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The complexity of cormorants: stable isotopes reveal multiple prey sources and feeding site switching

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Abstract: Conflict between cormorants (*Phalacrocorax* spp.) and humans over fisheries is currently one of the most widespread wildlife management issues in the world. Cormorant impact assessments typically assume a single source of prey near the breeding colony. However, cormorants can fly long distances (>20 km), resulting in fish removal from multiple areas. Knowledge of the source of cormorant prey is critical for fisheries impact assessments. Carbon and nitrogen stable isotopes values from fish in double-crested cormorant (*Phalacrocorax auritus*) regurgitations revealed several prey sources for breeding birds in north-central Saskatchewan, Canada. Cormorants also switched feeding locations on a daily and seasonal basis. Foraging patterns inferred by stable isotope analysis closely paralleled observations of relative cormorant densities on different lakes. Up to 80% of prey came from areas well removed from the breeding colony lake (≤30 km). Cormorant foraging ecology can be complex and may be driven by factors independent of breeding colony site selection. The approach of estimating biomass removal from breeding colony lakes as the guideline for management decisions may be invalid in many locations.

Résumé : Les conflits entre cormorans (*Phalacrocorax* spp.) et humains relatifs à la pêche constituent un des problèmes de gestion de la faune les plus répandus à l'échelle planétaire. Les évaluations des impacts des cormorans partent généralement de l'hypothèse d'une seule source de proies à proximité de la colonie de nidification. Les cormorans peuvent toutefois voler sur de longues distances (>20 km) et ainsi prélever du poisson de plusieurs secteurs. La connaissance des sources de proies des cormorans est essentielle à l'évaluation des impacts sur les pêches. Les concentrations d'isotopes stables du carbone et de l'azote de poissons dans les régurgitations de cormorans à aigrettes (*Phalacrocorax auritus*) révèlent l'existence de plusieurs sources de proies pour des oiseaux nidifiant dans le centre nord de la Saskatchewan (Canada). Ces cormorans changent également de sites d'alimentation sur des bases quotidienne et saisonnière. Les patrons de quête de nourriture tirés de l'analyse des isotopes stables concordent étroitement avec les observations sur la densité relative de cormorans dans différents lacs. Jusqu'à 80 % des proies proviennent de secteurs à bonne distance du lac de la colonie de nidification (≤30 km). L'écologie de la quête de nourriture des cormorans peut s'avérer complexe et dépendre de facteurs non reliés au choix du site de la colonie de nidification. L'approche reposant sur l'estimation du retrait de biomasse de lacs de colonie de nidification pour orienter les décisions de gestion pourrait s'avérer inadéquate pour de nombreux sites. [Traduit par la Rédaction]

Introduction

Conflicts between piscivorous birds and humans over fisheries and aquaculture resources are common and widespread, especially those involving cormorants (*Phalacrocorax* spp.; Doucette et al. 2011). A predominantly piscivorous diet, reputation for efficient foraging, and increasing populations of these birds have raised concerns over their impact on fisheries in a variety of locations worldwide (Hatch 1995; Frederiksen et al. 2001). In general, cormorants are perceived as major competitors with humans over economically valuable fisheries resources. As a result, cormorant population control programs occur across much of the Northern Hemisphere, where millions of dollars are spent on cormorant management annually (e.g., Shwiff et al. 2009). The extent of the conflict depends on estimates of cormorant impacts on fisheries, which differ dramatically among studies (reviewed by Doucette et al. 2011). The circumstances linking cormorant foraging and economically important fish loss remain uncertain and in need of further study.

Bioenergetics modeling is widely used to estimate cormorant consumption of fish (reviewed by Ridgway 2010). Central place foraging theory suggests that colonial birds should forage within the immediate vicinity of breeding colonies to decrease energy expended (Ashmole 1963; Gorke and Brandl 1986; Elliott et al. 2009). Thus, many assessments assume that all fish biomass removal by cormorants is from their nesting lake (e.g., Rudstam et al. 2004) or a particular area near the breeding colony (e.g., Diana et al. 2006). However, cormorants can use feeding sites that are distant from breeding colonies (Anderson et al. 2004). Several studies have shown that cormorants routinely forage within 20 km of breeding colonies (e.g., Custer and Bunck 1992; Platteeuw and Van Eerden 1995; Kotzerka et al. 2011), and maximum flight distances up to 30 km are commonly recorded (Hobson et al. 1989; Grémillet et al. 1995; Stapanian et al. 2002). Cormorants may thereby routinely have multiple prey sources, spreading their consumption over several fish populations. However, this feature of their foraging and feeding ecology is seldom considered during fisheries impact assessments.

Studies of cormorant foraging and feeding behaviour, including site selection, have been notoriously difficult. Radio telemetry generally allows detailed examination of only a few marked individuals from colonies containing hundreds to thousands of breed-

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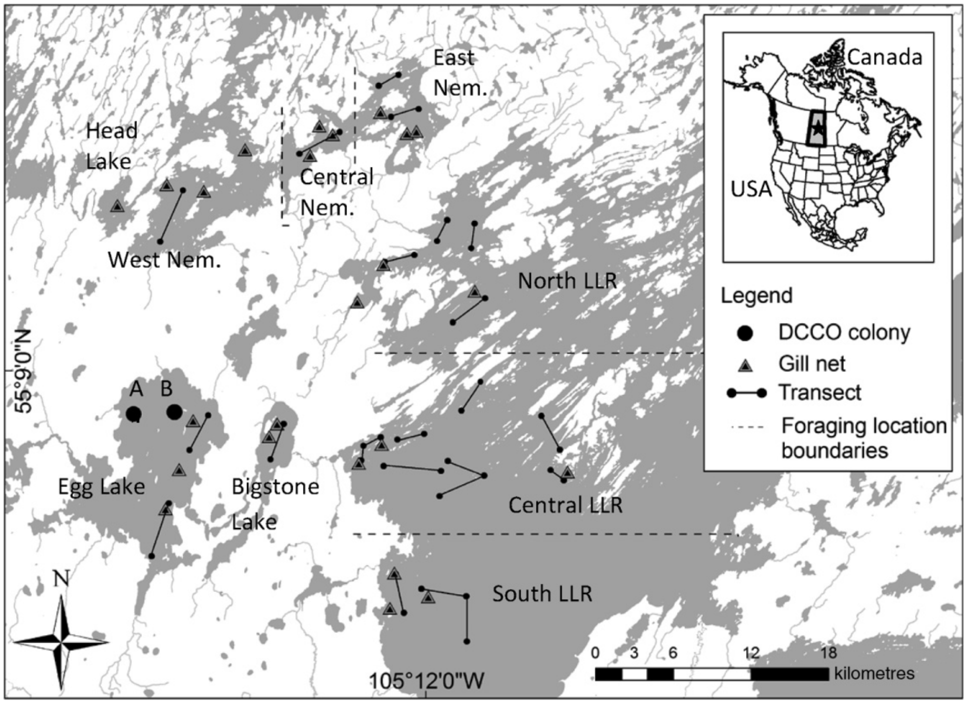
Fig. 1. Map of the study area (inset = North America; study area near Lac La Ronge is shown with a star) showing potential foraging locations for cormorants breeding on Egg Lake. Nemeiben Lake (Nem.) and Lac La Ronge (LLR) were each split into three areas because of habitat heterogeneity. Locations of gill nets to sample fish from known sites are shown (triangles). Line transects used to survey for foraging cormorants are also shown (lines with circles).



ing pairs (e.g., Custer and Bunck 1992; Coleman et al. 2005; Seefelt and Gillingham 2006), resulting in potential issues that apply to individual patterns being extrapolated colony-wide. In addition, telemetry studies only provide information on the location of birds, and when they are actively foraging (Coleman and Richmond 2007), but they do not indicate when cormorants are successfully obtaining prey in a given area. Thus, there is a need for alternative methods of determining where cormorants are feeding to refine biomass removal estimates when assessing fisheries conflicts.

Stable isotope analysis makes it possible to track movements of animals based on what they consume, and this technique does not rely on tagged individuals (Rubenstein and Hobson 2004). Stable isotopes offer a very useful tool for cormorant feeding studies (Hobson 2009; Doucette et al. 2011), but they have not been applied extensively for diet source tracking of cormorants (for exceptions see Bearhop et al. 1999; Ofukany et al. 2012). Isotopic characterization of cormorant tissues directly may not be useful for prey source tracking if cormorants are foraging in multiple locations, as these tissues would reveal an integrated signature from multiple sources. However, the prey items themselves (fish) may vary substantially in stable isotopes values based on their provenance (e.g., Overman and Parrish 2001; Murchie and Power 2004; Barks et al. 2010). Thus, if fish from multiple feeding locations are isotopically distinct, it may be possible to trace prey collected by cormorants back to their area of origin (Rubenstein and Hobson 2004). To our knowledge, no previous studies have taken advantage of stable isotopes values of prey to make inferences about cormorant foraging and feeding ecology.

The purpose of this study was to understand double-crested cormorant (*Phalacrocorax auritus*; hereafter, cormorant) foraging and feeding ecology in an environment where they have several lakes and foraging areas to choose from. We compared stable isotopes values for carbon (δ^{13}C) and nitrogen (δ^{15}N) in fish collected from known locations to fish regurgitated by cormorants in breeding colonies. Our main objectives were to (*i*) evaluate whether the variance in stable isotopes values over a small spatial scale within and among close bodies of water was sufficient for determining sources of cormorant prey and (*ii*) determine whether cormorants feed primarily from one or several sources of fish during the breeding season.

Materials and methods

Study area

We conducted our study in the La Ronge area of north-central Saskatchewan, Canada (55°09′N, 105°12′W; Fig. 1). We focused on the largest breeding colonies in the area, which are located on Egg Lake (Fig. 1): colony A in 2009 (55°07′14.88″N, 105°33′17.05″W; ~4000 breeding pairs) and colony B in 2010 (55°07′21.05″N, 105°30′20.11″W; ~800 breeding pairs). Egg, Bigstone, Nemeiben, and Head lakes and Lac La Ronge are suspected major foraging sites for breeding cormorants in the study area (Fig. 1). These sites were identified by local residents and also fall within a 20 km foraging radius of these cormorant colonies (Custer and Bunck 1992; Neuman et al. 1997). Egg (10 690 ha; mean depth 3 m) and Bigstone (1980 ha; mean depth 1.5 m) lakes are situated in the Boreal Plain ecozone and are characterized as shallow and mesotrophic (Cushing 1964). Nemeiben Lake (15 483 ha) is oligotrophic and situated in the Boreal Shield ecozone. It has three distinct basins: north (mean depth 30 m), central (mean depth 7 m), and outlet (mean depth 3 m; Duffy 2008). Head Lake (932 ha; mean depth 3 m) is a small outlet connected to the northwest side of Nemeiben Lake. Lac La Ronge (130 700 ha) also has three basins: north, central, and south. North Lac La Ronge is in the Boreal Shield ecozone and is characterized by deep (≥25 m), clear waters; south Lac La Ronge is in the Boreal Plain ecozone and has relatively shallow (≤10 m), productive waters; central Lac La Ronge is the transition zone between the two other areas (Duffy 2007).

Lac La Ronge and Nemeiben Lake have been used for commercial, sport, and subsistence fishing for decades, and their fisheries have declined in quality since the 1960s (Gloutney and Chen 1992; Wallace 1993). Of particular interest is the Lac La Ronge fishery, which has continued to decline since 1992 (Duffy 2007), coincident with the discovery of established cormorant breeding colonies of unknown age on nearby Egg Lake. Stakeholders are currently concerned that cormorants may cause further decline or inhibit recovery of fish populations.

Cormorant diet and selection of a representative prey species

We collected regurgitated stomach contents from nestling cormorants on Egg Lake in 2009 (n = 147) and 2010 (n = 701). Yellow perch (*Perca flavescens*; hereafter perch) made up 30% and 55% of the total fish biomass consumed by nestlings in 2009 and 2010, respectively (data not shown). In 2009, perch ranged in size from 45 to 190 mm (mean total length (TL) = 92.5 ± 29.1 mm); in 2010, TL ranged from 36 to 196 mm (mean TL = 78.9 ± 21.5 mm). Based on their importance to cormorants, we chose perch for all stable isotopes analyses.

Fish from known locations

We sampled fish from sites within four lakes that were identified as potential cormorant foraging locations (Fig. 1). Bottom-set, multipanel gill nets (mesh sizes: 1.3, 2.5, 3.8, 5.1, 6.4, and 7.6 cm) were set at depths ranging from 2 to 10 m overnight for 12–16 h. Gill nets were set at six sites in 2009 from 4 to 13 July: Egg Lake, Bigstone Lake, north and central Lac La Ronge, and central and eastern Nemeiben Lake. In 2010, gill nets were set from 23 June to 10 July at the same sites, and also south Lac La Ronge, west Nemeiben Lake, and Head Lake (Fig. 1). Gill nets were also set on 1 August 2010, to determine any temporal variation in stable isotope values of perch and to increase sample sizes for Egg and Bigstone lakes. No change in $\delta^{15}N$ values and only a small shift in $\delta^{13}C$ (mean difference = 0.9‰–2.1‰) to lower values was observed (data not shown). All captured perch were measured (TL) and frozen. We randomly chose up to 30 gill-netted perch (TL = 70–130 mm) from each potential cormorant foraging area for stable isotope analysis (n = 122 in 2009; n = 146 in 2010).

Fish from cormorant diet

We collected spontaneously regurgitated perch in the 70–130 mm size range from cormorant nestlings in colony A on 18 June and 5 July 2009 and expanded in 2010 by collecting regurgitated fish in colony B from 14 June to 22 July, on 10 separate days. Boluses were collected haphazardly throughout the colony to represent as many breeding pairs as possible. We analyzed a total of 186 prey items in 2009: 18 items from 18 June and 168 items from 5 July. In 2010, we analyzed up to 50 fish on each of 10 sampling days for a total of 391 individuals.

Stable isotopes analysis

We removed dorsal muscle tissue from perch and rinsed it in deionized water. Muscle samples were dried at 48 °C for ≥48 h and ground into a fine powder. All samples were weighed (0.5–1.0 mg) into tin capsules and analysed using a Finnigan Delta Plus isotope ratio mass spectrometer at the Environmental Quality Analysis Laboratory (Faculty of Science, University of Regina, Regina, Saskatchewan). Carbon and nitrogen stable isotopes values are expressed in δ notation (‰) relative to international standards, PeeDee belemnite (C) and atmospheric air (N_2; Peterson and Fry 1987). Lipids were not extracted from fish tissue; analyses of a subset of 2009 samples showed a mean C:N ratio of 3.6 ± 0.1 (n = 53), and arithmetic lipid normalization (Post et al. 2007) showed little difference (0.3‰ ± 0.1‰; n = 53) between $\delta^{13}C_{\text{untreated}}$ and $\delta^{13}C_{\text{normalized}}$ values. Based on this analysis, and no a priori need to standardize by lake (we wanted to maximize differences by site), we did not correct for lipids in this study. Fish tissue samples were analyzed along with two in-house laboratory standards: bovine liver ($\delta^{13}C$ = –21.6‰, $\delta^{15}N$ = 7.5‰) and wheat ($\delta^{13}C$ = –24.5‰, $\delta^{15}N$ = 3.5‰), both of which had standard deviation values of ±0.2‰ within runs. We also analyzed replicate samples of fish tissue from the same individuals (as per Bond and Hobson 2012), which had mean differences of 0.01‰ ± 0.2‰ for C samples and 0.02‰ ± 0.1‰ for N_2 samples.

Relative cormorant density

To relate cormorant foraging behaviour to patterns suggested from stable isotope analysis of regurgitated fish, and to characterize general cormorant foraging patterns in our study area, we surveyed cormorants in 2010 using line transects in potential foraging areas (Fig. 1). Transects were 600 m wide; observations were calibrated prior to surveying using spherical buoys placed 300 m from the boat (Gould and Forsell 1989). The number of transects per site and the total distance and area covered were as follows: Egg Lake: two transects, 7.3 km, 4.4 km²; Bigstone Lake: one transect, 4.3 km, 2.6 km²; Nemeiben Lake: four transects, 11.8 km, 7.1 km²; North Lac La Ronge: four transects, 9.2 km, 5.5 km²; Central Lac La Ronge: seven transects, 23.0 km, 13.8 km²; South Lac La Ronge: two transects, 10.1 km, 6.0 km². Line transects were driven at 15 km·h⁻¹ when visibility was >5 km, wave height was <1 m, and wind speed was <20 km·h⁻¹. Two observers counted cormorants inside the transect boundaries. Transects on all lakes were surveyed 23 times between 8 June and 24 August 2010. We also recorded the location of cormorant foraging flocks (≥10 individuals) observed during surveys and other boat travel from 9 June to 22 August 2010. The date, flock size, and approximate water depth were recorded; we used a geographic information system (GIS) to examine spatial and temporal patterns in cormorant foraging sites (ArcGIS Desktop10, ESRI, Redlands, California, USA).

Statistical analyses

We used a maximum likelihood approach to assign perch to their most likely area of origin based on stable isotope values (Royle and Rubenstein 2004). Areas of origin were determined based on geographic location (e.g., different lakes); however, delineation of origin boundaries was complicated by large bodies of water, in which different locations within a single lake could act as different sources (areas of origin), with corresponding differences in isotopic signatures. Thus, we created several models for our analyses by pooling and removing sites (see online Supplementary Tables S1–S6[1]). Our approach used a two-step process, where we first used linear discriminant analysis (LDA) with leave-one-out cross-validation to test isotopic distinctness of gill-netted perch among sites (Gillanders and Kingsford 2000) and to determine the best model for each year based on classification success. The leave-one-out method removes an individual perch of known origin from the analysis and reclassifies it based on the discriminant function of the remaining perch (n – 1). Following LDA classification, we used a multivariate ($\delta^{13}C$, $\delta^{15}N$) normal probability density function (MDF) to determine the likelihood that regurgitated perch originated from a given site based on the values for both isotopes (see supplementary online material for other models[1]). The LDA–MDF approach yields a single estimate of provenance for each unknown perch.

Second, to account for analytical error in isotope measurements and generate a measure of assignment confidence for our top models, we used a Bayesian error-based resampling simulation approach. This technique enables cross-validation of perch from known sampling locations (gill-netted perch) and the assignment of unknown origin (regurgitated) perch based on the best models from LDA–MDF assignments (Wunder et al. 2005; Wunder and Norris 2008; Franks et al. 2012). Because fish population den-

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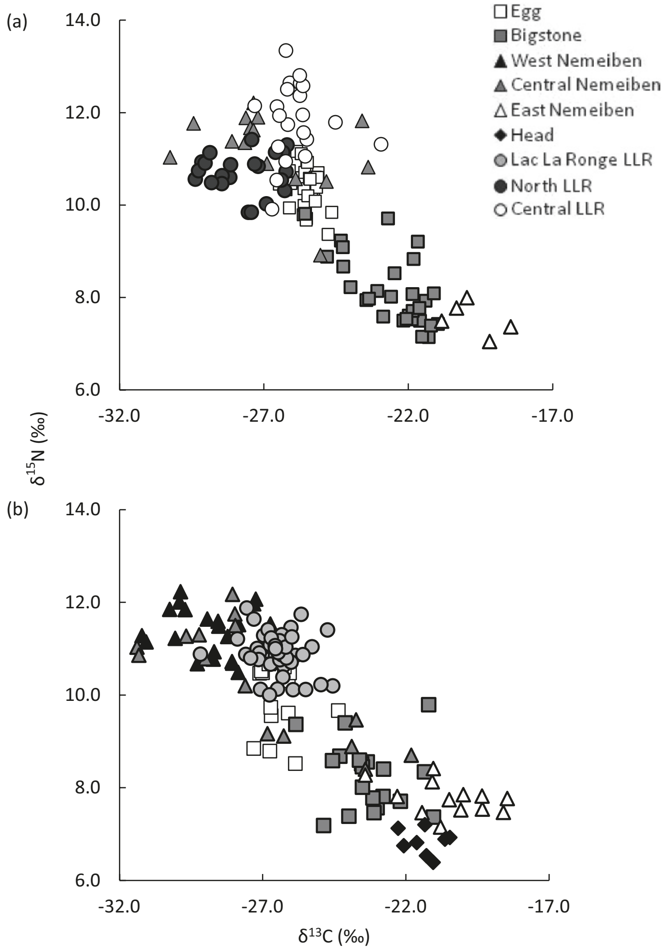
[1] Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2012-0237.

sity varies across space, we incorporated relative abundance (catch per unit effort of yellow perch based on gill netting) as the prior probability of origin (as in Franks et al. 2012). Briefly, for each isotope value for each perch, we randomly sampled 100 values from a normal distribution with a mean equal to the isotope value for that tissue and a standard deviation derived from repeated measures of lab standards; this produced 100 new isotopic data sets for all individuals. We randomly chose one data set to define the parameters (mean, variance–covariance) of the multivariate probability density functions for the sites of origin. We took two approaches for choosing the data set to define the parameters: (*i*) using all known-origin samples and (*ii*) using only samples correctly assigned during the cross-validation simulation (see below). Both approaches provided similar results; we present data using all known-origin samples because it better represents the extent of isotopic variation in the populations. For each individual in each data set, we determined the probability of assignment to a potential site of origin, which produced 100 assignment outcomes for each perch. Finally, we repeated the previous step 100 times, each time using a new data set to define the parameters of the probability density function. This produced 10 000 assignment outcomes for each individual. This approach also allowed us to assess our confidence in assignments. For example, an individual that was assigned to a given region 9000 times out of 10 000 simulations was considered to have a 90% confidence of assignment to that region. Regurgitated perch with assignment confidence levels ≥50% and 80% were used for determining the proportion of prey assigned to each location; here we present only data based on the 80% confidence threshold. The proportion of regurgitated perch assigned to each location was assumed to reflect the whole diet of cormorants. These values were chosen to represent low and high confidence thresholds in the probability of assignment (as in Franks et al. 2012). MDF assignments were analysed by collection date as well as chick rearing stage (early = chicks in nests; late = chicks in crèches).

To further examine our level of confidence in assignments of unknown-origin perch, we examined the ability of our isotopic data to correctly assign known origin (gill-netted) perch back to their source location. We used the resampling simulation approach described above with an exclusion criterion (i.e., leave-one-out cross-validation), whereby we calculated the parameters (mean, variance–covariance) of the probability density function, but excluded the individual to be assigned from the data set. We then examined the likelihood of that individual originating from each of the potential source regions, as above. The LDAs and MDFs were conducted in the statistical software package R 2.12.1, using the rrcov (Todorov and Filzmoser 2009), mvtnorm, and mvnmle packages (Genz et al. 2011).

We used a generalized linear model to compare cormorant densities among sites; the number of transects and transect length did not significantly influence density (data not shown). We performed a negative binomial regression on cormorant density based on site and chick rearing period. Density was used to standardize cormorant abundance among lakes. To eliminate non-integer values, density was multiplied by 100 and the decimal points were removed. Transect count data are reported as geometric means (± standard error); statistical tests of generalized linear models were performed in PASW Statistics 18 (SPSS Inc., IBM, Armonk, New York, USA).

Fig. 2. Carbon and nitrogen stable isotopes values of gill-netted yellow perch (TL = 70–130 mm) in (*a*) 2009 and (*b*) 2010. All gill-netted fish were collected from suspected cormorant foraging locations using bottom-set gill nets and represent known locations. In 2010, all Lac La Ronge zones were combined.



Results

Fish from known locations

Gill-netted perch showed a wide range of stable isotope values and varying degrees of overlap in $\delta^{13}C$ and $\delta^{15}N$ among sites. Carbon stable isotope values spanned a total of 11.8‰ (–30.2‰ to –18.5‰) in 2009 and 14.6‰ (–33.1‰ to –18.5‰) in 2010 (Fig. 2). Nitrogen stable isotope values spanned a total of 6.3‰ (7.1‰–13.3‰) in 2009 and 6.4‰ (5.9‰–12.2‰) in 2010 (Fig. 2). The best model for 2009 assumed distinct perch populations for Egg and Bigstone lakes, two populations in Lac La Ronge (north and central), and two populations from Nemeiben Lake (central and east). Eighty-one percent (99/122) of gill-netted perch were correctly assigned back to their lake of origin (Table 1; Table S1[1]). Of these, 89% (88/99) were assigned with greater than 80% confidence, and 99% (98/99) were assigned with greater than 50% confidence. Assignment probabilities were high for most sites; the highest correctly assigned rate was 100% (6/6) for perch from eastern Nemeiben Lake, while the lowest rate was 67% (14/21) for perch from central Lac La Ronge. The range of correct assignment rates for the remaining lakes was between 73% and 93% (Table 1).

The best model for 2010 assumed distinct perch populations for Egg Lake, Bigstone Lake, Head Lake, Lac La Ronge, and three distinct populations for Nemeiben Lake (west, central, and east). Sixty-seven percent (98/146) of gill-netted perch were correctly assigned back to their lake of origin (Table 1; Table S2[1]). Of these, 94% (92/98) were assigned with greater than 80% confidence, and 100% (98/98) were assigned with greater than 50% confidence. Correct assignment rates were low for Egg and central Nemeiben lakes at 44% (7/16) and 0% (0/17), respectively. Conversely, the remaining sites had high assignment rates ranging from 74% to 100% (Table 1).

Table 1. Cross-validation resampling simulation of gill-netted yellow perch (TL = 70–130 mm) from known locations, in 2009 using an MDF model with two Lac La Ronge (LLR) and Nemeiben Lake populations and in 2010 using an MDF model with one LLR and three Nemeiben Lake populations.

	Predicted sites								
Actual sites	Bigstone	Egg	Central Nemeiben	East Nemeiben	North LLR	West Nemeiben	Central LLR	Head	LLR
2009									
Bigstone (*n* = 29)	24 (0.83)	1 (0.03)	0 (0.00)	4 (0.14)	0 (0.00)	—	0 (0.00)	—	—
Egg (*n* = 30)	1 (0.03)	28 (0.93)	0 (0.00)	0 (0.00)	1 (0.03)	—	0 (0.00)	—	—
Central Nemeiben (*n* = 14)	0 (0.00)	2 (0.14)	11 (0.79)	0 (0.00)	1 (0.07)	—	0 (0.00)	—	—
Eastern Nemeiben (*n* = 6)	0 (0.00)	0 (0.00)	0 (0.00)	6 (1.00)	0 (0.00)	—	0 (0.00)	—	—
North LLR (*n* = 22)	0 (0.00)	2 (0.09)	3 (0.14)	0 (0.00)	16 (0.73)	—	1 (0.05)	—	—
Central LLR (*n* = 21)	0 (0.00)	2 (0.10)	3 (0.14)	0 (0.00)	2 (0.10)	—	14 (0.67)	—	—
2010									
Bigstone (*n* = 20)	16 (0.80)	1 (0.05)	0 (0.00)	2 (0.10)	—	0 (0.00)	—	1 (0.05)	0 (0.00)
Egg (*n* = 16)	0 (0.00)	7 (0.44)	1 (0.06)	0 (0.00)	—	0 (0.00)	—	0 (0.00)	8 (0.50)
Central Nemeiben (*n* = 17)	4 (0.24)	3 (0.18)	0 (0.00)	0 (0.00)	—	8 (0.47)	—	0 (0.00)	2 (0.12)
East Nemeiben (*n* = 13)	1 (0.08)	0 (0.00)	0 (0.00)	11 (0.85)	—	0 (0.00)	—	1 (0.08)	0 (0.00)
West Nemeiben (*n* = 24)	0 (0.00)	0 (0.00)	1 (0.04)	0 (0.00)	—	20 (0.83)	—	0 (0.00)	3 (0.13)
Head (*n* = 9)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	—	0 (0.00)	—	9 (1.00)	0 (0.00)
LLR (*n* = 47)	0 (0.00)	6 (0.13)	2 (0.04)	0 (0.00)	—	4 (0.09)	—	0 (0.00)	35 (0.74)

Note: Each perch was assigned to the site with the greatest number of assignments out of 10 000 simulations. In each simulation, perch were assigned to the site with the highest probability of origin. Values on the diagonal represent the number (and proportion) of correctly assigned individuals.

Fish from cormorant diet

Yellow perch regurgitated by cormorant nestlings had similar ranges in $\delta^{13}C$ and $\delta^{15}N$ values to those gill netted from potential foraging sites. Carbon stable isotope values spanned a total of 9.7‰ (−30.9‰ to −21.2‰) in 2009 and 14.2‰ (−31.6‰ to −17.2‰) in 2010 (Fig. 3). Nitrogen stable isotope values spanned a total of 5.5‰ (7.5‰–13.0‰) in 2009 and 7.4‰ (6.4‰–13.8‰) in 2010 (Fig. 3). Based on MDF analyses, confidence in assignment of regurgitated perch to their site of origin in 2009 was ≥80% for 94% (174/186) of individuals and ≥50% for 100% (186/186) of individuals, whereas in 2010, confidence was ≥80% for 85% (332/391) of individuals and ≥50% for 99% (389/391) of individuals. We present the following data using perch with assignments ≥80%. In 2009, 75% of perch were assigned to Bigstone Lake, followed by 18% to Egg Lake, 4% to north Lac La Ronge, 2% to central Nemeiben Lake, 1% to central Lac La Ronge, and 0% to eastern Nemeiben Lake. In contrast, in 2010, 24% percent of perch were assigned to western Nemeiben Lake, followed by 20% to Lac La Ronge, 17% to eastern Nemeiben Lake, 14% to central Nemeiben Lake, 10% to Bigstone Lake, 8% to Egg Lake, and 7% to Head Lake.

In both study years the proportions of perch assigned to each site changed by date (Fig. 4; Tables S3, S4[1]). For example, in 2009, 13% (2/15) and 81% (128/159) of regurgitated perch were assigned to Bigstone Lake on 18 June and 5 July, respectively (Fig. 4). Similar shifts were also observed in 2010: 88% (28/32) of perch collected on 1 July were assigned to western Nemeiben Lake, whereas 9% (4/43) of perch were assigned to the same site when collected on 4 July. The chick rearing stage also affected assignment location. During early chick rearing (n = 281), 62% of regurgitated perch were assigned to all Nemeiben Lake sites, with all other sites having <15% of assignments. In contrast, 20% of perch regurgitated during late chick rearing (n = 51) were assigned to Nemeiben Lake, 31% to Egg Lake, and 49% to Lac La Ronge. Analyses based on confidence in assignments ≥50% showed similar results (see also Tables S5, S6[1]).

Relative cormorant density

Variance in relative cormorant density was explained by site ($\chi^2 = 219.8$, df = 5, $p < 0.001$) and chick rearing stage ($\chi^2 = 16.2$, df = 1, $p < 0.001$) in a negative binomial regression model. There was a significant interaction between chick rearing stage and site ($\chi^2 = 150.6$, df = 5, $p < 0.001$). This interaction was driven largely by a reduction in cormorant density on Nemeiben Lake during the late chick rearing stage, with corresponding increases on Egg Lake and south Lac La Ronge (Fig. 5). Seasonal switching between foraging areas by cormorants is further supported by observations of foraging flocks (Fig. 6). We detected 66 cormorant flocks ranging from 10 to 2500 individuals (385.4 ± 56.3) in water depths of 1.2–13.1 m (4.5 ± 0.3 m). In the early chick rearing stage, 38% (13/34) of flocks were observed on Nemeiben Lake and 44% (15/34) on Lac La Ronge. During the late chick rearing stage, 66% (21/32) of flocks were observed on Egg Lake.

Discussion

Stable isotope values from prey and relative densities by site suggest that breeding cormorants foraged widely over much of the La Ronge area, including different lakes and regions within lakes. Cormorants also focused much of their feeding at sites that were well removed from the breeding colony lake and switched locations regularly; feeding site changes were common to many individuals within colonies. Therefore, cormorants are not foraging solely on the lake containing their breeding colony, or even on lakes closest to their breeding colony. Acentric colony locations on the perimeter of the foraging range have been observed in other colonial waterbirds and can lead to increased flight distances to foraging areas (Wittenberger and Dollinger 1984). Correspondingly, cormorants nesting on Egg Lake were collecting prey fish from areas over 20 km away from their breeding colony in different habitats and ecozones. Use of these distant areas was a major part of the foraging and feeding ecology of cormorants (>80% of fish in 2010), indicating a relatively weak spatial connection between the location of the breeding colonies and foraging sites. This insight into the feeding ecology of cormorants may profoundly affect assessment of potential fisheries impacts in our study area. Cormorants are spreading their fish biomass removal over a variety of sites, perhaps mitigating negative effects on fish in any given body of water. Conversely, multiple prey populations may be negatively affected by cormorant consumption, rather than just one.

Multiple foraging lakes and habitats may be a more common feature of cormorant ecology than previously thought. Our findings are supported by other studies on great cormorants in Europe, where the birds did not consistently forage on the lake they nested on. For example, great cormorants nesting on Lake Ymsen, Sweden, spent 20% of the time foraging at other nearby lakes, 7

Fig. 3. Carbon and nitrogen stable isotopes values of regurgitated yellow perch (TL = 70–130 mm) in (*a*) 2009 and (*b*) 2010. Regurgitated yellow perch are separated by collection date and chick rearing period (early = 17 June – 15 July; late = 16 July – 31 August) for 2009 and 2010, respectively. The approximate outline (rectangles) of stable isotopes values for yellow perch collected from known locations is shown for reference.

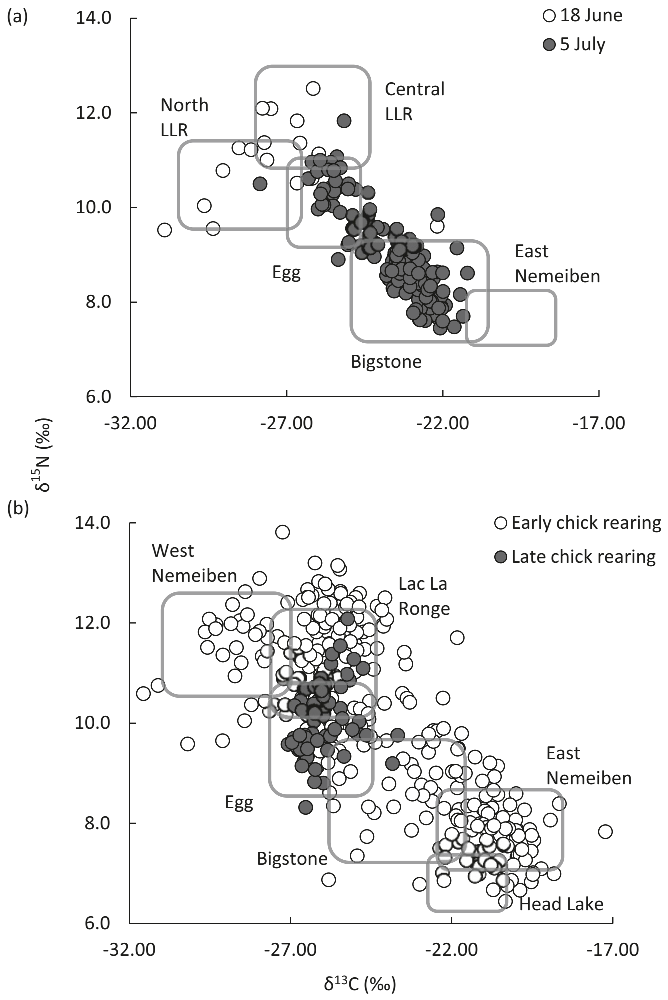


Fig. 4. The proportion of regurgitated yellow perch that were assigned to each site by collection date in 2009 and 2010.

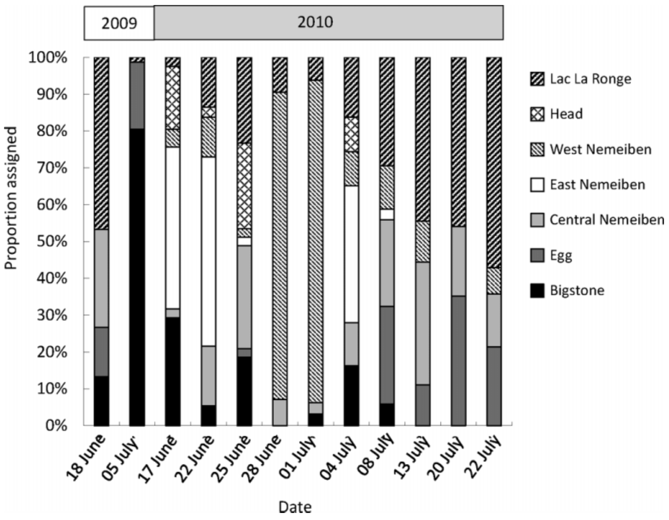
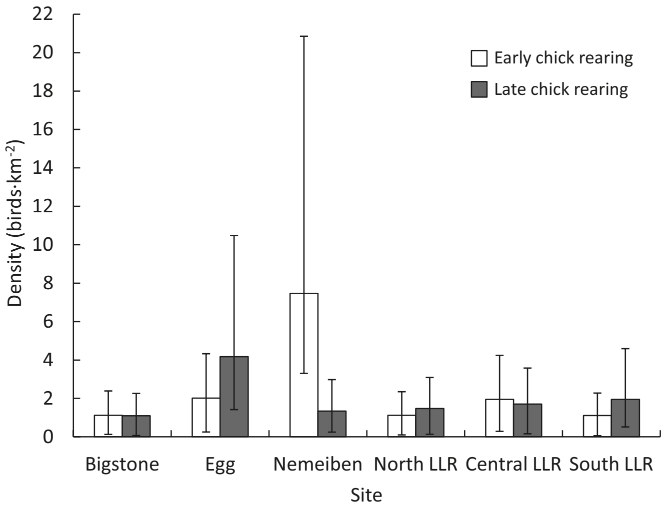


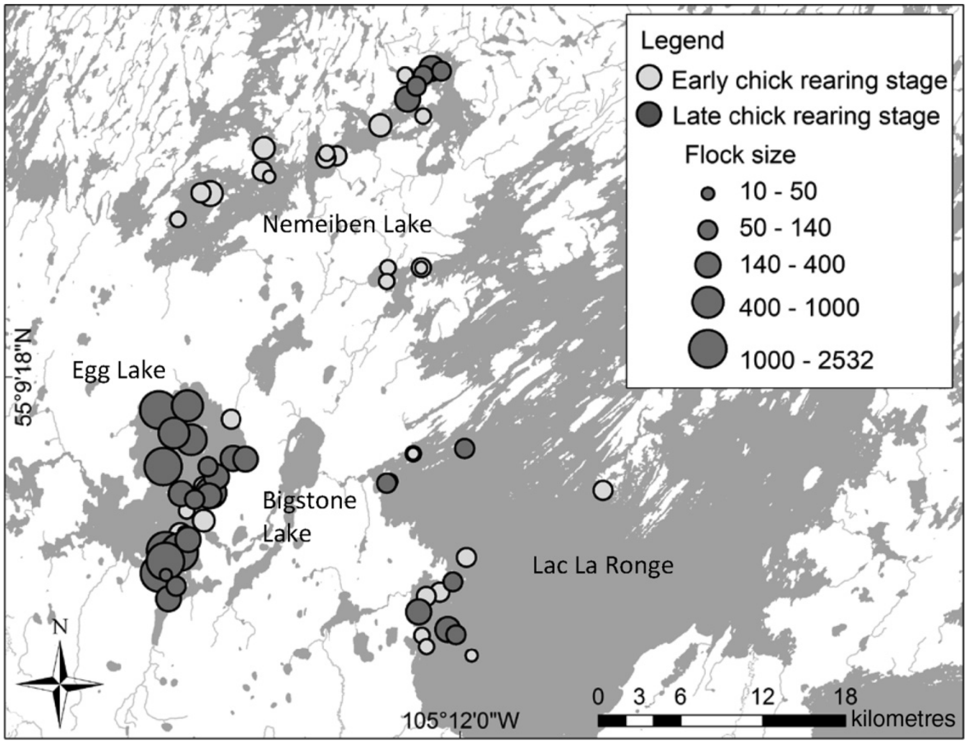
Fig. 5. Geometric mean (±SE) cormorant density at each site in the Lac La Ronge (LLR) study area during the early (17 June – 15 July; open bars) and late (16 July – 31 August; filled bars) chick rearing periods in 2010. Data were obtained from line transect surveys.



and 11 km away (Engström 2001). Similarly, great cormorants nesting on Lake Selent, Germany, foraged 50% of the time on that lake and the other 50% of the time in two different marine areas located approximately 30 km away (Grémillet et al. 1995). In an extreme case, great cormorants commuted 60 km from a breeding colony on Sheep Island in Northern Ireland, to feed in Lough Neagh (Warke et al. 1994; Warke and Day 1995). The distances travelled by cormorants in our study are comparable to those documented for cormorants in other areas. Thus, cormorants might commonly move large distances, 10–60 km away from their breeding colony. To our knowledge there are currently no published North American studies on double-crested cormorants that specifically address multiple foraging sites, despite evidence that cormorant movement may be a common phenomenon. For example, Eisenhower and Parrish (2009) reported that foraging cormorants in a basin of Lake Champlain declined in July of 3 years, indicating that they switched to other foraging areas. It is critical that cormorant foraging ecology, specifically where they consume prey, and how sites are selected, be more completely understood to inform management decisions.

Despite temporal changes in the sources of prey, cormorants were still consuming mainly small yellow perch (TL = 70–130 mm). It is currently unclear why cormorants switched locations to capture the same prey; however, prey availability likely played a role in their decisions (Warke et al. 1994; Warke and Day 1995; Eisenhower and Parrish 2009). Cormorant prey capture rate has been shown to relate more to prey density than to visual acuity (Hao 2008), and prey availability has a greater influence on daily food intake than water temperature and dive depth (Grémillet and Wilson 1999). This suggests that cormorants forage in locations that provide the most efficiently available prey. Our observations suggest a similar explanation: gill nets in pelagic zones on Egg Lake in 2010 yielded 0.34 perch·net^{-1}·h^{-1} in June when cormorants were foraging elsewhere, but catch per unit effort increased 54-fold in August when Egg Lake became a more important feeding site. Thus, cormorants may have foraged elsewhere when perch were not readily available in Egg Lake, perhaps because the perch were occupying unsuitable aquatic habitats. Recent research has shown that fish activity levels and movement may affect gill-net capture rates (Rennie et al. 2012), so seasonal differences in these parameters may also have influenced our perch catch per unit effort during the two sampling periods on Egg Lake. It is therefore not clear whether gill net capture data are a suitable

Fig. 6. Locations of cormorant foraging flocks (≥10 individuals) observed in the Lac La Ronge area in 2010. Flocks were divided into early and late chick rearing periods. Flock sizes ranged from 10 to 2500 individuals.



proxy for cormorant prey availability. In addition, cormorants may have also been selecting foraging sites and prey to suit rearing of nestlings, which may benefit from particular size ranges and species of prey. Future research examining the variables that affect cormorant decisions regarding foraging sites would be very useful for understanding which fish populations they are likely to interact with.

Our findings demonstrate the utility of stable isotopes for tracking the provenance of cormorant prey. Relative cormorant density in 2010 showed trends in foraging locations in accordance with stable isotope analysis. The MDF assigned 62% of regurgitated perch to Nemeiben Lake during the early chick rearing stage and 20% to the same lake in the late chick rearing stage. Relative cormorant densities and the locations of foraging flocks in 2010 showed a parallel shift, supporting our conclusions. Our analyses of stable isotopes indicate high confidence in our assignment of regurgitated perch; however, we recognize that the cross-validation success of gill-netted perch of known origin was <100%. Thus, assignments of regurgitated perch have some degree of uncertainty. Overall, assignment rates based on our stable isotopes data were similar to those that distinguished fish populations using multiple (four or five) trace elements (Thorrold et al. 1998; Gillanders and Kingsford 2000; Brazner et al. 2004). Successful assignment rates in these studies ranged from 63% to 76%, with individual sites ranging from 50% to 100% (Thorrold et al. 1998; Gillanders and Kingsford 2000; Brazner et al. 2004). Considering that our study was done on a smaller spatial scale with only two markers (δ^{13}C and δ^{15}N), the maximum likelihood approach performed well and is an approach that should be considered for additional studies of prey source tracking in colonial birds. For example, Hobson et al. (2012) showed marked spatial variation in baseline and fish stable isotope values within Lake Winnipeg (Manitoba, Canada), which supports our findings and may make source tracking possible on that lake as well. In addition, the general notion of using stable isotopes to determine the provenance of resources may be transferable to a wide variety of other central place foragers beyond birds, provided that they exist in landscapes with isotopically distinct patches (Cook and Dawes-Gromadzki 2005).

It is important to consider that the sites sampled in this study were assumed to be the only ones used by breeding cormorants from Egg Lake. It is possible that cormorants fed at other locations where prey had stable isotopes values similar to those sampled from our "known" sites. Thus, there is some uncertainty involved with assigning prey to specific locations. However, it is clear that multiple isotopic populations were involved. Stable isotopes values can only vary so much over a small spatial scale (e.g., Overman and Parrish 2001; Barks et al. 2010), so our technique likely has limitations in terms of the number of sites that can be sampled and the subsequent resolution of the MDF. A multivariate approach using several biogeochemical markers may greatly increase precision in detecting small spatial scale variation among fish populations (Thorrold et al. 1998; Gillanders and Kingsford 2000; Brazner et al. 2004). Future studies should examine variation among sites and evaluate resolving power before large spatial scale application of a stable isotope or chemical marker approach (see Hobson et al. 2012).

Bioenergetics modeling indicates that cormorants can consume large amounts of fish (Grémillet et al. 2003; Ridgway 2010). A single double-crested cormorant weighing 2.0 kg will eat ~500 g fish·day^{-1}, based on consuming 25% of its body mass daily (Dunn 1975; Glahn and Brugger 1995). A variety of studies have used such per-capita consumption rates to estimate biomass removal by cormorants during the breeding season and have assumed that prey originates near the colony (e.g., Johnson et al. 2002; Rudstam et al. 2004; Diana et al. 2006). For example, a small colony of 730 adult double-crested cormorants was estimated by Rudstam et al. (2004) to consume 47 300 kg of fish, whereas Johnson et al. (2002) estimated that a colony of 16 820 adults consumed 2.1 million kg of fish during one breeding season. The approach of estimating fish biomass consumed by cormorants solely from areas near breeding or roosting areas can be inaccurate for assessing impacts on fish populations. Our findings show that cormorants obtained prey from multiple distant (~30 km) locations, which negates the approach of simply assuming one prey source. In addition, simple applications of bioenergetic models present other serious problems for making management decisions. For example, fish biomass removal estimates by cormorants do not directly represent the fish biomass that would have otherwise been recruited into cohorts used by fisheries. Accumulating evidence, including our findings presented here, suggests that biomass removal estimates are only one small part of assessing cormorant impacts on fisheries resources and have limited usefulness.

Management implications

The conflict between cormorants and humans in the La Ronge area, and other locations worldwide, stems from the fact that some cormorant prey come from lakes with economically important fisheries that have declined in production over time. In our case, the majority of cormorant prey (75%) in 2010 was obtained from lakes that are heavily used by humans for fishing and recreational activities (Nemeiben Lake 55%, Lac La Ronge 20%) and have experienced declining fisheries quality. These feeding areas are well removed from the breeding colony location on Egg Lake; thus, it would be a major error to assume that cormorants primarily interact with fish populations on Egg Lake in the assessment of potential fisheries impacts. Egg Lake has essentially no sport fishery and only a small commercial harvest of lake whitefish, so it would be easy to erroneously conclude that there is little cormorant conflict. However, the possible influence of cormorant predation on sport fish populations in Lac La Ronge and Nemeiben Lake must be considered in any management planning exercise for our study area. We recommend at minimum that a much more detailed assessment of the species, size class, and age of cormorant prey fish be combined with a site-adjusted biomass removal model that accounts for multiple feeding sites and their relative importance to cormorants. This approach would enable fisheries managers to evaluate the potential importance of cormorants as a source of fish mortality compared with other factors at each site. For example, adult cormorants in 2010 consumed approximately 104 064 kg of fish (based on 542 $g\cdot bird^{-1}\cdot day^{-1}$ and 800 breeding pairs with a 120-day residence period; Ridgway 2010); however, only 57 235 and 20 813 kg of this total are predicted to be drawn from Nemeiben Lake and Lac La Ronge, respectively, based on our study. This raises two key points regarding management: (*i*) multiple feeding sites spread out cormorant biomass removal, reducing cormorant impact at individual sites, and (*ii*) the biomass removal may or may not be a significant fisheries management concern for a given body of water. Lac La Ronge, the site of primary concern in our study area, is a large lake (130 700 ha) in which 20 813 kg of fish biomass, comprising mostly yellow perch, cisco, and white suckers, is likely irrelevant to sport and commercial fisheries. Thus, we would not recommend any cormorant management action based on the Lac La Ronge fishery. The other sites, especially Nemeiben Lake, would need to be carefully assessed in a similar vein. As a final point, it is interesting that cormorants in our study area are choosing to nest on a lake that is isolated (Egg Lake; no road access) and has very little human use, but they travel long distances to feed on lakes in which food webs have been heavily disrupted by humans (Duffy 2007). It is highly probable that human disruption of food webs creates conditions more favourable for cormorants (e.g., by reducing abundance of top predator fish; Hobson et al. 1989; Gloutney and Chen 1992; Post et al. 2002), and thereby leads to the current situation. We suggest that effective long-term management of intact aquatic food webs is a key feature of preventing cormorant conflict with humans over fisheries resources.

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