake.htm.
- Custer, T.W., Bunck, C., 1992. Feeding flights of breeding double-crested cormorants at two Wisconsin colonies. *J. Field Ornithol.* 63, 203–211.
- DeBruyne, R.L., DeVault, T.L., Duerr, A.E., Capen, D.E., Pogmore, F.E., Jackson, J.R., Rudstam, L.G., 2012. Spatial and temporal comparisons of double-crested cormorant diets following the establishment of alewife in Lake Champlain, USA. *J. Great Lakes Res.* 38 (Supplement 1), 123–130.
- Derby, C.E., Lovvorn, J.R., 1997. Predation on fish by cormorants and pelicans in a cold water river: a field and modeling study. *Can. J. Fish. Aquat. Sci.* 54, 1480–1493.
- DesGranges, J.-L., 1982. Weight growth of young double-crested cormorants in the St. Lawrence Estuary, Quebec. *Colonial Waterbirds* 5, 79–86.
- Duerr, A.E., Donovan, T.M., Capen, D.E., 2007. Management induced reproductive failure and breeding dispersal in double-crested cormorants on Lake Champlain. *J. Wildl. Manag.* 71, 2565–2574.
- Dunn, E.H., 1975a. Caloric intake of nestling double-crested cormorants. *Auk* 92, 553–565.
- Dunn, E.H., 1975b. Growth, body components and energy content of nestling double-crested cormorants. *Condor* 77, 431–438.
- Enstipp, M.R., Grémillet, D., Jones, D.R., 2006. The effects of depth, temperature and food ingestion on the foraging energetics of a diving endotherm, the double-crested cormorant (*Phalacrocorax auritus*). *J. Exp. Biol.* 209, 845–859.
- Feltham, M.J., 1995. Consumption of Atlantic salmon smolts and parr by goosanders: estimates from doubly-labelled water measurements of captive birds released on two Scottish rivers. *J. Fish Biol.* 46, 273–281.
- Feltham, M.J., Davies, J.M., 1997. Daily food intake of cormorants: a summary. *Suppl. Ric. Biol. Selvaggina* 26, 259–268.
- Fowle, M.R., Capen, D.E., Buckley, N.J., 1999. Population growth of double-crested cormorants in Lake Champlain. *Northeast Wildl.* 54, 25–34.
- Garland, L., Chipman, R., Slate, D., Bruleigh, R., 1998. Environmental assessment of alternative strategies for the management of damage caused by ring-billed gulls and double-crested cormorants on Lake Champlain, Vermont and New York. Vermont Department of Fish and Wildlife, New York Department of Environmental Conservation, and U.S.D.A. Animal Plant Health Inspection Service, Wildlife Services.
- Glahn, J.F., Brugger, K.E., 1995. The impact of double-crested cormorants on the Mississippi Delta catfish industry: a bioenergetics model. *Colonial Waterbirds* 18, 168–175 (Special Publication 1).
- Grémillet, D., 1997. Catch per unit effort, foraging efficiency and parental investment in breeding great cormorants (*Phalacrocorax carbo*). *ICES J. Mar. Sci.* 54, 635–644.
- Grémillet, D., Schmid, D., Culik, B., 1995. Energy requirements of breeding great cormorants *Phalacrocorax carbo sinensis*. *Mar. Ecol. Prog. Ser.* 121, 1–9.
- Grémillet, D., Storch, S., Peters, G., 2000. Determining food requirements in marine top predators: a comparison of three independent techniques in great cormorants, *Phalacrocorax carbo carbo*. *Can. J. Zool.* 78, 1567–1579.
- Hatch, J.J., Weseloh, D.V., 1999. Double-crested cormorant (*Phalacrocorax auritus*). In: Poole, A., Gill, F. (Eds.), *The Birds of North America*. The Academy of Natural Sciences, Philadelphia, Pennsylvania, and The American Ornithologists' Union, Washington, D.C (Account 441).
- Hennemann, W.W., 1983. Environmental influences on the energetics and behavior of anhingas and double-crested cormorants. *Physiol. Zool.* 56, 201–216.
- Hennemann, W.W., 1985. Energetics, behavior and the zoogeography of anhingas and double-crested cormorants. *Ornis Scand.* 16, 319–323.
- Hennemann, W.W., 1988. Energetics and spread-winged behavior in anhingas and double-crested cormorants: the risks of generalization. *Am. Zool.* 28, 845–851.
- Hewett, S.W., Johnson, B.L., 1992. Fish bioenergetics model 2. Report UW Sea Grant Technical Report No. WIS-SG-92-250. Madison, WI. University of Wisconsin, Madison.
- Kendeigh, S.C., Dolnik, V.R., Gavrilov, R.M., 1977. Avian energetics. In: Kendeigh, S.C., Penoski, J. (Eds.), *Granivorous Birds in Ecosystems*. Cambridge University Press, Cambridge.
- Kernohan, B.J., Gitzen, R.A., Millsapugh, J.J., 2001. Analysis of animal space use and movements. In: Millsapugh, J.J., Marzluff, J.M. (Eds.), *Radio Tracking and Animal Populations*. Academic Press, San Diego, CA, pp. 125–166.
- King, D.T., Andrews, K.J., King, J.O., Flynt, R.D., Glahn, J.F., 1994. A night-lighting technique for capturing cormorants. *J. Field Ornithol.* 65, 254–257.
- King, D.T., Glahn, J.F., Andrews, K.J., 1995. Daily activity budgets and movements of winter roosting Double-crested Cormorants determined by biotelemetry in the Delta Region of Mississippi. *Colonial Waterbirds* 18, 152–157 (Special Publication 1).
- King, D.T., Tobin, M.E., Bur, M., 2000. Capture and telemetry techniques for double-crested cormorants (*Phalacrocorax auritus*). Proceedings of the 19th Vertebrate Pest Conference. University of California, Davis, CA, pp. 54–57.
- Lantry, B.F., Eckert, T.H., Schneider, C.P., Chrisman, J.R., 2002. The relationship between the abundance of smallmouth bass and double-crested cormorants in the eastern basin of Lake Ontario. *J. Great Lakes Res.* 28, 193–201.
- Lasiewski, R.C., Dawson, W.R., 1967. A re-examination of the relation between standard metabolic rate and body weight in birds. *Condor* 69, 13–23.
- Leger, C., McNeil, R., 1987. Brood size and chick position as factors influencing feeding frequency, growth, and survival of nestling double-crested cormorants, *Phalacrocorax auritus*. *Can. Field Nat.* 101, 351–361.
- Lewis, H. F., 1929. The natural history of the double-crested cormorant *Phalacrocorax auritus auritus* (Lesson). Ph.D. Dissertation, Cornell University, Ithaca, NY. 94 pp.
- Marsden, J.E., Hauser, M., 2009. Exotic species in Lake Champlain. *J. Great Lakes Res.* 35, 250–265.
- Mendall, H.L., 1936. The home-life and economic status of the double-crested cormorant *Phalacrocorax auritus* (Lesson). *Maine Bull.* 39, 1–159.
- Pennycuik, C.J., 1989a. Bird Flight Performance: A Practical Calculation Manual. Oxford University Press, New York, NY. (11 pp.).
- Pennycuik, C.J., 1989b. Span-ratio analysis used to estimate effective lift:drag ratio in the double-crested cormorant *Phalacrocorax auritus* from field observations. *J. Exp. Biol.* 142, 1–15.
- Ricklefs, R.E., 1967. A graphical method of fitting equations to growth curves. *Ecol.* 48, 978–983.
- Ridgway, M.S., 2010. A review of estimates of daily energy expenditure and food intake in cormorants (*Phalacrocorax* spp.). *J. Great Lakes Res.* 36, 93–99.
- Rudstam, L.G., VanDeValk, A.J., Adams, C.M., Coleman, J.T.H., Forney, J.L., Richmond, M.E., 2004. Cormorant predation and population dynamics of walleye and yellow perch in Oneida Lake. *Ecol. Appl.* 14, 149–163.
- Schartz, R.L., Zimmerman, J.L., 1971. The time and energy budget of the male dickcissel (*Spiza americana*). *Condor* 73, 65–76.
- Schmid, D., Grémillet, D.J.H., Culik, B.M., 1995. Energetics of underwater swimming in the great cormorant (*Phalacrocorax carbo sinensis*). *Mar. Biol.* 123, 875–881.
- Seefelt, N.E., Gillingham, J.C., 2008. Bioenergetics and prey consumption of breeding double-crested cormorants in the Beaver Archipelago, northern Lake Michigan. *J. Great Lakes Res.* 34, 122–133.
- Storch, S., Grémillet, D., Culik, B.M., 1999. The telltale heart: a non-invasive method to determine the energy expenditure of incubating great cormorants *Phalacrocorax carbo carbo*. *Ardea* 87, 207–215.
- Trapp, J.L., Lewis, S.J., Pence, D.M., 1999. Double-crested cormorant impacts on sport fish: literature review, agency survey, and strategies. Proceedings of Symposium on Double-Crested Cormorants: Population Status and Management Issues in the Midwest. USDA/APHIS Technical Bulletin No. 1879, pp. 87–96.
- VanDeValk, A.J., Adams, C.M., Rudstam, L.G., Forney, J.L., Brooking, T.E., Gerken, M.A., Young, B.P., Hooper, J.T., 2002. Comparison of angler and cormorant harvest of walleye and yellow perch in Oneida Lake, New York. *Trans. Am. Fish. Soc.* 131, 27–39.
- Vermont Monitoring Cooperative, 2006. Basic meteorological monitoring: Colchester Reef meteorology (38m). (URL: <http://sal.snrvvm.edu/vmc/air/>) (Accessed 15 March 2006).
- Wanless, S., Harris, M.P., Morris, J.A., 1995. Factors affecting daily activity budgets of south Georgian shags during chick rearing at Bird Island, South Georgia. *Condor* 97, 550–558.
- Wilson, R.P., Culik, B.M., 1991. The cost of a hot meal: facultative specific dynamic action may ensure temperature homeostasis in post-digestive endotherms. *Comp. Biochem. Physiol.* A 100, 151–154.
- Wires, L.R., Cuthbert, F.J., Trexel, D.R., Joshi, A.R., 2001. Status of the double-crested cormorant (*Phalacrocorax auritus*) in North America. Final report to USFWS, University of Minnesota, Department of Fisheries and Wildlife, St. Paul, MN. (359 pp).