

Management-Induced Reproductive Failure and Breeding Dispersal in Double-Crested Cormorants on Lake Champlain

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ABSTRACT We studied breeding dispersal of double-crested cormorants (*Phalacrocorax auritus*) associated with management practices that suppressed their reproduction on Lake Champlain in the northeastern United States. We implemented an experiment on one colony by spraying corn oil on cormorant eggs in portions of the colony and leaving other portions untreated. Gulls (*Larus* spp.) consumed cormorant eggs during the oiling process, but we reduced and then eliminated predation levels after the first year of the study. We used mark-recapture techniques within the experimental framework to measure rates of breeding dispersal for cormorants from the experimental colony and an unmanaged colony in Lake Champlain. Egg oiling increased the movement rate to the unmanaged colony by 3% during the year with no egg predation by gulls. When gulls depredated cormorant eggs at high rates during egg oiling, movement to the unmanaged colony increased by 20%. When cormorants are managed to reduce population sizes, methods that limit dispersal away from the managed colony may be most effective. Such methods would mitigate effects to nontarget populations and allow for a greater portion of the metapopulation to be managed. (JOURNAL OF WILDLIFE MANAGEMENT 71(8):2565–2574; 2007)

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The process of dispersal is an important component of metapopulation dynamics, where movement of individuals among local populations influences growth and persistence of these populations (Hanski 1991, Hanski and Gilpin 1991). Dispersal can occur as the movement of adults between breeding sites (breeding dispersal) or as movement from a natal area to the first breeding site (natal dispersal; Greenwood and Harvey 1982). Rates of breeding and natal dispersal are associated with habitat quality (Fretwell and Lucas 1969, Suryan and Irons 2001). Because management can alter habitat quality, management also may alter rates of dispersal. Therefore, when assessing options for management, it is important to determine how specific management actions affect dispersal.

One example is management of the rapidly expanding population of double-crested cormorants (*Phalacrocorax auritus*) in the Great Lakes region. During the early 1980s, cormorants colonized several inland regions in New England, including Lake Champlain (Krohn et al. 1995), which straddles the Vermont and New York, USA, and Quebec, Canada, borders. Before 1980, they were rare migrants on the lake (Green Mountain Audubon Society 1976). Since 1981, populations have expanded geometrically (Fowle et al. 1999), with concomitant destruction of vegetation in nesting colonies and displacement of other species of birds. Currently 4,200 pairs breed at 4 colonies on Lake Champlain, with 96% of the population nesting in 2

colonies: Four Brothers Islands, New York, and Young Island, Vermont.

In response to habitat loss on nesting islands and concerns about the increasing size of the cormorant population, Vermont Fish and Wildlife Department (VTFWD) and United States Department of Agriculture Wildlife Services (WS) began actively managing cormorants in the Vermont portion of Lake Champlain in 1994 (Garland et al. 1998). Initially, VTFWD and WS removed nests from several islands in Vermont to prevent cormorants from establishing new colonies. In 1999, these agencies began applying corn oil to cormorant eggs on Young Island to reduce recruitment into the population. The oil addles eggs, preventing them from hatching (Gross 1951, Shonk et al. 2004). Adults continue to incubate addled eggs for several weeks without renesting. The egg-oiling program successfully eliminated almost all cormorant reproduction on Young Island in 1999 and 2000 (D. E. Capen, University of Vermont, unpublished data).

Although egg oiling was effective in reducing cormorant productivity on Young Island, it apparently caused a shift in the size and distribution of cormorant colonies on Lake Champlain (Fig. 1). During the 2 years following initiation of the egg-oiling program on Young Island, the size of the colony decreased by 1,759 pairs (58%; D. E. Capen, unpublished data). Meanwhile, the Four Brothers colony increased by 1,065 nests (78%). Additionally, cormorants attempted to establish 10 new colonies on Lake Champlain in 2001 and were reported to be more numerous in the St. Lawrence River of Quebec, about 100 km north of Lake

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Champlain. Population increases in nontarget colonies on Lake Champlain accounted for 1,405 nests or 80% of the decline observed on the target colony, Young Island. These observations suggested that cormorants responded to nest failure from management activities by dispersing from Young Island to other locations to breed.

To determine if egg oiling could have caused the observed breeding dispersal, we initiated an experiment on Young Island in 2001. This experiment involved oiling eggs in a portion of nests on Young Island, and leaving another portion of nests untreated. While flushing cormorants from their nests to apply oil to their eggs, we observed gulls (*Larus* spp.) eating cormorant eggs. Because VTFWD and WS oiled cormorant eggs in the same manner in 1999 and 2000, predation of cormorant eggs could have triggered or contributed to observed dispersal.

Dispersal rates also vary with quality (i.e., productivity) of the breeding colony (Danchin et al. 1998, Cadiou 1999). In another study, we found that cormorants from the Four Brothers colony had lower fledging rates and traveled farther from the colony to forage than did cormorants from Young Island (Duerr 2007). These measures indicate colony quality may not be equal; therefore, dispersal rates could differ between colonies independent of management activities.

Based on observations of colony dynamics from 2000 to 2001, our experimental hypothesis was 1) oiling cormorant eggs would increase breeding dispersal in the following year. After we initiated the egg-oiling experiment, we developed 2 more hypotheses about breeding dispersal in cormorants: 2) predation of cormorant eggs increases dispersal, and 3) dispersal rates for Young and Four Brothers islands differ. Because the last 2 hypotheses included factors that we did not include in the controlled experiment, we termed these as observational hypotheses and tested them separately from the experimental hypothesis.

To test these 3 hypotheses, we implemented a 4-year mark-recapture study of adult cormorants on Young and Four Brothers islands. On Young Island, we implemented an experiment to determine the response of adult cormorants to egg oiling and altered this experiment to account for egg predation. We used multistrata analyses (Brownie et al. 1993, Lebreton et al. 2003) to estimate breeding dispersal of cormorants. Multistrata modeling allows for estimation of apparent survival, resight probability, and movement rates among strata. For this study, we considered 3 strata: Four Brothers Islands, the oiled treatment on Young Island, and the control (not-oiled) treatment on Young Island. Apparent survival (Φ) is the product of true survival and fidelity to the study area or system. We assumed survival of adult cormorants did not differ between colonies, so differences in apparent survival would be due to differences in emigration rates. Resight probability (p) is the probability that we observed a marked bird in a given year, given the bird was alive and present in the system. Movement (Ψ) is the probability that an individual that survived and remained in the system moved from one stratum to another.

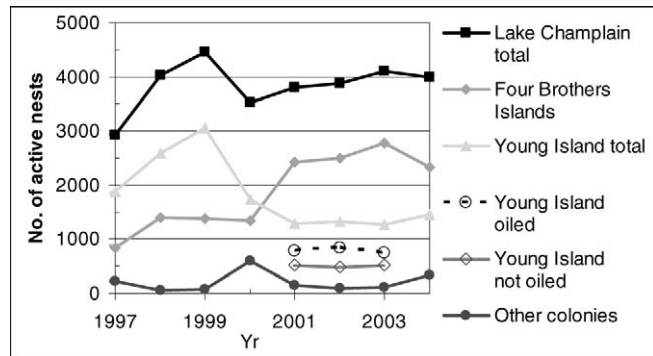


Figure 1. Number of active nests of double-crested cormorants on Lake Champlain from 1997 to 2004. Nests on the Four Brothers Islands were not managed. Nests on Young Island were not managed before 1999. From 1999 to 2000, we sprayed eggs in all nests on this colony with corn oil to prevent hatching. From 2001 to 2003, we implemented an experiment in which we oiled eggs from some nests while we did not oil others.

Therefore, dispersal can occur as either movement (Ψ) within the system or emigration from the system ($1 - \Phi$).

STUDY AREA

Young Island was a 2-ha island owned by the State of Vermont and managed by VTFWD. It was located about 1 km west of Grande Isle, Vermont, and about 31 km northwest of Burlington, Vermont. The Nature Conservancy owned the Four Brothers Islands (named A, B, C, and D), New York, which total about 7 ha in area. They were located 35 km south of Young Island, about 2.5 km east of Willsboro Point, New York, and about 10.5 km west of Burlington, Vermont. The Nature Conservancy had not actively managed cormorant populations on the Four Brothers Islands.

METHODS

Experimental Design

The egg-oiling experiment on Young Island began in 2001 and continued through 2003. We helped VTFWD oil eggs from cormorant nests according to a randomized design that we established. We identified treatment blocks by establishing a 10×10 m grid on Young Island with grid corners marked by 1-m tall wooden stakes. We randomly assigned oiled ($n = 8$), not-oiled ($n = 5$), and variably oiled ($n = 7$) treatments to grid blocks that contained cormorant nests in 2001. We also randomly assigned new blocks that were occupied in 2003 to oiled ($n = 3$) and not-oiled ($n = 3$) treatments. Every year, we sprayed all eggs in oiled blocks with corn oil at least twice during the nesting season; first 1–2 weeks after cormorants initiated most clutches (about mid-May), and again 1 or 2 more times each season. We never sprayed eggs in the not-oiled treatment (our experimental control) with corn oil, but flushed cormorants from these nests and counted eggs; therefore, disturbance to both treatment groups was the same. We oiled cormorant eggs in the variably oiled treatment in some years but not in other years.

During each of 3 daytime applications of oil to eggs in

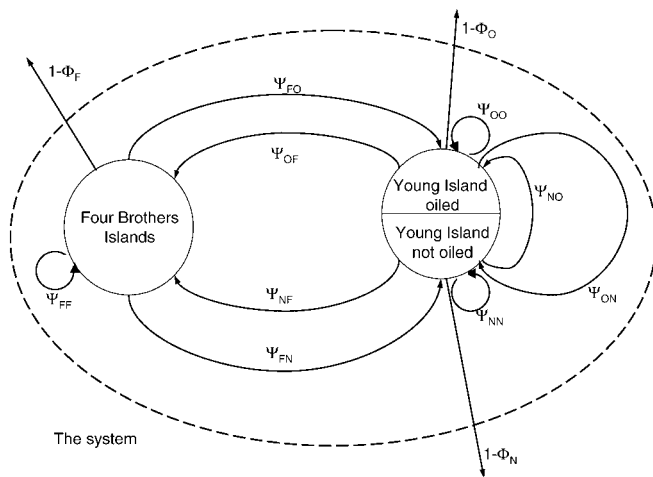


Figure 2. Multistrata model of population dynamics for adult double-crested cormorants at the two largest colonies on Lake Champlain from 2001 to 2004. Demographic parameters include apparent survival (Φ) and movement (Ψ). Movement is conditional upon survival. Strata are Four Brothers Islands (F), Young Island oiled (O), and Young Island not oiled (N). Subscripts indicate strata specific rates for apparent survival and movement rates between strata.

2001, gulls consumed cormorant eggs from both oiled and not-oiled nests throughout the colony. In 2002, we applied oil to cormorant eggs twice, once during the daytime and once at night. In 2003, we completed 2 oil applications during the nighttime. Gulls only preyed upon cormorant eggs when we oiled eggs during the daytime, resulting in a temporal trend in predation levels (or predation events). Levels of predation were high in 2001 (3 events), low in 2002 (1 event), and absent in 2003.

We captured adult cormorants on nests from each treatment block on Young Island and banded them in 2001–2003. We captured most cormorants at night, but captured as many as 25 cormorants per year during daytime. These captures were incidental to other management activities on the island and thus did not add to predation levels. We captured and banded adults from Four Brothers Islands in 2002 and 2003. We banded all adults with a United States Geological Survey metal band and a plastic colored band engraved with unique alphanumeric codes. The University of Vermont, Institutional Animal Care and Use Committee approved all methods involving animals.

We resighted cormorants with colored bands in both nesting colonies in 2002–2004. Within a breeding season, we searched for banded cormorants 8 to 20 times on each colony, and then pooled observations within a year. We treated the Four Brothers Islands as a single colony and pooled observations from all 4 islands. On Young Island, we resighted birds from an abandoned house on the island that we could access without flushing cormorants from their nests, thereby preventing egg predation by gulls. To ensure that we measured breeding dispersal between years, we included only observations of birds up to the middle of the nestling period (i.e., up to the time when nestlings were half grown). Observations after this time could be of individuals that may have attempted to breed elsewhere, failed, and

moved to a second colony within a year. We included observations of birds that we observed on a nest, exchanging nesting material, or feeding nestlings, but not those whose breeding status we did not ascertain.

We gathered capture and resight histories for 254 uniquely banded cormorants. Each capture history consisted of 4 letters or zeros for each cormorant; that is, one character for each year of the study. Letters indicated the colony and experimental treatment (strata) where we originally banded ($n = 254$) or observed nesting in subsequent years ($n = 338$) for each bird. Zeros indicated that we did not know the breeding location of an individual (even if observed, $n = 110$). We removed cormorants observed in the variably oiled treatment from analyses ($n = 33$) to prevent these observations from contributing to estimates of apparent survival, resight probability, or movement rates. By including only observations of adults whose nesting status we confirmed, estimates of apparent survival reflect rates that birds survive, remain in the system, and nest in the following year. Estimates of resight rates are rates that we observe birds and confirm their nesting status, and estimates of movement are rates that cormorants disperse from one breeding location to another within the system and between years.

We used multistrata modeling (Brownie et al. 1993, Lebreton et al. 2003) in program MARK (White and Burnham 1999) to analyze the capture-history data. Our system consisted of 3 strata: Young Island oiled (O), Young Island not oiled (N), and Four Brothers Islands (F; Fig. 2). Program MARK calculates the most likely values for apparent survival (Φ), resight probability (p), and movement rates (Ψ) given the set of capture histories and a model of interest (White and Burnham 1999). Each model is a linear combination of effects on apparent survival, resight probability, and movement rates after transformation through a link function. We developed a design matrix for each model, where each row in the matrix corresponded to a parameter estimate, and each column corresponded to either an intercept or an effect (β estimate) for a given parameter.

We denoted effects on parameters with a lowercase subscript. We included resighting effort/nest (e), colony (c), treatment or egg-oiling (t), and egg-predation (p) effects (e.g., Φ_t is a treatment effect on apparent survival). We denoted strata with capital subscripts and included oiled (O) and not-oiled (N) strata on Young Island and the Four Brothers (F) stratum (e.g., Φ_F was apparent survival for Four Brothers strata and Ψ_{ON} was movement from the oiled to the not-oiled strata on Young Island). Superscripts denoted time intervals by the first year in the interval (e.g., Φ^{2001} is apparent survival from 2001 to 2002).

Effects for apparent survival included egg oiling, egg predation, and colony effects. If egg oiling increased emigration from the system, apparent survival would be lower for the Young Island oiled stratum than for Young Island not-oiled and Four Brothers strata. An egg oiling (treatment) effect Φ_t would allow $(\Phi_O) \neq (\Phi_N) = (\Phi_F)$ by applying the treatment β_t only to the oiled stratum on Young Island. If egg predation caused emigration from

the system, emigration rates from both strata on Young Island would be greater for 2001 than for 2002. In 2003, emigration rates would be the same for all strata because no predation occurred in that year. An egg predation effect Φ_p would apply $3 \times \beta_p$ to (Φ_O^{2001}) and (Φ_N^{2001}) and would apply $1 \times \beta_p$ to (Φ_O^{2002}) and (Φ_N^{2002}) . Thus, a predation effect Φ_p would allow $[(\Phi_O^{2001}) = (\Phi_N^{2001})] < [(\Phi_O^{2002}) = (\Phi_N^{2002})] < [(\Phi_O^{2003}) = (\Phi_N^{2003}) = (\Phi_F^{2001-2003})]$. A colony effect would provide separate estimates of apparent survival for Young Island (oiled and not-oiled strata would be equal) and for Four Brothers Islands. A colony effect Φ_c would allow $(\Phi_O) = (\Phi_N) \neq (\Phi_F)$ by applying the β_c only to the Young Island strata. We constrained estimates of apparent survival to the interval [0,1] with the sin link. For simulated data, the sin link provided less biased estimates of apparent survival for our data than the logit link.

We limited the number of alternative models for resight probability to one biologically relevant model that included effects that we felt influenced resight probability based upon our experiences searching for banded cormorants on Young and Four Brothers colonies. We constrained resight probability to be a function of the number of hours spent searching for banded cormorants per nest on each colony for each year. We used the logit link to constrain resight probability to the interval [0,1].

We included egg-oiling, egg-predation, and colony effects for movement. We included effects on movement in a similar manner as effects on apparent survival; however, movement could depend upon conditions in the strata that a cormorant leaves or enters. Movement away from the oiled stratum would be different than movement away from not-oiled stratum. A from-treatment (egg oiling) effect on movement $\Psi_{\text{from } t}$ would allow $\Psi_{ON} = \Psi_{OF} \neq \Psi_{NO} = \Psi_{NF} = \Psi_{FO} = \Psi_{FN}$ by applying the $\beta_{\text{from } t}$ only to estimates of movement away from the oiled stratum on Young Island. Similarly, a to-treatment effect would allow movement to the oiled stratum to differ from movement to not-oiled strata ($\Psi_{NO} = \Psi_{FO} \neq \Psi_{ON} = \Psi_{OF} = \Psi_{NF} = \Psi_{FN}$). We used multinomial logit links to model movement and constrain the sum of the movement probabilities away from each stratum to the interval [0,1].

Experimental Analysis

We determined if egg oiling caused dispersal from a colony by analyzing 6 candidate models. We started with a model that included colony and egg predation effects for apparent survival and movement rates and an effort/nest effect for resight probability ($\Phi_{c+p} \text{ Pe } \Psi_{\text{from } c \text{ to } c + \text{ from } p \text{ to } p}$). We included these effects to account for variation in the data associated with differences in colony quality and influences of predation, but not to assess the influence of these factors, per se. We added treatment effects to the starting model to create 5 more models: 1) treatment effect on apparent survival, 2) treatment effect on movement from a colony, 3) treatment effect on movement from and to a colony, 4) treatment effect on apparent survival and movement from a colony, and 5) treatment effect on apparent survival and

movement to and from a colony. We used the information theoretic approach using Akaike's Information Criterion adjusted for small sample size (AIC_c) to compare models in the experimental model set (Burnham and Anderson 2002, 2004).

Observational Analysis

In our observational analysis, we evaluated 168 candidate models to assess the influence of combinations of egg-predation and colony effects. We retained effects of egg oiling to explore the influence of that treatment when inclusion of other effects varied among models. Each model included 1 of 8 possible combinations of effects for apparent survival, one effect for resight probability, and 1 of 21 possible combinations of effects for movement. Combinations of effects for apparent survival included no effects, each effect singly, and additive combinations of effects. Similarly, we defined 21 combinations for movement (Table 1). Combinations of effects on movement included colony, treatment, and predation effects for strata cormorants left (from effects) and for strata cormorants entered (to effects). We only included effects for strata that cormorants entered when we included the same effect for strata cormorants left.

Again, we used an information-theoretic approach to determine which combination of effects influence cormorant demographics (Burnham and Anderson 2002, 2004). We averaged parameter estimates from each model in our model set through model averaging procedures in program MARK. Averaging models incorporates model selection uncertainty into parameter estimates (Buckland et al. 1997, Burnham and Anderson 2004). Model averaging uses AIC_c weights for each model to calculate a weighted average for each parameter estimate (Burnham and Anderson 2002, 2004). To determine effect sizes, we averaged over the subset of models that included the parameter of interest (Buckland et al. 1997).

Goodness-of-Fit

The only method developed to assess fit of data to assumptions for multistrata mark-recapture analyses is through Program U-CARE (Choquet et al. 2003, Pradel et al. 2003). U-CARE assesses fit of data only for fully time-dependent models. A fully time-dependent model does not belong in our experimental or observational model sets given that we assembled model sets to assess effects associated with management. However, we temporarily added a fully time-dependent model solely for purposes of assessing fit. Information theoretic approaches using AIC will select models that fit the data provided such a model is included in the model set (Burnham and Anderson 2004). It follows that any models ranked higher than the fully time-dependent model will fit the data, provided we do not find evidence of lack of fit for that model.

RESULTS

Goodness-of-Fit

We found no evidence of lack of fit of the data to multistrata models (U-CARE Global Multisite Test $\chi^2 = 4.627$, $df =$

Table 1. Models of movement rates between cormorant colonies on Lake Champlain, 2001–2004, include 21 combinations of egg-oiling, egg-predation, and colony effects for strata that double-crested cormorants leave and enter.

Model no.	Effects for strata cormorants leave	Effects for strata cormorants enter
1	None	None
2	Egg oiling	None
3	Egg predation	None
4	Egg oiling + egg predation	None
5	Egg oiling	Egg oiling
6	Egg predation	Egg predation
7	Egg oiling + egg predation	Egg oiling + egg predation
8	Colony	None
9	Colony + egg oiling	None
10	Colony + egg predation	None
11	Colony + egg oiling + egg predation	None
12	Colony + egg oiling	Egg oiling
13	Colony + egg predation	Egg predation
14	Colony + egg oiling + egg predation	Egg oiling + egg predation
15	Colony	Colony
16	Colony + egg oiling	Colony
17	Colony + egg predation	Colony
18	Colony + egg oiling + egg predation	Colony
19	Colony + egg oiling	Colony + egg oiling
20	Colony + egg predation	Colony + egg predation
21	Colony + egg oiling + egg predation	Colony + egg oiling + egg predation

13, $P = 0.98$). The fully time-dependent model ranked below all experimental models ($\Delta AIC_c = 11.6$, AIC_c wt = 0.001) and was the 55th best model ($\Delta AIC_c = 11.9$, AIC_c wt = 0.0006) when included in the observational model set. Therefore, the experimental models and the top 54 observational models, with a combined AIC_c weight of 0.98, also adequately fit the data.

Experimental Analysis

We found support for effects of egg oiling on movement, but not on apparent survival, after accounting for variation in the data due to colony and predation effects. The highest ranked experimental model only included the from-treatment effect on movement from the oiled (treatment) strata (Table 2). This model had 3.0 (AIC_c wt ratio) times more support in the data than the starting model (model rank = 3). The size of the egg-oiling effect on the movement rate from Young Island to Four Brothers Islands for the top experimental model was small (0.02, SE = 0.014) for the year with no egg predation on Young Island.

Evidence for the to-treatment effect on movement is equivocal. The second best experimental model included

from- and to-treatment effects, and had 2.1 times more support in the data than the starting model (model rank = 3). However, support for the second model could be driven by support in the data for the from-treatment effect because the best model had 1.4 times more support in the data than the second best model. The size of the to-treatment effect from the second model was 0.07 (SE = 0.057).

We found little support in the data for a treatment effect on apparent survival. Models that included this effect were ranked lower than models without this effect (Table 2). For the best model than for a similar model that also included the treatment effect on apparent survival (model 4). In summary, we found little or no evidence supporting a treatment effect on apparent survival or a to-treatment effect on movement. We found strong evidence for a from-treatment effect on movement; however, the effect size was small.

Observational Analysis

The 10 highest ranked models had a combined AIC_c weight of 0.82 and illustrated the relative importance of egg-oiling, egg-predation, and colony effects on apparent survival and

Table 2. Ranking criteria and model effects for an experimental model set used to determine if oiling eggs of double-crested cormorants increased dispersal away from Young Island during an egg-oiling experiment on Lake Champlain from 2001 to 2004.

Model rank	Model ^a	ΔAIC_c^b	AIC_c wt	K^c	Deviance
1	$\Phi_{c+p} Pe \Psi_{\text{from } c + \text{ to } c + \text{ from } p + \text{ to } p + \text{ from } t}$	0	0.36	11	126.5
2	$\Phi_{c+p} Pe \Psi_{\text{from } c + \text{ to } c + \text{ from } p + \text{ to } p + \text{ from } t + \text{ to } t}$	0.6	0.26	12	124.9
3	$\Phi_{c+p} Pe \Psi_{\text{from } c + \text{ to } c + \text{ from } p + \text{ to } p}$	2.1	0.12	10	130.8
4	$\Phi_{c+p+t} Pe \Psi_{\text{from } c + \text{ to } c + \text{ from } p + \text{ to } p + \text{ from } t}$	2.1	0.12	12	126.5
5	$\Phi_{c+p+t} Pe \Psi_{\text{from } c + \text{ to } c + \text{ from } p + \text{ to } p + \text{ from } t + \text{ to } t}$	2.8	0.09	13	124.9
6	$\Phi_{c+p+t} Pe \Psi_{\text{from } c + \text{ to } c + \text{ from } p + \text{ to } p}$	4.2	0.04	11	130.7

^a Model effects include colony (c), predation (p), and treatment (t) effects on apparent survival (Φ) and movement (Ψ) from a strata and an effect of search effort/nest (e) on resight probability (p).

^b AIC_c = Akaike's Information Criterion adjusted for small sample size.

^c No. of parameters in each model.

Table 3. Ranking criteria and model effects for the top 10 models used to determine the influence of colony (c), egg-oiling (t), and egg-predation (p) effects on apparent survival (Φ) and movement (Ψ) from or to strata for double-crested cormorants on Lake Champlain from 2001 to 2004.

Model rank	Model	ΔAIC_c^a	AIC_c wt	K^b	Deviance
1	$\Phi, p_e \Psi_{\text{from c} + \text{to c} + \text{from t} + \text{to t} + \text{from p} + \text{to p}}$	0.00	0.22	10	125.9
2	$\Phi_c p_e \Psi_{\text{from c} + \text{to c} + \text{from t} + \text{to t} + \text{from p} + \text{to p}}$	1.18	0.12	11	124.9
3	$\Phi_p p_e \Psi_{\text{from c} + \text{to c} + \text{from t} + \text{to t} + \text{from p} + \text{to p}}$	1.64	0.10	11	125.4
4	$\Phi, p_e \Psi_{\text{from c} + \text{to c} + \text{from p} + \text{to p}}$	1.87	0.09	8	132
5	$\Phi_t p_e \Psi_{\text{from c} + \text{to c} + \text{from t} + \text{to t} + \text{from p} + \text{to p}}$	2.03	0.08	11	125.8
6	$\Phi_c p_e \Psi_{\text{from c} + \text{to c} + \text{from p} + \text{to p}}$	2.73	0.06	9	130.8
7	$\Phi_{c+t} p_e \Psi_{\text{from c} + \text{to c} + \text{from t} + \text{to t} + \text{from p} + \text{to p}}$	3.33	0.04	12	124.9
8	$\Phi_{c+p} p_e \Psi_{\text{from c} + \text{to c} + \text{from t} + \text{to t} + \text{from p} + \text{to p}}$	3.33	0.04	12	124.9
9	$\Phi_{c+p} p_e \Psi_{\text{from c} + \text{to c} + \text{from p} + \text{to p}}$	3.44	0.04	9	131.5
10	$\Phi_{t+p} p_e \Psi_{\text{from c} + \text{to c} + \text{from t} + \text{to t} + \text{from p} + \text{to p}}$	3.76	0.03	12	125.4

^a AIC_c = Akaike's Information Criterion adjusted for small sample size.

^b No. of parameters in each model.

movement probabilities (Table 3). For apparent survival, 5 models included a colony effect, 4 included a predation effect, 3 included a treatment effect, and 2 models included no effects. We inferred the importance of each effect on apparent survival by examining β estimates for each model (Table 4). We found little evidence supporting effects on apparent survival because 95% confidence intervals for β estimates overlapped 0 by a relatively large margin for all top 10 models. The magnitude of β estimates was much greater for the colony effect than for egg oiling or egg predation effects on apparent survival.

All top 10 models included to- and from-colony and to- and from-predation effects for movement, and 7 of these models included treatment effects (Tables 3 and 4). In contrast to effects on apparent survival, examination of β

estimates for each model indicated there was strong evidence supporting effects on movement within the Lake Champlain system. Confidence intervals for β estimates for $\Psi_{\text{from t}}$, $\Psi_{\text{to c}}$, $\Psi_{\text{from p}}$, and $\Psi_{\text{to p}}$ never overlapped zero, but did include zero for 7 of 10 models for the $\Psi_{\text{from c}}$ effect. This pattern mirrors the importance of the $\Psi_{\text{from t}}$ effect and lack of support for the $\Psi_{\text{to t}}$ effect that we found in the experimental analysis. We also found a correlation between cormorant movement and certain conditions of the strata at both ends of a move. We found associations between cormorant decisions to leave a stratum and predation and treatment effects where they left and between decisions to settle in a stratum and predation and colony effects where they settled.

After incorporating model selection uncertainty, the best

Table 4. Estimates of β for effects included in the top 10 models used to determine the influence of colony (c), egg-predation (p), and egg-oiling (t) effects on apparent survival (Φ), resight probability (p), and movement (Ψ) from and to strata for double-crested cormorants on Lake Champlain from 2001 to 2004.

Model rank ^a	Φ								p			
	β_{int}	SE	β_c	SE	β_p	SE	β_t	SE	β_{int}	SE	β_c	SE
1	0.83	0.166							0.32	0.497	-9.06	14.237
2	0.63	0.222	0.28	0.271					0.75	0.686	-21.43	19.263
3	0.72	0.202			0.09	0.129			0.44	0.547	-11.18	15.204
4	0.83	0.165							0.33	0.509	-9.50	14.453
5	0.81	0.172					0.10	0.305	0.37	0.525	-10.77	15.229
6	0.60	0.218	0.32	0.267					0.86	0.723	-24.30	20.054
7	0.63	0.222	0.27	0.284			0.02	0.322	0.75	0.687	-21.55	19.326
8	0.63	0.222	0.26	0.412	0.01	0.183			0.74	0.707	-20.99	20.836
9	0.71	0.200			0.09	0.129			0.47	0.565	-11.82	15.586
10	0.72	0.205			0.08	0.130	0.05	0.282	0.47	0.565	-12.12	15.990

Model rank ^a	Ψ											
	β_{int}	SE	$\beta_{\text{from c}}$	SE	$\beta_{\text{to c}}$	SE	$\beta_{\text{from p}}$	SE	$\beta_{\text{to p}}$	SE	$\beta_{\text{from t}}$	SE
1	-4.15	0.628	0.87	0.543	1.74	0.555	0.72	0.261	-1.14	0.350	1.27	0.534
2	-4.12	0.622	0.78	0.542	1.83	0.553	0.72	0.261	-1.15	0.351	1.24	0.537
3	-4.15	0.627	0.86	0.539	1.75	0.552	0.71	0.261	-1.14	0.350	1.26	0.534
4	-3.94	0.591	1.45	0.488	1.87	0.519	0.58	0.243	-1.00	0.338		
5	-4.14	0.628	0.85	0.545	1.76	0.556	0.72	0.261	-1.14	0.350	1.26	0.534
6	-3.90	0.582	1.33	0.489	1.96	0.513	0.57	0.243	-1.01	0.339		
7	-4.12	0.622	0.78	0.542	1.83	0.553	0.72	0.261	-1.15	0.351	1.24	0.537
8	-4.12	0.623	0.78	0.548	1.82	0.558	0.72	0.262	-1.15	0.352	1.24	0.537
9	-3.94	0.589	1.44	0.485	1.88	0.516	0.57	0.244	-1.00	0.338		
10	-4.14	0.627	0.85	0.541	1.76	0.554	0.71	0.261	-1.14	0.350	1.26	0.534

^a Corresponds to models in Table 3.

Table 5. Apparent survival (Φ), resight probability (p), and movement rates (Ψ) for double-crested cormorants from 3 strata in Lake Champlain from 2001 to 2004.

Yr ^a	Φ_O^b	SE	Φ_N	SE	Φ_F	SE	p_O	SE	p_N	SE	p_F	SE
2001	0.89	0.076	0.89	0.070	0.83	0.080	0.46	0.085	0.46	0.085	0.59	0.108
2002	0.88	0.070	0.88	0.061	0.83	0.080	0.51	0.052	0.51	0.052	0.55	0.076
2003	0.87	0.080	0.87	0.071	0.83	0.080	0.48	0.064	0.48	0.064	0.56	0.083
	Ψ_{OF}	SE	Ψ_{NF}	SE	Ψ_{ON}	SE	Ψ_{NO}	SE	Ψ_{FO}	SE	Ψ_{FN}	SE
2001	0.40	0.165	0.23	0.092	0.10	0.071	0.09	0.063				
2002	0.14	0.053	0.07	0.032	0.27	0.064	0.21	0.050	0.05	0.024	0.03	0.020
2003	0.07	0.037	0.04	0.024	0.37	0.092	0.29	0.076	0.13	0.051	0.08	0.037

^a Predation levels varied among yr on Young Island with high predation levels in 2001, low predation levels in 2002, and no predation in 2003.

^b Strata include Young Island oiled (O), Young Island not oiled (N), and Four Brothers Islands (F).

estimates of apparent survival, resight probability, and movement probabilities varied for each strata. Apparent survival rates varied from 83% to 89% (Table 5). After model averaging, apparent survival appeared to be greater on Young Island than Four Brothers Islands even though we found no evidence of a colony effect on apparent survival for any of the top 10 models. The appearance of this effect is a result of the magnitude of the colony effect on apparent survival (Φ_c ; Table 6). Resight probabilities varied from 46% to 59% and rates that cormorants moved among strata varied from 3% to 40% (Table 5). Movement rates from Young Island to Four Brothers Islands were lowest (4% to 7%) when there was no predation on Young Island and greatest (23% to 40%) during the year of high egg predation. Movement from Young Island to Four Brothers without oiling or egg predation (4%) was less than movement rates from Four Brothers to Young Island (8% to 13%). The to-colony effect, which we found support for in the data (Tables 3 and 4), drives differences in movement rates between colonies.

Sizes of effects on movement varied widely (Table 6). Predation, colony, and treatment effects appeared to

influence movement. For the not-oiled treatment on Young Island, high levels of egg predation (3 events) increased movement to the Four Brothers colony by 20% and low levels (one event) increased movement by 3%. Oiling cormorant eggs increased movement from Young Island to Four Brothers by 3% in the absence of egg predation.

Some of the experimental models were a subset of the observational model set. Experimental model 2 was ranked 8 ($\Delta AIC_c = 3.3$), experimental model 3 was ranked 13 ($\Delta AIC_c = 4.8$), experimental model 5 was ranked 14 ($\Delta AIC_c = 5.5$), and experimental model 6 was ranked 16 ($\Delta AIC_c = 7.0$). Experimental models 1 and 4 were not part of the observational dataset but would have fallen between models with rank of 5 and 6 ($\Delta AIC_c = 2.7$) and 13 and 14 ($\Delta AIC_c = 4.9$) in the observational model set, respectively.

DISCUSSION

We designed this study to determine if reproductive failure from oiling cormorant eggs increased dispersal of cormorants away from the colony where we applied this treatment. In all years and for all predation levels, cormorants moved from Young Island to Four Brothers Islands at greater rates

Table 6. Size of colony (c), predation (p), and egg oiling (t) effects on apparent survival (Φ) and movement (Ψ) to and from strata as measured for double-crested cormorants on Lake Champlain from 2001–2004.

Parameter effect	Measured as	Measured for	Effect size ^a	SE	No. models averaged	AIC_c wt ^b
Φ_c	$\Phi_N^{2003} - \Phi_F^{2003}$	No predation	-0.10	0.109	84	0.35
Φ_p	$\Phi_N^{2001} - \Phi_N^{2003}$	3 predation events	0.06	0.139	84	0.29
Φ_p	$\Phi_N^{2002} - \Phi_N^{2003}$	1 predation event	0.02	0.056	84	0.29
Φ_t	$\Phi_O^{2001} - \Phi_N^{2001}$	3 predation events	0.02	0.095	84	0.26
Φ_t	$\Phi_O^{2002} - \Phi_N^{2002}$	1 predation event	0.02	0.097	84	0.26
Φ_t	$\Phi_O^{2003} - \Phi_N^{2003}$	No predation	0.02	0.103	84	0.26
$\Psi_{from\ t}$	$\Psi_{OF}^{2001} - \Psi_{NF}^{2001}$	3 predation events	0.17	0.123	96	0.71
$\Psi_{from\ t}$	$\Psi_{OF}^{2002} - \Psi_{NF}^{2002}$	1 predation event	0.07	0.045	96	0.71
$\Psi_{from\ t}$	$\Psi_{OF}^{2003} - \Psi_{NF}^{2003}$	No predation	0.03	0.025	96	0.71
$\Psi_{to\ t}$	$\Psi_{FO}^{2003} - \Psi_{FN}^{2003}$	No predation	0.06	0.031	48	0.68
$\Psi_{from\ p}$	$\Psi_{NF}^{2001} - \Psi_{NF}^{2003}$	3 predation events	0.20	0.092	96	0.96
$\Psi_{from\ p}$	$\Psi_{NF}^{2002} - \Psi_{NF}^{2003}$	1 predation event	0.03	0.014	96	0.96
$\Psi_{to\ p}$	$\Psi_{FN}^{2002} - \Psi_{FN}^{2003}$	1 predation event	-0.05	0.025	48	0.94
$\Psi_{from\ c}$	$\Psi_{NO}^{2003} - \Psi_{FO}^{2003}$	To oiled treatment	0.16	0.073	112	0.99
$\Psi_{to\ c}$	$\Psi_{ON}^{2003} - \Psi_{OF}^{2003}$	Oiled treatment	0.31	0.101	56	0.97

^a We calculated effect sizes from the subset of models from the observational model set that included the effect.

^b AIC_c = Akaike's Information Criterion adjusted for small sample size. AIC_c wt are the summed wt for the subset of models and indicate wt of support for the subset of models, but they should not be used to compare the relative strength of each parameter effect unless the no. of models averaged is equal.

from the oiled treatment compared to the not-oiled treatment. Our experimental results show that reproductive failure for cormorants increased breeding dispersal similar to what others have reported in both experimental (Haas 1998) and observational studies of other birds (Gavin and Bollinger 1988, Aebischer 1995, Aebischer et al. 1995, Schjørring et al. 2000, Styrsky 2005). However, the effect that we found was small and variation around the effect size was large, leading us to conclude that dispersal in response to egg oiling without egg predation may be relatively unimportant when employing egg oiling as a management technique.

Rates of breeding dispersal were different for each colony on Lake Champlain. In the year with no predation on Young Island, cormorants moved from Four Brothers to Young Island at approximately twice the rate than *visa versa*. Black-legged kittiwakes (*Rissa tridactyla*) disperse from low-quality colonies at higher rates than from high-quality colonies (Danchin et al. 1998, Cadiou 1999). Following this pattern, Young Island is a higher quality site than Four Brothers, a hypothesis confirmed by other aspects of our research. Cormorants breeding on Young Island travel shorter distances to forage and have higher productivity levels when not managed than do cormorants on Four Brothers Islands (Fowle et al. 1999, Duerr 2007).

A major finding of our study was that predation of eggs by gulls during the oiling process reversed the flow of cormorants between colonies on Lake Champlain. In the year with one predation event, cormorants moved from Young Island to Four Brothers at more than twice the rate than cormorants moved from Four Brothers to Young Island. This was a complete reversal of movement compared to the year with no predation during oiling events, and is a result of increased movement away from Young Island and decreased movement to Young Island. These responses allowed cormorants to move between colonies to avoid egg predation, a pattern that Cadiou (1999) also found in black-legged kittiwakes.

Cormorants appear to have different responses to egg oiling than egg predation such that high levels of egg predation had a larger effect on breeding dispersal for cormorants than did oiling of eggs. One explanation for this pattern is that egg predation and egg oiling present different cues. Predation of eggs occurs at the colony level because gulls consumed eggs in both the oiled and not-oiled treatments when we applied oil during the daytime. Therefore, predation should indicate that a cormorant chose a poor quality colony and the appropriate response to avoid future predation of eggs would be to disperse to another colony. In contrast, cormorants whose reproductive attempt failed because they nested in the oiled treatment could perceive that unoiled portions of the colony are high quality, but they chose either a poor quality nest site or a poor or infertile mate. Cormorants could respond to avoid similar reproductive failure by dispersing to another colony, dispersing to the not-oiled treatment, or choosing another mate within the same colony. Thus cormorants faced with

egg oiling should disperse to another colony at lower rates than those faced with egg predation.

The influence of egg oiling and egg predation on reproductive success could also provide different cues of habitat quality to cormorants that may be prospecting. Prospecting is the process of obtaining information about breeding sites to use in future choices of breeding locations (Reed et al. 1999). Black-legged kittiwakes time their prospecting to coincide with the end of the nestling stage so they gather appropriate and useful information such as the reproductive success of conspecifics (Boulinier et al. 1996). The optimal time window for prospecting for cormorants should also be later portions of the nestling stage. A cormorant breeding on Four Brothers Islands that prospecting on Young Island during the year without egg predation would have observed empty or available nests in oiled portions of Young Island because cormorants with oiled eggs would have abandoned their nesting attempt by the end of the nestling stage. Nests still occupied in not-oiled portions of Young Island would contain nestlings, possibly presenting a cue of good nesting success on the island. In years with egg predation, these prospecting individuals would observe reduced reproductive success in not-oiled portions of the colony, a cue of lower reproductive success. In contrast, cormorants prospecting and breeding on Young Island may be able to track reproductive success of conspecifics throughout the breeding season and recognize that oiled portions of the colony are poor quality nesting sites and not-oiled portions are high quality nest sites. Thus, prospecting on Young Island may provide more detailed information or different cues to cormorants breeding on Young Island than those breeding on Four Brothers Islands. This could explain why movement rates from Four Brothers to Young Island followed the expected pattern for egg predation (i.e., dispersal increased as predation decreased), but not the expected pattern associated with egg oiling (i.e., no evidence was found for different dispersal rates to oiled and not-oiled treatments).

Understanding how wildlife perceive cues can help managers create an ecological trap, a strategy that would provide an excellent method of reducing overabundant or nuisance wildlife populations. An ecological trap occurs when there is a mismatch between cues used by animals in selecting habitat and the quality (fitness) of the habitat that is selected (Gates and Gysel 1978, Donovan and Thompson 2001, Schlaepfer et al. 2002). Enticing wildlife to stay in a location where managers are implementing population control measures will reduce or eliminate dispersal to nontarget populations. Management actions during the last year of our study appeared to have created an ecological trap on Young Island. For prospecting cormorants, the cue of high reproductive success for not-oiled portions of Young Island indicated high-quality habitat. The mismatch occurred when cormorants did not recognize portions of the colony (oiled) that appeared available or unoccupied at the time of prospecting as low-quality habitat and selected those locations over available high-quality habitat. Cormor-

ants that bred on Young Island and failed to reproduce due to egg oiling tended to move within Young Island, failing to respond to the overall or average reproductive success on the colony. Cormorants that appeared to escape the trap are those that moved to Four Brothers in response to egg oiling, but the rate of breeding dispersal due to egg oiling was small, especially compared to the rate of immigration to Young Island. Even though oiling cormorant eggs increased breeding dispersal slightly, it appeared to be an effective management strategy when completed without inducing predation of eggs. The perception of higher quality habitat on Young Island by cormorants depends upon successful reproduction by cormorants on the colony. In this study, we did not oil half of the treatment blocks, which resulted in 40% of nests producing nestlings. Further investigation is needed to determine if the trap can be maintained while oiling a greater portion of nests.

We did not find strong evidence that breeding dispersal took the form of emigration from the Lake Champlain system. Assuming true survival is constant among colonies, evidence of emigration from our study system would include differences in apparent survival rates between colonies, treatments on Young Island, or among years with different levels of egg predation. We found that effect sizes for egg predation, egg oiling, and breeding colony on apparent survival were large enough that we considered them biologically relevant; however, variance estimates for each effect were also large. Given that we found evidence for effects on movement within the system, it is possible that effects on apparent survival are real and that large variances were due to small sample sizes. We are aware that color-banded cormorants have moved among colonies located in Lake Ontario, New York and Ontario; Oneida Lake, New York; the St. Lawrence River, Quebec; and Young and Four Brothers Islands (Duerr 2007; C. Maisonneuve, Quebec Ministère des Ressources naturelles et de la Faune, personal communication; I. Mazzochi, New York Department of Environmental Conservation, personal communication; D. V. C. Weseloh, Canadian Wildlife Service, personal communication). Further investigation is needed to determine the extent to which colonies on Lake Champlain interact with colonies outside of Lake Champlain. Such investigations will provide additional insight into the scale at which cormorant colonies interact.

MANAGEMENT IMPLICATIONS

Based upon the results of this study, cormorant colonies on Lake Champlain interact through movement of individuals between local populations in a metapopulation. Managers should expect to influence the size and distribution of cormorant colonies throughout Lake Champlain when they control cormorant populations at any one site, such as Young Island. Our results also suggest that managers may be able to establish an ecological trap on Young Island, the highest quality nesting site on Lake Champlain, through oiling cormorant eggs. Establishing such a trap would require that managers minimize predation of eggs during

the oiling process and allow a portion of the eggs to hatch to maintain the cue of high-quality habitat (production of nestlings) for prospecting cormorants.

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