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Migration and Winter Movements of Double-crested Cormorants Breeding in Georgian Bay, Ontario

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Abstract.—Double-crested Cormorants (*Phalacrocorax auritus*) breeding in the Great Lakes and wintering in the southeastern United States were implanted with satellite transmitters to assess their movements. During 2007 and 2008, 26 cormorants from Georgian Bay, Ontario, Canada, were tracked in order to, variously, identify staging areas, characterize migration routes, winter habitat use, and home range size, assess philopatry of returning breeders, and test for a relationship between winter habitat use and arrival at the breeding ground. Females left summer areas earlier and spent more time in staging areas than did males. However, both sexes left the staging areas and arrived in the wintering grounds at approximately the same time. There was no difference in latitude between wintering males and females, or in winter residency time (n = 136 days for both sexes). The predominant winter habitat types were lakes and coasts with only seven of 26 (26.9%) birds wintering on aquaculture sites. Contrary to expectations, winter home ranges of birds on aquaculture sites ($\bar{x}$ = 2760 km^2) were significantly larger than birds on non-aquaculture sites ($\bar{x}$ = 81 km^2). A carryover effect of aquaculture was not detected; winter residency time was similar for birds on both aquaculture and natural winter habitats, with birds from both habitats returning north at the same time. Fidelity to the previous summer's location was observed in 15 of 20 returning individuals. *Received 8 November 2009, accepted 16 February 2010.*

Key words.—aquaculture, Double-crested Cormorants, foraging, Great Cormorants, home range, migration, satellite telemetry, staging areas, winter.

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Double-crested Cormorants (*Phalacrocorax auritus*) breeding in the Great Lakes region winter in the southeastern USA from North Carolina to the Gulf of Mexico (Hatch and Weseloh 1999). In the wintering area, cormorants are found both on the coasts and inland along rivers and lakes, including where aquaculture is prominent (Hatch and Weseloh 1999). Over recent decades, many changes have occurred in the number of cormorants nesting in the Great Lakes and in their wintering habitat. In the 1990s alone, the number of cormorants wintering in the Mississippi delta region tripled (Werner *et al.* 2000). Many factors, including habitat alteration, regulatory protections, reduced environmental contamination and expanded commercial aquaculture, have likely contributed to the recent increase in the cormorant population (Blackwell *et al.* 2002; Stapanian 2002; Dorr *et al.* 2004). The population increase has in turn produced a range expansion throughout both the breeding and wintering grounds (Blackwell *et al.* 2002; Stapanian 2002; Taylor and Dorr 2003; Dorr *et al.* 2004; Ridgway *et al.* 2006; Hebert *et al.* 2008). For example, Christmas Bird Counts from 1959-1988 showed an increase of 18.7% per year in inland areas of Mississippi, and a 7.3% increase for all interior areas combined (Hatch and Weseloh 1999). Winter survival of this species may have been improved due to the expansion of the aquaculture industry in the Mississippi delta region (Glahn *et al.* 1997; Blackwell *et al.* 2002; Stapanian 2002; Taylor and Dorr 2003; Dorr *et al.* 2004). In 2001 and 2002, respectively, approximately 16,500 and 22,000 cormorants were counted in winter night roosts in the primary aquaculture areas of eastern Mississippi and western Alabama (Dorr *et al.* 2004).

Much about cormorant migration is unknown, so our main objectives were to determine the migration routes, staging areas and wintering grounds of cormorants breeding in Georgian Bay, in Lake Huron, Ontario. The birds nesting in Georgian Bay are part of a larger Great Lakes metapopulation

(Scherr 2009); however, their cohesion among seasons (e.g. whether or not they migrate together, winter in the same areas, and return to the same breeding grounds each year) was unknown. We also assessed cohesion between sexes, since differential energy investment between sexes during breeding (Moreno 1989) may affect patterns of staging and migration. At the start of fall migration in September, many cormorants from throughout the Great Lakes region appear to move into Lake Erie. In this area, cormorants form large social gatherings. Such staging areas provide opportunities for birds to rest and replenish the fuel stores needed to reach their final destinations (Hedenstrom and Alerstam 1997). After staging, it appears that birds from Lake Erie migrate over the interior of the eastern USA and into the Mississippi delta region (Dolbeer 1991; Hatch and Weseloh 1999). We used satellite transmitters to assess the migration routes and staging areas of cormorants from Georgian Bay.

Given recent suggestions that cormorant population increases are due, at least in part, to winter foraging benefits associated with aquaculture (Blackwell *et al.* 2002; Dorr *et al.* 2004; Hebert *et al.* 2008), we were interested in effects of aquaculture on cormorant movements, both during winter and during return migration. We first tested for an effect of aquaculture on winter home range size, reasoning that cormorants near aquaculture ponds should have small home ranges if home range size varies inversely with food abundance (Naef-Daenzer 2000). We also tested for a carryover effect of aquaculture, which we defined as a relationship between winter habitat quality and subsequent arrival time to the breeding grounds. Early arrival time on a breeding ground is a measure of good physical condition for migrating species (Marra *et al.* 1998; Norris and Marra 2007). Hebert *et al.* (2008) found that cormorants returning to breeding grounds were in better physical condition if they had fed in freshwater rather than marine environments. They suggested that enhanced foraging opportunities at aquaculture facilities (freshwater habitats) may improve fitness of birds feeding there. Based on these observations, and assuming that birds in the best condition would return to the breeding grounds earliest (Marra *et al.* 1998; Norris and Marra 2007), we predicted that cormorants wintering on or near aquaculture facilities would return to the breeding grounds earlier than birds wintering in other environments.

Finally, nesting cormorants were experimentally disturbed in 2007 and 2008, to disrupt breeding behavior and cause colony abandonment (Scherr 2009). Many of these birds relocated following disturbance to new summer locations throughout the Great Lakes. We assessed fidelity by comparing summer locations of return migrants to their breeding or post-disturbance locations the previous summer.

Thus, our research was an examination of cormorant migration and winter habitat selection. We used implanted satellite transmitters to assess: (1) location of staging sites, (2) migration routes, (3) winter movements and habitat use, and (4) fidelity of returning breeders.

METHODS

Twenty-eight breeding adult cormorants were captured at their nests with modified and padded foothold traps designed to specifications provided by King *et al.* (2000). Each cormorant was outfitted with a Platform Terminal Transmitter (PTT) (Microwave Telemetry, Inc.). Backpack-mounted satellite transmitters have been used before on cormorants, but transmitter loss is a problem with this method (King *et al.* 2000). Thus, we sought, for the first time, to surgically implant transmitters in cormorants. The PTT units were implanted in the abdomen of each bird (Scherr 2009). The fourteen-month battery life was expected to allow collection of location data during the initial breeding season, the subsequent fall migration and winter, and a second breeding season. PTTs were programmed to transmit location information at varying intervals depending on the activity of the birds (Table 1). Duty cycles were always one hour less than the previous cycle so that the four- hour on period drifted and birds were recorded at all times of day. All data from the PTTs were received by Service Argos Inc. equipment situated on two National Oceanographic and Atmospheric Administration (NOAA) polar-orbiting satellites (Werner *et al.* 2001) and transmitted to us electronically via weekly e-mail. Accuracy of telemetry locations varied with location class (LC; an estimate of reliability from Service Argos Inc.), but errors tend to be small enough at all classes for assessment of large-scale movements such as those associated with migration. For example, mean errors in

Table 1. Duty-cycle of the platform terminal transmitters (PTTs) implanted in 28 Double-crested Cormorants (*Phalacrocorax auritus*) in Georgian Bay, Ontario, Canada in 2007 and 2008 to monitor movement in response to disturbance, and to follow birds throughout the fall, winter and spring.

Time Frame	Duty Cycle
Breeding Season (May to August)	On 4 hrs/ 23 hrs
Fall Migration (September to November)	On 4 hrs every three days
Winter Roosting (December to February)	On 4 hrs every week
Spring Migration (March to April)	On 4 hrs every three days

one recent study varied from 0.3 km for LC3 (the most reliable locations) to 76.1 km for LC B (the least reliable) (Soutullo *et al.* 2007). Transmitters in two birds stopped transmitting before fall migration and were omitted from the analysis but the 26 remaining individuals were monitored throughout the fall migration, winter and spring migration. Location data were received from 13 birds from spring 2007 to summer 2008, and another 13 birds from spring 2008 to summer 2009.

We overlaid locations for each bird on North American base maps to outline its migration route and final winter destination. Winter home ranges were overlaid on images from Google Earth, which we classified into coarse habitat categories. Aquatic habitat within home ranges was classified as either natural (lake, coastal, river, swamp) or aquaculture facility. Aquaculture ponds were easy to identify; they occurred in distinctive clusters as linear aquatic features with regular borders. We consider it unlikely that we overlooked ponds within the study area, although we recognize that we could have overestimated their abundance if other aquatic features had a similar appearance.

We calculated approximate speed of travel of each bird during the migration period by dividing the longest distance between two consecutive transmitted locations by the number of days between fixes. As location data were not received daily in the fall (Table 1) and exact times of departure and arrival could not be determined, this gave a minimum estimate of how far an individual was able to travel in a given day rather than an accurate hourly speed.

Habitats and movements of greatest interest included breeding sites, staging and wintering areas, and the timing of departure from the breeding colony, arrival at a staging area, departure from the Great Lakes, and arrival at a wintering location. The staging period was defined as the time between departure from a breeding colony or post-disturbance location (Scherr 2009) and when the bird left the Great Lakes altogether. Staging areas were regarded as areas used by greater than one bird for multiple days before initiating migration to the winter range. Wintering areas were identified as any area where an individual remained over an extended period of time between December and March. Total migration distances from the breeding colony or post-disturbance location to the final destination were calculated by summing all the segments' distances (i.e. the distance between two consecutive points of data). Independent t-tests were used to determine if significant differences existed between the sexes in the time spent in staging areas, migration distances travelled, number of days taken to reach the wintering area and travel speed. Pearson correlations were used to estimate the strength of association between the amount of time males and females spent in their staging area, and the amount of time it took for them to travel to their wintering areas.

One PTT stopped transmitting from an unknown cause soon after the bird reached its wintering area. Winter home ranges were estimated for the 25 remaining birds using one point per week only; the first class 3 or 2 location of each week was used to prevent pseudoreplication. Home ranges were estimated using the 95% minimum convex polygon in ArcGIS with the Hawth's Tool extension. Mann-Whitney U-tests were used to determine whether significant differences existed between the home range sizes of birds foraging on aquaculture sites and those of birds foraging on natural sites, as well as birds foraging on freshwater sites (both natural and aquaculture) and birds foraging in marine habitats. We used a non-parametric test for this comparison because the home-range size data had a positive skew. The mean home range centroid for each sex was compared with a t-test to test the prediction that males winter farther north than females.

Arrival times at the breeding grounds were monitored to determine whether there was a relationship between winter home range size, habitat type and return to the breeding grounds (i.e. a carryover effect). During each bird's second summer in the study, we determined which colony they had settled in by assigning them to the colony closest to the geographic centroid of their set of locations during the breeding season. Fidelity to the original breeding site was simply determined by recording if a bird settled on its capture colony. For birds that moved from their breeding colony following the experimental disturbance, we determined whether they returned to either their original breeding colony, or their post-disturbance location by measuring the distance between centroids of the second summer location and the post-disturbance location. Centroids were used to account for the movement of these birds in response to experimental disturbance, and the response to the surgical implantation of the transmitters (Scherr 2009). Dolbeer (1991) showed with band recoveries that median distance of 3-year old breeders from their natal sites was 25 km. We used this distance to define fidelity—if the distance between the two centroids was < 25 km (Hatch and Weseloh 1999) then these birds were considered to show fidelity.

RESULTS

Staging Areas and Fall Migration

Two staging areas were identified during this study: Long Point and Middle Island, both in Lake Erie. Seven birds stopped at both sites. An additional seven birds stopped only at Middle Island and another seven stopped only at Long Point. These 21 birds showed a funneling effect through Lake Erie (Fig. 1). They all initiated migration from Lake Huron, Georgian Bay or inland waters nearby. Of the remaining five monitored birds, four began migration from east of the Bay of Quinte on Lake Ontario, where they had relocated following experimental disturbance. Three of these birds, one from Bay of Quinte, one from near the Little Galloo cormorant colony and one from the Montreal, Quebec region, traveled along the Atlantic Coast. A fourth made a flight from Bay of Quinte through the continental interior to its wintering area. The fifth bird flew directly from Muskoka Lake, Ontario (east of Lake Huron) and traveled to its winter area without indication of visiting any staging area.

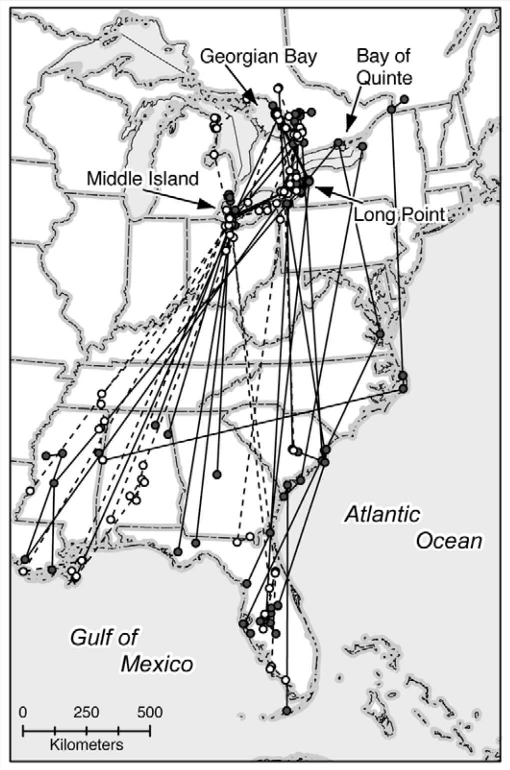

Figure 1. Migration routes of 26 Double-crested Cormorants (*Phalacrocorax auritus*) breeding in Georgian Bay, Ontario, Canada, from southern Ontario including staging areas in Lake Erie (Long Point and Middle Island) to southeastern USA wintering areas. Female cormorants are indicated by white circles and dashed lines and males by black circles and lines. Birds beginning migration in areas other than Georgian Bay traveled to those locations from Georgian Bay following experimental disturbance.

For both years combined, the earliest date that migration from a staging area began was 1 September, and the latest date was 25 October. The earliest date that an individual reached its destination was 30 September and the latest date was 9 December. Over both years, females had a mean [SE in days] departure date from their summer location of 12 September [4], which was significantly earlier than the males' average departure date of 7 October [3] (t = -4.41, d.f. = 24, $P < 0.05$). From the summer to the winter location, the longest migration was 87 days by a male, and the shortest was six days by a male. The mean [SE] duration of migration was 41 [5] days, with no significant differences between the sexes with females arriving on average in 42 [8] days (N = 10), and males arriving in 35 [6] days (N = 16) (t = 1.05, d.f. = 24, P = 0.30).

The mean [SE] migration distance that birds traveled from their summer to their winter location was 2060 [127] km, with females traveling a mean of 2264 [282] km (N = 10) and males traveling 1932 [107] km (N = 16) with no difference between sexes (t = -0.69, d.f. = 24, P = 0.50) (Table 2, Fig. 1). Distances were also measured from each bird's final staging location in the Great Lakes to its winter range (Table 2). No difference in distance traveled was found (t = -0.12, d.f. = 23, P = 0.90) between males (1473 [132], N = 15) and females (1449 [140], N = 10). There was also no difference in the number of days en route (t = 0.89, d.f. = 13, P = 0.39) between males (14 [2], N = 15), and females (19 [5], N = 10); however, females spent more days (33 [6], N = 10) staging in the lower Great Lakes before the final travel to their winter roosts (t = 2.13, d.f. = 23, P = 0.04) than did males (17 [4], N = 15) (Table 2). No relationship was found between staging time and duration of migration for either sex (Female: r = 0.06, P = 0.87, Male: r = -0.14, P = 0.62). Males flew a mean [SE] of 176 [24] km/d (N = 16), and females flew a mean of 171 [24] km/d (N = 10) with no difference between sexes (t = -0.46, d.f. = 24, P = 0.65). The greatest overall rate of movement was 343 km/d by a female. No difference was observed between the mean [SE] latitude of wintering males (30.6°N [0.7], N = 16) and females (30.3°N [0.7], N = 10) (t = -0.33, d.f. = 24, P = 0.74). Mean [SE] winter residency time was the same for males (137 [5] days) and females (136 [12] days) (t = -0.05, d.f. = 18, P = 0.961).

Habitat Selection

In winter, birds were spread throughout six southeastern coastal states (Fig. 1). Florida had the largest number of birds (10), followed by Louisiana (5), Alabama (4), Mississippi and South Carolina (3 each) and Georgia (1). Of the 26 birds, seven birds wintered in or near areas that contained aquaculture facilities. One of these seven roosted on a large river in Alabama; however, there were a few aquaculture facilities within 25 km of its location. Although this bird appeared to be in a natural habitat, it is possible that it may have also visited the aquaculture ponds and therefore we included it with the aquaculture birds. The remaining 19 birds wintered in five different habitat types that were classified as natural habitats containing no aquaculture. Two birds roosted on rivers, one on a swamp, one on an oceanic island in the Florida Keys, eight on lakes (which included one golf course lake) and seven wintered in marine areas along the coast.

Winter home ranges varied widely between birds in different habitats. Birds wintering near aquaculture had much larger home ranges than non-aquaculture birds (U = 12.0, n = 25, P = 0.002) (Table 3).

Three of the twelve birds from 2007 stopped transmitting, and two of 13 birds from 2008 stopped transmitting, before spring migration began in 2008 and 2009, respectively. Of the remaining 20 birds with active transmitters that returned to Georgian Bay, 15 wintered on natural habitats and five on aquaculture. No difference was detected between these two groups in the mean [SE] number of days to return to the breeding ground: natural habitats (28 [3], N = 15) and aquaculture (40 [12], N =

Table 2. Migration statistics for Double-crested Cormorants (*Phalacrocorax auritus*) from summer colonies in Georgian Bay, Ontario, Canada to winter areas in the southeastern United States in 2007 and 2008. The total distance is a sum of the segments of the migration path from the location on the day they left their breeding ground to the location on the day they arrived in their winter area. Independent t-tests were used to identify differences between males and females. Dates, distances (km) and duration (days) are means (standard errors are shown in brackets).

	Departure from breeding	Departure from staging	Duration of total migration	Duration of migration after staging	Distance migrated	Distance migrated from staging	Duration of staging	Arrival on winter range
Females [n = 10]	15-Sep [4]	20-Oct [6]	49 [8]	19 [5]	2264 [282]	1449 [140]	33 [6]	4-Nov [7]
Males [n = 16]	5-Oct [3]	19-Oct [4]	35 [6]	19 [5]	1932 [107]	1479 [123]	16 [4]	7-Nov [4]
t-test	P = 0.0008	P = 0.71	P = 0.08	P = 0.48	P = 0.29	P = 0.90	P = 0.0298	P = 0.85

Table 3. Winter home range size, date of return from spring migration and spring migration duration for Double-crested Cormorants (*Phalacrocorax auritus*) breeding in Georgian Bay, Ontario, Canada and wintering in two different habitat types (aquaculture or natural habitats). Home ranges are 95% minimum convex polygon (MCP). Units are km^2 for home range size and days for timing of migration (standard errors are in brackets).

	Mean MCP	Date of return	Migration duration
Aquaculture	2760 [1831] n = 7	22-Apr [4] n = 5	40 [12] n = 5
Natural habitats	81 [35] n = 18	21-Apr [2] n = 15	28 [3] n = 15

5) (Mann Whitney U = 31.0, P = 0.57). Similarly, there were no differences in mean [SE] winter residency time between cormorants in natural (141 [6] days) and aquaculture (123 [10] days) habitats (t = 1.40, d.f., 18, P = 0.18). Arrival at the breeding grounds occurred between 9 and 30 April for non-aquaculture birds and from 11 April to 3 May for aquaculture birds (Table 3).

Fidelity

Over the two years, 20 birds with active transmitters were monitored during return migration in spring. Six of these birds did not move from their original breeding colony in response to the experimental disturbance, and all six of these birds (100%) returned to the same colony the next year. Of the 14 birds that moved to a new location in the first summer following the experimental disturbance, two (14.3%) returned to their original breeding location. Instead, seven of the 14 (50%) returned during the second summer to the post-disturbance location. One bird (74301) showed fidelity to both its capture colony and its post-disturbance location by spending May and June 2008 at the 2007 breeding colony before returning to its post-disturbance site on Lake Simcoe, Ontario, for the rest of the 2008 breeding season (Table 4). Overall, 15 of 20 birds (75%) showed fidelity to either the breeding colony or the post-disturbance location (Table 4).

DISCUSSION

We found that cormorants breeding in Georgian Bay tended to stage in Lake Erie at either Long Point or Middle Island. Then they migrated over the continent interior to a large wintering area across the southeastern USA (Fig. 1). We found few differences between male and female cormorants with regard to migration timing and behavior, and no evidence of carryover effects on return migration. There were differences in winter movements however, between birds that roosted near aquaculture sites and those using natural habitats. Birds roosting near aquaculture had larger home ranges (Table 3).

Staging Areas

In both years, there was a pattern of birds funneling into Lake Erie and remaining in staging areas there for multiple days before continuing south. Females left the summer areas earlier, and spent more time staging in the Great Lakes before making the final leg of their migration than did males (Table 2). One function of staging is to load fuel prior to migration, which allows individuals to complete their migration without having to stop frequently along the way to forage (Hedenstrom and Alerstam 1997; Weber *et al.* 1998). The sex-biased staging times we observed may be related to differential investment during breeding, associated with additional reproductive stress in females (e.g. Moreno 1989). Females may need to load more fuel than males prior to migrating.

Migration

Recent ideas about migration routes use by Double-crested Cormorants have in-

Table 4. Fidelity to summer locations of Double-crested Cormorants (*Phalacrocorax auritus*) breeding in Georgian Bay, Ontario, Canada. Females are denoted with a *. Fidelity was determined in two ways: first by whether or not the bird returned to its original capture colony; second by whether it returned to its post-disturbance location if it abandoned its capture colony. The latter was determined by measuring the distance from the location during the second summer to the centroid of the previous summer range. If the distance between both points was less than 25 km, then the bird was considered to have fidelity.

Bird ID	Spring migration	Capture colony	Post-disturbance location	Location during second summer	Fidelity to capture colony	Distance to post-disturbance location (km)	Fidelity to post-disturbance location
*74292	March 23 - April 22	GB 6	GB 6	GB 6	yes	1.4	—
*81063	March 25 - April 9	GB 15	GB 15	GB 15	yes	0.2	—
*74298	February 5 - May 3	GB 12	North Channel	North Channel	no	5.3	yes
*81061	March 24 - April 24	GB 15	Lake Simcoe	GB 9	no	105.3	no
*81065	March 27 - April 13	GB 7	Lake Simcoe	GB 6	no	92.4	no
*81067	March 28 - April 20	GB 7	North Bay	GB 2	no	146.8	no
*81068	April 1 - 29	GB 7	GB 16	GB 16	no	1.5	yes
*81071	April 2 - 17	GB 7	GB 9	GB 9	no	0.1	yes
74293	March 18 - April 16	GB 6	GB 6	GB 6	yes	10.9	—
74294	March 26 - April 17	GB12	Muskoka Lake	GB 12	yes	45	no
74300	March 8 - April 19	GB 6	GB 6	GB 6	yes	3.7	—
74301	March 28 - April 11	GB 19	GB 19	GB 19 and Lake Simcoe	yes	5.6	—
51060	March 19 - April 30	GB 7	Lake Simcoe	GB 7	yes	97.1	no
81070	March 24 - April 25	GB 15	GB 15	GB 15	yes	0.2	—
74295	March 27 - April 25	GB 12	North Bay and North Channel	North Bay and North Channel	no	2.7	yes
74297	March 29 - April 26	GB 19	Inland north of Parry Sound	Inland north of Parry Sound	no	20.1	yes
74302	March 14 - April 19	GB 12	Montreal	Southern Georgian Bay	no	487	no
81058	April 20 - 26	GB 15	GB 16	GB 16	no	0.4	yes
81062	March 7 - April 29	GB 15	Toronto	Southern Georgian Bay	no	138	no
81066	March 26 - April 20	GB 7	North Bay	North Bay	no	1.3	yes

cluded the notion that there is a split in migration routes between birds that travel through the Great Lakes and the interior of United States to wintering locations, and those that travel along the Atlantic Coast. Dorr *et al.* (2002) found that 77% of 52 satellite tracked birds caught on Little Galloo Island in eastern Lake Ontario migrated east of the Appalachian Mountains and down the east coast to their winter grounds in the Gulf of Mexico. Cormorants breeding east of the Bay of Quinte may migrate down the Atlantic coast (the Bay of Quinte is situated on the north shore of Lake Ontario; Fig. 1) with birds that breed west of this area migrating through the interior (D.T. King, pers. comm.). Our data are consistent with this suggested split in migration routes, as three of four transmittered birds summering east of the Bay of Quinte migrated down the Atlantic Coast. All of the remaining birds migrated through the continental interior, west of the Appalachian Mountains (Fig. 1).

Reymond and Zuchuat (1995) found that female Great Cormorants (*Phalacrocorax carbo*) wintered farther south than males in northern Switzerland. Van Eerden and Munsterman (1995) reported similar results in northern Europe and they suggested that males remained farther north so that they could be closer to the breeding grounds. Myers (1981) termed this sex difference in distribution the "arrival time hypothesis" stating that when arrival at breeding grounds is advantageous to any sex or age class, then wintering as close as possible to breeding areas should be favored. Male cormorants that return first to the breeding colonies may have an advantage in establishing and defending nest sites or claiming complete nests from the year before, which would save time and energy in constructing a new one. We found no difference in the distances that males and females traveled to winter areas and in the latitude at which they wintered; sexes were relatively equally dispersed throughout the wintering grounds. Thus, our data do not support the arrival time hypothesis.

Habitat Selection

The expansion of the aquaculture industry in the Mississippi delta region has enhanced the food supply for wintering cormorants, and may have increased their survival and body condition (Blackwell *et al.* 2002; Stapanian 2002; Dorr *et al.* 2004; Hebert *et al.* 2008). Predation by cormorants on cultured fish has led however, to financial losses for the aquaculture industry (Blackwell *et al.* 2002; Taylor and Dorr 2003). As a result, the United States Fish and Wildlife Service has implemented depredation orders that allow the take of unlimited numbers of cormorants if they are found depredating ponds (Stapanian 2002). Management of cormorants at fish ponds includes shooting birds to reduce numbers, frightening them off ponds and dispersing them from night roosts near ponds (Taylor and Dorr 2003; Dorr *et al.* 2004). Harassment of night roosts near ponds effectively reduces cormorant predation of cultured fish; however, harassment can move birds to roosts near other ponds (Dorr *et al.* 2004). Cormorant harassment has likely increased movements of birds around aquaculture facilities, and is likely a key contributor to the large size of the home ranges we observed in birds wintering near aquaculture facilities.

We found no evidence of an effect of winter habitat on either winter residency time or arrival time on the breeding grounds. Similarly, we could detect no difference between birds wintering in different habitats in the duration of their return migration. The trend in duration of return migration however, was opposite our expectation if aquaculture birds were in better body condition (40 vs 28 days for birds from aquaculture and natural habitats, respectively). Overall, our winter residency and migration data provide no support to the notion that birds using aquaculture are in better condition than birds wintering in natural habitats (e.g. Hebert *et al.* 2008). The absence of such an effect may be related to the USDA depredation order. We speculate that the energetic benefits that cormorants can obtain from feeding on cultured fish may be lost through the large movements made in response to harassment on winter roosts. The behavioral response to harassment could be costly for cormorants, and may explain why we observed no carryover effect of winter habitat (Marra *et al.* 1998).

Fidelity

Henaux *et al.* (2007) found that disturbances, such as culling caused experienced breeding Great Cormorants to abandon their colonies and relocate to nearby undisturbed colonies. The fidelity of these birds to their original breeding colonies in the following year was reduced as a result of their failed breeding experience; many birds did not return to their original colonies the following year, but rather were sighted on nearby colonies to which they had relocated post-disturbance. A similar mechanism of relocation has been observed in other species (e.g. *Larus cachinnans*; Bosch *et al.* 2000), and our results were also consistent with this pattern. Fifty percent of birds that moved following disturbance returned the second summer to their post-disturbance location rather than to the original colony where they were disturbed. Only 14.3% of birds that moved following disturbance returned to their original breeding colony, compared to 100% site fidelity of birds that did not abandon their breeding colony. Thus, it appears possible to reduce fidelity of cormorants to breeding colonies through disturbance, but the birds can be expected to develop fidelity to new breeding sites.

Our study illustrated the diversity in migration routes and wintering grounds used by a small group of cormorants that shared a small common breeding ground. The birds were widely dispersed in winter throughout six of the southeastern coastal states. The winter distribution of birds from Georgian Bay underscores the connected nature of Double-crested Cormorant populations across their range, providing support for those who have suggested large scale, inter-jurisdictional approaches to cormorant management (Glahn *et al.* 2000).

Contrary to expectation based on previous studies, few cormorants from our study wintered near aquaculture facilities. Most birds wintered on natural inland lakes and coasts. Furthermore, the cormorants that did winter near aquaculture ponds had relatively large home ranges, which may be the result of harassment programs intended to disperse the birds away from these facilities. We did not test for differences in body condition, but found no evidence that birds wintering near aquaculture facilities returned to the breeding grounds earlier as might be expected if there was a carryover effect of aquaculture. Thus, we observed no evidence of positive effects of aquaculture on cormorant populations. We speculate that additional costs to cormorants of responding to harassment at aquaculture ponds might negate any benefits gained from feeding on cultured fish. Taken together, these findings suggest that recent cormorant population increases cannot be easily attributed to aquaculture activities on the wintering grounds, at least in the years since the depredation order activities were implemented.

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