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Research Paper

## Understanding widespread declines for Common Terns across inland North America: productivity estimates, causes of reproductive failure, and movement of Common Terns breeding in the large lakes of Manitoba

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**ABSTRACT.** Common Tern (*Sterna hirundo*) breeding populations in inland North America have declined significantly since the 1970s. A 2012 survey of the large Manitoba lakes, previously the largest known inland population stronghold, reported a 57–67% decline in 20 years. A further 38% decline by 2017 highlights the urgent need for research and management. We use ground-based estimates of productivity and analysis of microsatellite markers to provide the first detailed insight into breeding status and movements of Common Terns in this region. At six breeding colonies in 2012, we recorded breeding success in fenced plots, counted fledglings, documented predators and floods, and collected blood samples for microsatellite analysis of movement. Productivity ranged from 0.0 to 2.0 chicks fledged per nest, being highest at large colonies (> 1000 nests) located far away from human settlements (20–30 km). Large-scale breeding failure from predation occurred at smaller colonies close to human settlement. The most common predators were Black-crowned Night Herons (*Nycticorax nycticorax*) and Great Horned Owls (*Bubo virginianus*), but we also report three novel predators: Bald Eagles (*Haliaeetus leucocephalus*), gray wolves (*Canis lupus*), and river otters (*Lontra canadensis*). Microsatellite analysis suggested little eastward emigration, but instead a 100-fold increase in immigration from the Great Lakes between the 1990s and 2010s. Substantial population declines in the Manitoba Lakes despite this influx imply that net losses are occurring within inland-breeding populations. Terns now appear to switch frequently between breeding colonies in the region, possibly in response to predation and/or flooding. Although some colonies achieved productivity during the one-year study, continued population decline indicates that monitoring and studies of adult survival and movement are needed, especially given the on-going environmental changes within the region. Only by coupling these data with further efforts in unsurveyed boreal regions can the status of inland-breeding Common Terns be determined and strategies developed to curb apparent, large-scale population declines.

## Comprendre la diminution généralisée de Sternes pierregarins dans les régions intérieures de l'Amérique du Nord : productivité, causes de l'échec de la reproduction et déplacements des Sternes pierregarins nichant sur les grands lacs du Manitoba

**RESUME.** Les populations nicheuses de Sternes pierregarins (*Sterna hirundo*) dans les régions intérieures de l'Amérique du Nord ont diminué de façon marquée depuis les années 1970. Un relevé réalisé en 2012 sur les grands lacs du Manitoba, qui constituaient auparavant le plus grand bastion connu de la population intérieure, a révélé une baisse de 57 à 67 % en 20 ans. Une nouvelle diminution de 38 % en 2017 souligne le besoin urgent de recherche et de gestion. Nous avons utilisé des estimations de productivité réalisées sur le terrain et l'analyse de marqueurs microsatellites pour fournir le premier rapport détaillé du statut de reproduction et des déplacements des Sternes pierregarins dans cette région. En 2012, dans six colonies de nidification, nous avons noté le succès de reproduction dans des parcelles clôturées, compté les oisillons, documenté les prédateurs et les inondations, et collecté des échantillons sanguins en vue d'effectuer une analyse microsatellite des déplacements. La productivité a varié de 0,0 à 2,0 oisillons envolés par nid, étant la plus élevée dans les grandes colonies (> 1000 nids) situées loin des établissements humains (20-30 km). Des échecs de reproduction à grande échelle attribuables à la prédation se sont produits dans les petites colonies proches des établissements humains. Les prédateurs les plus courants étaient le Bihoreau gris (*Nycticorax nycticorax*) et le Grand-duc d'Amérique (*Bubo virginianus*), mais nous signalons également trois nouveaux prédateurs : le Pygargue à tête blanche (*Haliaeetus leucocephalus*), le Loup gris (*Canis lupus*) et la Loutre de rivière (*Lontra canadensis*). L'analyse des microsatellites a indiqué une faible émigration vers l'est, mais révélé une immigration en provenance des Grands Lacs multipliée par 100 entre les années 1990 et 2010. Les baisses substantielles de population dans les lacs du Manitoba, malgré cet afflux, sous-tendent que des pertes nettes se produisent au sein des populations se reproduisant à l'intérieur des terres. Les sternes semblent maintenant changer fréquemment de colonie de nidification dans la région, peut-être en raison de la prédation et/ou des inondations. Bien que certaines colonies aient atteint un niveau de productivité satisfaisant au cours de l'étude d'un an, la baisse

continue de la population indique que le suivi et l'étude de la survie et des déplacements des adultes sont nécessaires, en particulier compte tenu des changements environnementaux en cours dans la région. Ce n'est qu'en associant ces données à d'autres activités réalisées dans des régions boréales non étudiées que l'on pourra déterminer le statut des Sternes pierregarins nichant à l'intérieur des terres et élaborer des stratégies pour enrayer le déclin apparent et à grande échelle des populations.

Key Words: *gene flow; habitat change; Lake Winnipeg; metapopulation dynamics; population connectivity; population decline; productivity; waterbird*

## INTRODUCTION

Waterbird populations are sensitive to a range of anthropogenic threats, including habitat loss and degradation, water regulation, and the intensification of agriculture (Amano et al. 2018). Population trends among North American waterbirds are variable with some showing remarkable recoveries from historic population lows, e.g., American White Pelican (*Pelecanus erythrorhynchos*; King and Anderson 2005) and Double-crested Cormorant (*Phalacrocorax auritus*; Wires and Cuthbert 2006), but several others continuing to decline, including inland-breeding populations of Common Terns (*Sterna hirundo*; Morris et al. 2012, Arnold et al. 2020).

Common Terns have a broad breeding distribution across North America, from southern Labrador to South Carolina in the east and inland through the Great Lakes and other large inland lakes and rivers in the northern prairies (United States and Canada) and boreal regions, as far west as Montana, Alberta, and the Northwest Territories (Arnold et al. 2020). Breeding populations were nearly extirpated on the Atlantic Coast and severely reduced elsewhere in the range by the millinery trade in the late 1800s, with some recovery by the 1930s, although not to historical numbers (Arnold et al. 2020). Further population declines in the 1950s until the 1970s have been associated with organochlorines (DDE, PCBs) and other anthropogenic toxins, particularly at freshwater colonies (Fox 1976, Gilbertson et al. 1976, Courtney and Blokpoel 1983, Cuthbert et al. 2003, Arnold et al. 2020). Common Tern populations in the North American Great Lakes have been studied and managed intensively since then, and concentrations of these compounds have been reduced below toxic levels (Weseloh and Braune 1989, Cuthbert et al. 2003), but decadal census data indicate a continuing decline basin-wide, averaging ~20% numerically and 23% of breeding sites (Morris et al. 2010, 2012). Declines in this region have been particularly acute for Canadian breeding colonies, averaging 41% between 1976 and 2009 censuses (Morris et al. 2012). These declines contrast with the generally stable Atlantic Coast populations but are significant because evidence suggests that inland populations may be the ancestral strongholds of this species in North America (Szczyz et al. 2017). Also, inland colonies rarely receive immigrants from coastal colonies (Haymes and Blokpoel 1978, Szczyz et al. 2017) and inland Common Terns exhibit ecological differences from their coastal counterparts (e.g., Burson 1990, Arnold and Oswald 2013, Arnold et al. 2016).

Boreal populations of Common Terns are largely unstudied despite the considerable area of small lakes and rivers within the boreal region. Moreover, estimates of Common Tern abundance in these areas are few and far between. Across two surveys conducted by Canadian Wildlife Service in 2011–2012 in Ontario, Canada, a minimum of 845 breeding pairs was recorded within a 112,000 km<sup>2</sup> area (~20% of Ontario's boreal forest; D. J. Moore,

D. V. C. Weseloh, R. Weeber, *personal communication*, reported in Arnold et al. 2020). Higher breeding densities were reported in boreal regions of Manitoba (Wilson 2013) with a minimum of 779 breeding pairs across 11 boreal lakes covering an area of approximately 7000 km<sup>2</sup> in west-central Manitoba in 2011. However, extrapolation of these results may be difficult as these areas may be heavily supplemented by influxes of birds from the large lakes of southern Manitoba (Lakes Winnipeg, Manitoba, and Winnipegosis; hereafter “Manitoba Lakes”) in high water years, such as 2011, when many breeding sites may be underwater (McKellar et al. 2021).

The Manitoba Lakes maintain the highest densities of Common Terns of all surveyed boreal areas. Surveys between 1979 and 1999 estimated 20,000 to 30,000 breeding pairs (Nisbet 2002, Morris et al. 2012), two to three times greater than the Great Lakes population (Nisbet 2002, Morris et al. 2012). Reexamination of original survey data suggested slightly lower numbers: between 15,140 and 19,997 breeding pairs, excluding Lake Winnipegosis (Wilson et al. 2014). However, this still represented the largest known inland grouping in North America. This status changed with a comprehensive aerial survey conducted in 2012 that indicated much lower abundances. This survey found a total of 7950 nesting pairs estimated from aerial overflight images, constituting a 57–67% decline in this region within as little as 20 years (Wilson et al. 2014). A follow-up survey conducted in 2017, using similar methods, reported no abatement of this decline for breeding Common Terns in the region (~38% decline in five years over a subset of 23 colonies), and also reported variations in waterbird abundance with lake water levels (McKellar et al. 2021), suggesting a link between nesting numbers and climate-induced changes in flood frequency (Schindler et al. 2012). If this decline continues unchecked, Common Terns may effectively be lost as a breeding species in the Manitoba Lakes within two decades. Given that this is the only lake system, other than the Great Lakes, known to support over 1000 breeding pairs (Arnold et al. 2020), the dramatic and continuing demise of this breeding stronghold for Common Terns requires urgent research and management efforts to understand and reverse these population declines.

Despite the importance of the Manitoba Lakes for inland Common Tern populations, information on breeding success for these colonies is currently limited to a two-year study at a single site that recorded low productivity in the 1980s and attributed this to predation by a Great Horned Owl (*Bubo virginianus*; Hebert 1985). Predation is a common cause of breeding failure for Common Terns, and in inland areas the most common nest predators reported are Black-crowned Night Herons (*Nycticorax nycticorax*), Great Horned Owls, Herring Gulls (*Larus argentatus smithsonianus*), and Ring-billed Gulls (*L. delawarensis*), American mink (*Neovison vison*), red fox (*Vulpes vulpes*), and raccoon (*Procyon lotor*; Cuthbert et al. 2003, Arnold et al. 2020). Other factors often described as important limiting factors of

**Table 1.** Location and characteristics of Common Tern breeding islands/spits and fieldwork dates for the six colonies visited during this study (see Fig. 4 for mapped locations).

Breeding Location	Latitude, Longitude	Selection criteria	Description	Area (ha)	Common Tern colony size (pairs) <sup>†</sup>	Distance from mainland (km)	Distance from human settlement (km)	Other breeding waterbirds <sup>‡</sup>	First visit	Second visit
Mexico Island	52°17'23" N, 98°1'44" W	Within largest regional population center in W Lake Winnipeg	Loose limestone slab, vegetated center	2.80	1,652	11	36		3 July	23 July
Egg Islands	51°55'36" N, 97°4'52" W	Within largest population center in E Lake Winnipeg	Limestone with sandy beaches and marshes	15.60	1,154	13.6	15	RBGU, FRGU	30 June	21 July
McLeod's Island	51°50'22" N, 96°48'4" W	Characteristic shield island	Granite shield island with limestone slab, heavily vegetated	6.50 <sup>§</sup>	452	2.3	5	RBGU, HERG	1 July	22 July
Shoal Islands	50°16'27" N, 97°36'32" W	Small lake colony in inter-lake region	Flooded farmland, mud and gravel	0.25 <sup>‡</sup>	285	0.3 <sup>¶</sup>	8	CATE	5 July	25 July
Riverton Spit	50°59'60" N, 96°54'59" W	Mainland site in S Lake Winnipeg	1.6-km long sand spit, little vegetation	3.25 <sup>§</sup>	73	0	5.5	RBGU	20 July	26 July
Long Point Spit	52°56'10" N, 98°48'42" W	Mainland site in N Lake Winnipeg	5.5-km long sand spit, little vegetation	0.30 <sup>§</sup>	50	0	42		4 July	-

<sup>†</sup>estimated from aerial photos (Wilson et al. 2014), except for Riverton Spit where ground counts were used as no nests were present during aerial overflights; <sup>‡</sup> RBGU: Ring-billed Gull (*Larus delawarensis*), FRGU: Franklin's Gull (*Leucophaeus pipixcan*), HERG: Herring Gull (*Larus argentatus smithsonianus*), CATE: Caspian Tern (*Hydroprogne caspia*); <sup>§</sup> terns nested on a small part of island/spit; <sup>¶</sup> combined size of four islands, largest is 0.17 ha; <sup>‡</sup> in year of study surrounding farmland was flooded to ~0.5–2 m depth

productivity at inland colonies include competition for nesting space with Ring-billed Gulls, vegetation encroachment, and flooding (Courtney and Blokpoel 1983, Cuthbert et al. 2003, McKellar et al. 2021).

Long-term banding records (Haymes and Blokpoel 1978, Cuthbert et al. 2003), results from bird-borne geolocators (Nisbet et al. 2011, Bracey et al. 2018), and genetic analyses of population connectivity (Burson 1990, Szczys et al. 2017) have greatly added to our understanding of migration and movements of Common Terns between breeding colonies within North America (Arnold et al. 2020). Inland-breeding Common Terns show lower site fidelity and increased sub-regional movement than coastal colonies (Haymes and Blokpoel 1978, Burson 1990, Szczys et al. 2017), and movement from the large Atlantic coast colonies to inland regions is rare (Haymes and Blokpoel 1978, Szczys et al. 2017). Emigration of breeding Common Terns from inland regions has been reported for the Great Lakes region, and although some birds have settled in coastal colonies, the majority are unaccounted for (Szczys et al. 2017). Breeders from the Manitoba Lakes may follow the same fall migration routes as Great Lakes birds and their wintering distributions overlap on the west coast of South America, but there is little evidence for overlap across the annual cycle between Manitoba populations and Common Terns breeding on the Atlantic Coast (Szczys et al. 2017, Bracey et al. 2018, Arnold et al. 2020). Furthermore, of the ~1.2 million Common Terns banded outside the Manitoba Lakes only a single bird, banded 250 km to the west, has ever been re-encountered within them (USGS Bird Banding Laboratory 2021). The extent to which loss of inland colonies in population strongholds results from chronic breeding failure, adult mortality away from breeding sites, or emigration, as well as the various drivers affecting each population process, remain uncertain. Estimates of breeding productivity and movement between the Manitoba Lakes populations and other regions are vital steps toward understanding and addressing these losses.

To help address the urgent plight of Common Terns in the Manitoba Lakes, we report detailed data on Common Tern breeding productivity, causes of breeding failure (flooding and predation) and metapopulation connectivity estimated from microsatellite genetic markers collected during ground surveys of six breeding sites throughout the Manitoba Lakes region in 2012 (Table 1). We use these data to provide further insight into breeding status and movements within this important population, detailing (1) estimates of fledging success at each colony; (2) causes of nesting failure; and (3) migration (gene flow) among breeding colonies within the region and also to and from Great Lakes and Atlantic Coast colonies.

## METHODS

The six studied colonies were too remote to be able to visit daily, so fieldwork was completed during two expeditions (27 June to 6 July and 19 to 27 July 2012; Table 1), the timing of which was based on estimates from aerial census (Wilson et al. 2014) photographs taken during the second week of June, to approximate the peak hatching period and immediately prior to the peak fledging period for Common Terns. During the first site visit, we constructed fenced plots for subsequent productivity estimates, deployed remote equipment to detect causes of nest failure, and took blood samples for genetic analysis of population connectivity and dispersal. During the follow-up visit, we assessed productivity in plots and by whole-colony fledgling counts and then removed all fences and equipment. We found that the colony on Long Point Spit had been abandoned earlier in the season, so we did not make a second visit to this site and simply examined field signs (condition of eggs, evidence of predator presence, etc.) during our first visit. No nests were recorded at Riverton Spit during the aerial census and thus this site was not visited or fenced during the initial field effort. However, during an opportunistic site visit on 20 July, active nests were recorded and we returned on 26 July to evaluate their status.

## Productivity estimates

At each site except Long Point Spit and Riverton Spit, we individually fenced between eight and 11 study nests within habitat representative of the majority of the breeding colony. Fenced plots are necessary to follow survival of mobile, semi-precocial tern chicks and are commonly employed in colony-based studies (e.g., Nisbet and Drury 1972, Arnold et al. 2016) and have been found not to bias productivity estimates (Hall and Kress 2004). Occasionally, if substrate prevented individual enclosures, multiple nests (two to three) were fenced within the same enclosure. Only active nests with complete clutches (three eggs/chicks in all but one case) that were close to hatching (preferably, at least one chick younger than two days of age) were selected. If signs of hatching (chick, pipped or starred eggs) were not visible we determined incubation stage using egg floatation (Hays and LeCroy 1971). All hatched chicks within fenced enclosures were banded with standard USGS, incoloy leg bands. Fenced enclosures were not used at Riverton Spit because we did not want to draw attention to sensitive breeding areas, given that this site is often used for recreation.

Fences were 2 feet high, 0.5 inch mesh, poly hardware cloth (<http://homehardware.ca>, Quest Brands, item #5258963), with 16-GA wire threaded through the upper perimeter for stability and attached by zip ties to 1 × 1 inch wooden posts hammered into the ground (Fig. 1). Fences were either dug 2–4 inches into the ground or, for hard substrates, weighed down by being zip-tied to stones piled around the base to prevent the escape of chicks (Fig. 1). All fences were at least 0.5 m distant from each study nest, providing a minimum of 0.8 m<sup>2</sup> potential nesting territory, larger than the typical nesting territory (mean nesting Common Tern density ranges between 0.06 and 0.5 nests/m<sup>2</sup>; Arnold et al. 2020). Teepee-style chick shelters (made from two 1 × 1 foot plywood boards) were provided for all study nests in each enclosure. Shelters are only used by chicks when insufficient cover is present (McGowan et al. 2018) and nearly all our sites provided vegetative cover. However, because fences preclude adults from moving their young to more sheltered locations, providing shelters is important when studying conservation-important populations.

**Fig. 1.** Examples of fenced nest enclosures constructed on different substrates: (A) a single nest in soft substrate (mud, sand, soil, or gravel), and (B) multiple nests in hard substrate (rock or cobble). In both cases, to prevent possible escape of chicks from enclosures, material (e.g., mud or rocks) was piled against the base of fences, especially if fences could not be dug in.



During our second visit to the site, we recorded all chicks within these fenced plots, estimated their age using a morphometric photographic tool (Wails et al. 2014), and weighed them by using appropriate spring balances to determine chick health based on mass (Wails et al. 2014, Arnold et al. 2016). We also searched plots thoroughly for any egg or chick remains. Productivity for each study nest was calculated in two ways: the number of chicks that survived to (1) 11 d or (2) 18 d old (closer to true fledging age: 22+ d, Arnold et al. 2020).

For a broader estimate of productivity at all sites except Long Point Spit, we performed whole-island nest counts, counting the number of nests during our first visit and the number of chicks 11+ d old and fledging age (18+ d) during the second visit. Whole-colony productivity was then calculated as follows: # fledglings / (# nests × mean clutch size). Clutch size was estimated at 2.9 (Arnold et al. 2020) to standardize it across study sites and # fledglings was either number of chicks 11+ d of age or number of chicks 18+ d of age to produce two different comparable estimates to the fenced-enclosure method.

We analyzed the relationship between distance to human settlement or colony size and estimated productivity using linear regression in R (R Development Core Team 2021). Because colony size was strongly correlated with distance to human settlement (Spearman rank correlation:  $\rho = 0.83$ ,  $P < 0.001$ ), these were analyzed in separate models. This analysis was only undertaken on whole-colony counts because of the inadequate sample size of colonies at which plots were fenced.

## Causes of breeding failure

On each visit, we undertook detailed searches in parts of large colonies and throughout small colonies for evidence of predation, such as field signs on predated eggs, or remains of adults or chicks. During our first visit, we also set up automated methods to record timing and causes of nest desertion and predation. To examine evidence of desertion caused by flooding, we used boulders or tent pegs to secure a lidded, 7-cup kitchen storage container to the ground within a nesting area at each site. The container had small holes in the sides, ~100 mm above ground level, such that extensive flooding (but not rain) resulted in the collection of floodwater and consequent staining of the inside of the container.

We also mounted motion-sensitive, infrared trail cameras (Bushnell Trophy Cam HD Max 119576C, Overland Park, Kansas, USA) to overlook large sections of breeding colonies, including fenced enclosures, to identify types of predators and evidence of flooding at the colonies. Cameras were either mounted on 1 m-high, 1 × 1 inch wooden stakes or on sturdy branches, where necessary. In addition to motion-sensitive triggering, cameras also recorded time-lapse images every 1 h regardless; all triggered events took three sequential images. Cameras ran continuously between the two visits made to study colonies. All images were reviewed for evidence of predation or flooding.

## Population connectivity and gene flow

At all sites (except Long Point Spit), we collected small (< 50  $\mu$ g) blood samples from 17–28 unrelated Common Tern chicks by pricking the femoral vein with a hypodermic needle and collecting blood in capillary tubes (Szczyz et al. 2005, 2017). To avoid

**Table 2.** Mean ( $\pm$  SD) productivity for Common Terns (*Sterna hirundo*) at the six study colonies, estimated as the number of chicks either reaching 11 or 18 days of age. Productivity was estimated in two different ways: either for fenced nests in multiple study plots or by whole colony counts. Predators were detected either by trail cameras (on the number of days indicated) or from field signs (common name is given for mammalian predators, alpha code for avian predators: BCNH = Black-crowned Night Heron, *Nycticorax nycticorax*, BAEA = Bald Eagle, *Haliaeetus leucocephalus*, GHOW = Great Horned Owl, *Bubo virginianus*).

Colony	11 d Productivity (Fenced)	11 d Productivity (Island Count)	18 d Productivity (Fenced)	18 d Productivity (Island Count)	Predators recorded	
					Camera (# days)	Field Signs
Mexico Island	1.38 $\pm$ 1.3	1.64	1.33 $\pm$ 1.51	1.57	-	BCNH, BAEA
Egg Islands	2.33 $\pm$ 1.12	0.58	2.00 $\pm$ 1.41	0.12	-	-
McLeod's Island	0.24 $\pm$ 0.28	0.46	0.00 $\pm$ 0.00	0.46	BAEA (5)	BCNH, river otter
Shoal Islands	0.75 $\pm$ 0.89	0.54	0.40 $\pm$ 0.89	0.54	BCNH (7), GHOW (1)	
Riverton Spit	-	0.04	-	0.01		BAEA <sup>†</sup> , domestic dog <sup>‡</sup>
Long Point Spit	-	-	0	0		gray wolf

<sup>†</sup> Remains of Herring Gull (*Larus argentatus*) found that was indicative of a kill by a large raptor, possibly an eagle or Peregrine Falcon (*Falco peregrinus*)

<sup>‡</sup> Tracks may result from human recreational use, rather than predation

sampling siblings, we chose nestlings that were still clearly associated with a specific nest, mostly chicks < 2 d of age.

Genotypes for a total of 132 individuals were obtained for six microsatellite markers: RBG 13, 27, and 28 (Given et al. 2002), AAT 20 and 27, and AAC 20 (Szczyz et al. 2005), following methods of Szczyz et al. (2012). We combined this new Manitoba Lakes dataset with data from the 12 Common Tern colonies within inland and coastal North America reported by Szczyz et al. (2017). Replicating the approach of Szczyz et al. (2017), we used estimates of  $F_{ST}$ , Jost's D, and Bayesian Clustering Analysis (STRUCTURE 2.3.4; Pritchard et al. 2000) to estimate population differentiation and the number of genetic clusters in the data. Cluster analysis was repeated to control for sampling unevenness across regions (Meirmans 2019). To examine contemporary gene flow between colonies we used BAYESASS 3.3 (Wilson and Rannala 2003) to infer  $m$ , the proportion of a population consisting of individuals from another population, per generation. These methods assume low migration rates, so if migration rates are high (e.g.,  $F_{ST}$  roughly < 0.05; Table A1.2), migration can change allele frequencies in the population quickly so estimates of non-migrant ancestry must exceed 67% (Tables A1.3A and A1.5A) to ensure accuracy. To estimate the historical mutation-scale migration rate we used Migrate-n (Beerli 2006) and converted values to effective migration rate for comparison with contemporary estimates. In this case, contemporary time periods represent two to three generations (since ~1990, based on a generation time of 10 years; Sæther et al. 2013) and historical time represents > five generations (prior to ~1960). These two analyses were implemented as in Szczyz et al. (2017), except that we undertook regional analysis by grouping colonies into either Manitoba Lakes (data from current study), Inland, or Coastal (the latter two as described in Szczyz et al. [2017]) and did not further subdivide into sub-regions. Sampling fewer sites and more individuals per site increases precision of both contemporary and historical estimates. Initially, we ran this regional analysis twice, once with the boreal Ontario site Lake St. Joseph designated as inland, and once with it combined instead with the Manitoba Lakes. Because the results indicated the most parsimonious combination was to combine Lake St. Joseph with the Manitoba Lakes, we report those here, although the alternative analysis

yielded similar conclusions. Finally, we also used these same contemporary and historical dispersal analytical approaches to look at local gene flow among the five sites sampled within Manitoba Lakes (not including Lake St. Joseph).

## RESULTS

### Productivity estimates

Productivity estimates for sites visited ranged from a mean of 0.0 to 2.3 chicks surviving to 11 days per nest and 0.0 to 2.0 chicks surviving to 18 days per nest (Table 2). Productivity estimates using fenced plots (Fenced) generally agreed with those estimated by counting fledglings across the whole colony (Island Counts). There were two exceptions: at McLeod's Island, where 18-day counts were much higher for whole-colony counts, and at Egg Islands, where fenced plot estimates suggested this colony was the most productive (2.0 chicks per nest) but whole colony counts implied that it was one of the least productive (0.12 chicks per nest).

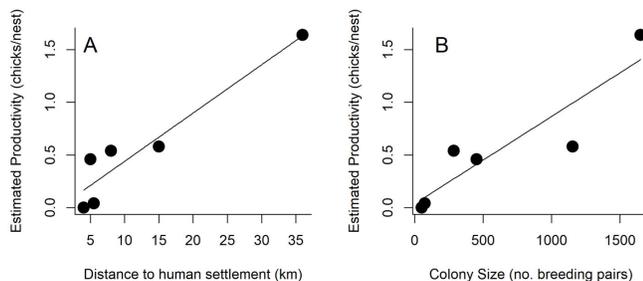
Despite the small number of colonies studied, productivity estimated from whole-island counts increased with distance to human settlement (11-d estimates:  $F_{1,4} = 37.1$ ,  $P < 0.01$ , 18-d estimates:  $F_{1,4} = 12.9$ ,  $P < 0.05$ , Fig. 2). Distance to human settlement was correlated with colony size, so there were similar positive relationships with 11-d productivity estimates ( $F_{1,4} = 18.8$ ,  $P < 0.05$ ) but no relationship with 18-d estimates ( $F_{1,4} = 5.1$ ,  $P = 0.09$ ) because of the low, 18-d whole-colony productivity for Egg Islands (Table 2). Sample sizes for colonies with fenced plots were too small to permit analyses, but productivity trends were similar (Table 2).

### Causes of breeding failure

Predation was recorded at five of the six Common Tern colonies studied and it led to wide-spread nesting failure for terns at two sites, Riverton Spit and Long Point Spit (Table 2). The most common predators of terns were Bald Eagles (*Haliaeetus leucocephalus*) and Black-crowned Night Herons (Table 2). We recorded three novel predators for Common Terns, previously absent from the literature (Arnold et al. 2020): Bald Eagle, gray wolf (*Canis lupus*), and river otter (*Lontra canadensis*). At

McLeod's Island, both immature and adult Bald Eagles were repeatedly photographed feeding on Common Tern chicks in flocks of up to six birds, and we found remains of > 100 pre-fledged chicks (~16 d or older) scattered around the colony on 22 July. Although a pair of Bald Eagles nested among the Common Terns on Mexico Island, we also disturbed 10 eagles feeding on Common Tern chicks in a different part of the island on 23 July. We found extensive tracks of gray wolves (likely an adult and subadult) and predated Common Tern eggs with distinctive teeth marks at Long Point Spit on 4 July. The colony had been abandoned and all intact eggs were cold but appeared to be recently laid, i.e., there was no sun-bleaching of shell color. Because this is too late in the season to be a first breeding attempt it is likely that these were replacement clutches laid by birds that had attempted to breed here earlier in the summer. We observed a river otter taking young chicks and eggs of Common Terns on 1 July at McLeod's Island. From the behavior of the otter and the terns that were dive-bombing it aggressively, it appeared that this was not the first time this predator had been in the colony.

**Fig. 2.** Effect of (A) distance to nearest human settlement and (B) Common Tern (*Sterna hirundo*) colony size on productivity across six colonies within the Manitoba Lakes. Productivity data shown are the number of Common Tern chicks surviving to 11 d of age, calculated from whole colony counts divided by estimated clutch size. Points indicate individual colonies. Lines are predictions from separate, significant linear regressions.



Flooding was only detected by flood buckets and cameras at the Shoal Islands, where it caused desertion of many nests; however, we also found washed-out nests at both Mexico Island and Riverton Spit. Extensive vegetation growth likely led to premature abandonment of nests in a silty depression on Mexico Island where ~15 pairs of Common Terns nested, but not for study nests at any other sites. Human disturbances were recorded at Riverton Spit (for recreation, including extensive ATV tracks), Long Point Spit (flotsam and jetsam from a nearby fishing launch), and McLeod's Island (people recorded by trail cameras on one occasion).

### Population connectivity and gene flow

Indices of genetic diversity for Common Terns breeding in Manitoba were similar to Inland and Coastal breeders (Supplementary Material, Table A1.1; Szczys et al. 2017). Two genetic clusters (Fig. 3) were identified by all estimates of population structure (Table A1.2), whereby Manitoba Lakes are more similar to the Great Lakes than to the Atlantic Coast.

Asymmetrical contemporary migration was detected out of the Great Lakes colonies to Manitoba Lakes and to the Atlantic Coast (Fig. 3; Szczys et al 2017). Further, contemporary migration

rates were much higher out of the Great Lakes into Manitoba over the last 20 to 30 years (contemporary time) compared to the low and symmetrical movements historically (Fig. 3).

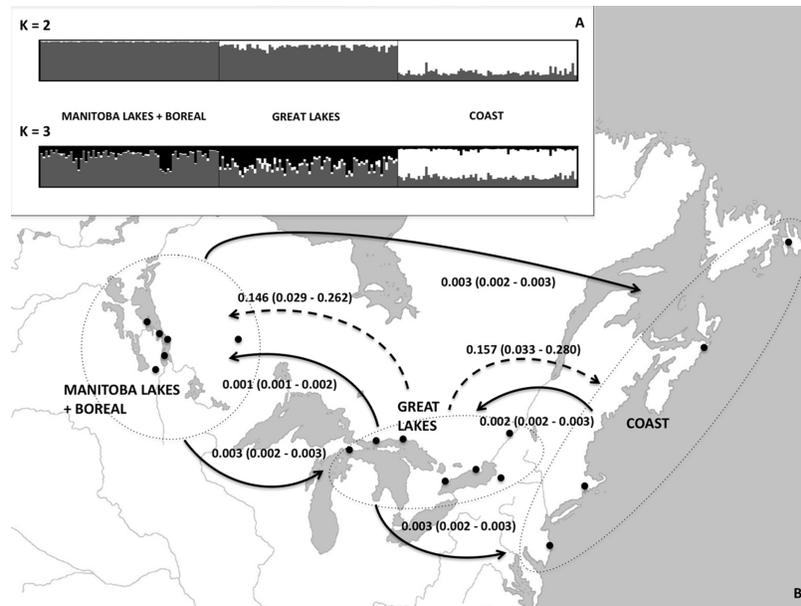
Within Manitoba, colonies exhibited relatively low levels of population genetic structure (Table A1.4). This corresponds with the high, asymmetrical rates of movement (mean = 0.179) among some colonies detected in contemporary time periods within Manitoba Lakes (Fig. 4) but contrasts to low and symmetrical migration rates (mean = 0.002) in historical time periods (Table A1.5).

## DISCUSSION

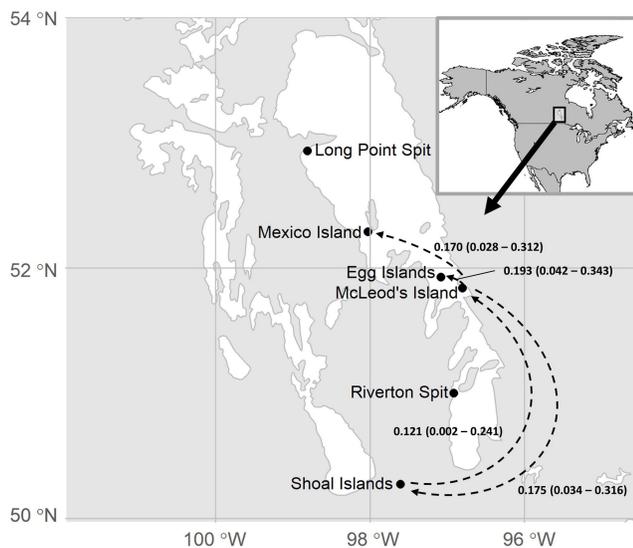
Only two Common Tern population strongholds in inland North America have been surveyed regularly enough to determine numerical trends: the Laurentian Great Lakes (including the St. Lawrence River) and the large Manitoba Lakes. Abundance is lower in other lake and river systems (each < 1000 breeding pairs; Arnold et al. 2020) and, although much of Canada's extensive boreal forest remains unsurveyed, results from existing survey efforts suggest much lower population densities across this bioregion. The Great Lakes populations (9223 nesting pairs in 2010; Morris et al. 2012) have been declining since the 1970s (Morris et al. 2010, 2012), leading to extensive management efforts to restore and protect Common Tern colonies (Arnold et al. 2020). Although the Manitoba Lakes supported more breeding Common Terns than any other inland region in prior status assessments (Nisbet 2002), breeding numbers declined by 57–67% to 7950 pairs between the 1990s and 2012 (Wilson et al. 2014). This trend continues unabated (a further 38% decline within the same survey area, 5313 breeding pairs recorded throughout the region in 2017; McKellar et al. 2021) but without eliciting the same management efforts. By examining breeding productivity and connectivity of terns in this region, our study represents a first, vital step toward understanding and addressing this decline.

Population declines in breeding areas must result from emigration, adult mortality, and/or chronic breeding failure. Our data indicate high productivity (up to two chicks fledged per nest) at large, remote colonies in the Manitoba Lakes but poor success and colony-wide breeding failure at small colonies close to the mainland. Thus, at least in the year of this study, breeding failure on a regional scale was not evident. However, because this represents a single annual snapshot, we cannot rule out that low productivity has prevailed in other years, or continues to do so. As is common for waterbird surveys (Green et al. 2008, Wilson et al. 2014) our estimates are for peak-nesting individuals, and we also limited study nests to those that survived to hatch the modal clutch of three chicks. These generally comprised the majority of nests at Common Tern colonies and in the year of study we have no reason to suspect that our productivity estimates are not representative of the majority of birds breeding at each colony. Although our data provide some hope that Common Terns are achieving adequate breeding success in the region, they are now almost 10 years old and further regular monitoring of breeding productivity is required to conclude that population declines are not the result of ongoing breeding failure. Given that many colonies are difficult to access, monitoring could make use of mid-July fledgling counts from ground surveys (to a subset of colonies) that coincide with survey efforts for other colonial waterbirds in these lakes.

**Fig. 3.** Regional population genetic structure: (A) Manitoba Lakes Common Tern (*Sterna hirundo*) colonies cluster with Great Lakes colonies, and (B) contemporary migration (two to three generations; dashed arrows) among regions is 100x greater than historical migration (> five generations; solid arrows) and limited to movement out of the Great Lakes compared to near-isolation historically. Values represent the proportion of individuals in a population with immigrant ancestry per generation.



**Fig. 4.** Population genetic structure among Common Tern (*Sterna hirundo*) colonies within the Manitoba Lakes (dashed lines indicate non-zero, contemporary migration rates). High rates of migration were largely asymmetrical among colonies during the contemporary time period (last two to three generations). Historical (> five generations) migration among colonies was low (pair-wise estimates range from 0.002 to 0.004; see Table A1.5). No samples were available for Long Point Spit.



Poor productivity in our study was largely due to predation by birds or mammals, although on low-lying islands, such as the Shoal Islands, nests were also abandoned after flooding. These scattered islets were not the historical nesting areas in the Shoal Lakes and were likely used in 2012 because water levels were still above normal following extensive floods in 2011. This site was also visited by Black-crowned Night Herons and Great Horned Owls, both common predators that are known to cause widespread breeding failure at tern colonies in inland regions (Hunter and Morris 1976, Cuthbert et al. 2003, Arnold et al. 2020). Bald Eagles were also observed preying on tern chicks at several sites, which has not been reported previously for Common Terns in the literature, although they have recently been witnessed preying on eggs of Aleutian Terns (*Onychoprion aleuticus*; Corcoran et al. 2018) and adult Caspian Terns (*Hydroprogne caspia*; Collar et al. 2017). This may simply represent underreporting in the literature, because eagle populations have increased dramatically in recent years along most of the east coast of North America, where the majority of research on Common Terns has been conducted. In our study, flocks of up to 10 eagles were recorded preying on tern chicks, suggesting that this may not simply be the action of specialized birds nesting close to the colony. Interestingly, the largest Common Tern colony studied (Mexico Island, 1652 pairs) also supported a nesting pair of eagles, as well as evidence of Black-crowned Night Heron predation, and yet still achieved moderately high productivity. Mammalian predators included river otter and gray wolf, neither of which have been previously reported to prey on terns, although river otters have been observed preying on Arctic Terns (*Sterna paradisaea*; Duffy 1995).

Our data on productivity and causes of breeding failure are the first multi-site data for this region, the only other being a study of a single colony (now abandoned) in Lake Manitoba in the 1980s, where Great Horned Owls were found to be reducing tern productivity (Hebert 1985). In our study, Common Tern breeding success was highest at sites far from human settlements (where the colonies were large) and lowest at sites physically connected to the mainland (sandy spits). Because only six colonies were studied, we cannot distinguish between the influence of colony size and remoteness on breeding success. There was no evidence of predator activity at the Egg Islands, presumably a result of remoteness, yet the larger colony at Mexico Island, although almost as remote from human settlement, was visited by predators but was able to withstand predation by both eagles and night herons without extensive colony abandonment. We hypothesize that human disturbance and predation, especially from mammalian predators, was responsible for complete colony failure at the two spit sites studied.

Common Tern chicks generally fledge between 22 and 29 days of age (Arnold et al. 2020). We recorded survival to 18 d as an index of fledging within fenced plots, because it was not logistically possible to record survival to fledging age, but mortality after 18 d is comparatively low (Arnold et al. 2020) and the degree of concordance between our 18-d estimate and counts of all fledglings observed at a colony suggest that this provides a good estimate of productivity. There were cases where these two measurements differed: whole colony fledgling counts gave much lower estimates for Egg Islands, and higher estimates for McLeod's Island than survival in fenced plots (Table 2). Egg Islands was a large island chain, well-vegetated and swampy in places with many places where fledglings could hide or fly to, out of sight of investigators. It is also possible that the plots chosen, in the consolidated vegetation at the center of the island, were occupied by higher quality breeders than those in other areas, such as the sandy and swampy locations. Bald Eagles decimated the colony at McLeod's Island, and only early-hatched chicks, that fledged prior to the eagles' arrival, survived. Although all chicks in plots were predated, these early-fledged chicks were still roosting around the island during our second visit.

Our analysis of microsatellite markers indicated that during contemporary time periods (1990s–2012) population structure was low, with terns moving between some colonies (Fig. 3). This movement is generally from small to large colonies, but there was symmetrical exchange between Shoal Lake and McLeod's Island and no discernible movement from/to Riverton Spit. We interpret large colonies as being most attractive for nesting, especially given their high productivity, and that terns unable to secure breeding territories at large colonies attempt (and often fail) to breed successfully at smaller colonies and frequently switch between these locations in response to predation or flooding. Interestingly, inter-colony movement was estimated to be much lower and symmetrical during historical (i.e., before 1960) time periods, suggesting that dynamics between colonies have changed recently. This situation matches that at a regional scale, whereby migration was low and symmetrical between the Great Lakes and Manitoba Lakes historically, but over the past 20 years immigration of terns from the Great Lakes to our Manitoba colonies increased over 100-fold. Szczys et al. (2017) detected increased emigration from the Great Lakes to the Atlantic Coast during this same time period

and suggested that degradation of habitat due to human development was driving this exodus.

Our finding of significant contemporary gene flow from the Great Lakes to Manitoba is the first strong evidence that population declines in the Great Lakes have also included losses from westward emigration: despite ~1.2 million Common Terns banded in North America to date (D. Bystrak, *personal communication*), there are insufficient reencounters in the Manitoba Lakes (three to date; USGS Bird Banding Laboratory 2021) to estimate emigration from banding data. This is likely on account of the relatively sparse recapture efforts in the Manitoba Lakes. Although our results suggest a potential mechanism behind Great Lakes population declines, losses from the Great Lakes (~5000–6000 nests between 1960 and 2010; Morris et al. 2010) are smaller than the population increases in the Manitoba Lakes prior to 2000 (~10,000–15,000 nests; Morris et al. 2012, Wilson et al. 2014, McKellar et al. 2021). Also, maximal losses from the Great Lakes occurred 20–30 years before the growth of the Manitoba Lakes populations (1960–1970s; Courtney and Blokpoel 1983, Morris et al. 2010). Even so, the Manitoba populations have now declined precipitously and are still in decline despite the contemporary immigration from the Great Lakes that we report. Thus, population declines in Manitoba comprise both loss of birds from this region and immigrants from other inland regions, indicating that these are net losses for inland-breeding populations rather than simply between-region movements. Such losses may lead to genetic erosion for Common Terns in the Manitoba Lakes, and so genetic monitoring should be implemented. This could build upon our results and would be feasible after further colony surveys, ideally every two to three generations. Tissue sampling from as few as 24 random individuals per colony could provide reliable estimates of changes in allelic diversity, a key metric of genetic diversity (Hoban et al. 2014), and differentiation over time (Hale et al. 2012).

Anthropogenic eutrophication from livestock farming in the region increased primary productivity of Lake Winnipeg throughout most of the 20th century (Schindler et al. 2012), which may have increased some forage fish populations. Common Terns are known to forage successfully in shallow, eutrophic waters (Pinkowski 1980, Arnold et al. 2020), and this may have made Lake Winnipeg attractive to nesting terns. Since the 1990s, however, the lake has entered a new regime, with seasonal blooms from nitrogen-fixing, cyanobacteria (Kling et al. 2011, Bunting et al. 2016). During this time, Common Tern populations in the Manitoba Lakes exhibited a 57–67% decline (Wilson et al. 2014) to the year of our study (2012) and this has not slowed since (McKellar et al. 2021). The remaining, large colonies are now still found in productive areas of the lake but only where such blooms are less common, e.g., Mexico Island, Egg Islands (Fig. 4; Binding et al. 2018), suggesting that this, as well as major floods in recent years (1997, 2005, 2009, 2011; Schindler et al. 2012) may cause returning birds to settle further north (McKellar et al. 2021) and may therefore partially explain the large decline in abundance of nesting Common Terns recorded in the last decade (Wilson et al. 2014, McKellar et al. 2021). However, in addition to scant information on productivity, without sufficient data on return rates of Common Terns breeding in the Manitoba Lakes, it is not possible to rule out extensive adult mortality as the cause of population declines. Because this would reflect a continent-wide

population decline, rather than a geographical change in distribution, such studies are urgently required. Currently, only a single study of migration between 2015 and 2017 in this region exists (Bracey et al. 2018). In this study, archival light-level geolocators were attached to 30 breeding Common Terns and 30 control birds were fitted with only color bands at the Egg Islands. In both cases, 10/30 were recovered or resighted in a subsequent year at the colony. This suggests only ~30% return rate but it is not possible to infer adult survival from this because of the possibility of emigration. A potential future approach to estimate survival and movement of Common Terns, both within the Manitoba Lakes system and beyond, might be marking breeding adults with band-mounted radiotags together with the establishment of Motus towers within the Manitoba Lakes region. With calibration for radiotag lifespan (up to three years), this effort would allow for the estimation of movement within and between breeding seasons as well as seasonal and annual survival when marked individuals are detected by towers across the extensive Motus network in North America (Taylor et al. 2017).

## CONCLUSION

At more than 5000 breeding pairs in 2017 (McKellar et al. 2021), the Manitoba Lakes Common Tern population is the second largest inland population surveyed to date and remains of key conservation importance. We hypothesize that widespread changes in lake ecology such as eutrophication, invasive species, increased flooding, and climatic change (Schindler et al. 2012, Shrestha et al. 2012, Depew et al. 2020) within the Manitoba Lakes are marginalizing breeding habitat for Common Terns. Thus, Common Terns are being adversely affected by human activities within the Manitoba population strongholds, a conclusion similar to that reached by Szczys et al. (2017) concerning population declines in the Great Lakes. We advocate continued, regular census efforts (e.g., McKellar et al. 2021), studies of adult survival within the region, and monitoring productivity at major colonies, e.g., Mexico Island and Egg Islands, to distinguish between possible drivers of these declines, track population trends, and inform potential management solutions. Given that we did not detect eastward movement of Common Terns from the Manitoba Lakes, any emigrating birds are most likely dispersing to the boreal regions to the north or west (Wilson 2013, McKellar et al. 2021). Although surveys have occurred in some boreal locations, these report much lower numbers in these less nutrient-rich systems than either the Great Lakes or Manitoba Lakes (Arnold et al. 2020). Thus, emigrating birds are being pushed into likely more marginal habitat, at a time when boreal habitats themselves are under broad-scale threats from increasing human activity and climate change (Schindler and Lee 2010). Most survey data for Common Terns in boreal areas are now several decades old (e.g., Stelfox and Brewster 1979, Sirois et al. 1995) and so the status of these populations is largely unknown.

The extensive population declines for Common Terns evident in monitored inland regions are worrying and, although birds may be moving to remote boreal lakes, we cannot assume this is the case: declines could be occurring throughout inland Canada. Broad aerial surveys across boreal areas of Canada (such as those in boreal Ontario in 2011–2012; D. J. Moore, D. V. C. Weseloh, R. Weeber, *personal communication*, reported in Arnold et al. 2020) are therefore urgently required. These surveys also offer

opportunities for partnership with local communities and First Nations in these areas and echo the Government of Canada's current environmental pledges (Government of Canada 2021). Additional repeat surveys, either aerial or ground efforts, of important boreal lakes, including the Manitoba Lakes, are required to provide a continental perspective on declines for Common Terns throughout inland North America. Finally, research on survival, movement, and productivity within and among regions is needed to identify the drivers and extent of population declines. Without all these initiatives, the significance of continuing losses within the Manitoba Lakes and the status of inland populations across North America will remain unknown.

*Responses to this article can be read online at:*  
<https://www.ace-eco.org/issues/responses.php/2067>

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## LITERATURE CITED

- Amano, T., T. Székely, B. Sandel, S. Nagy, T. Mundkur, T. Langendoen, D. Blanco, C. U. Soykan, and W. J. Sutherland. 2018. Successful conservation of global waterbird populations depends on effective governance. *Nature* 553:199-202. <https://doi.org/10.1038/nature25139>
- Arnold, J. M., I. C. T. Nisbet, and S. A. Oswald. 2016. Energetic constraint of non-monotonic mass change during offspring growth: a general hypothesis and application of a new tool. *Journal of Animal Ecology* 85(2):476-486. <https://doi.org/10.1111/1365-2656.12467>
- Arnold, J. M., and S. A. Oswald. 2013. First confirmed record of a Common Tern *Sterna hirundo* breeding at one year of age. *Bird Study* 60(2):275-279. <https://doi.org/10.1080/00063657.2013.768590>
- Arnold, J. M., S. A. Oswald, I. C. T. Nisbet, P. Pyle, and M. A. Patten. 2020. Common Tern *Sterna hirundo*, version 1.0. In S. M. Billerman, editor. *Birds of the World*. Cornell Lab of Ornithology, Ithaca, New York, USA. <https://doi.org/10.2173/bow.comter.01>
- Berli, P. 2006. Comparison of Bayesian and maximum-likelihood of population genetic parameters. *Bioinformatics* 22(3):341-345. <https://doi.org/10.1093/bioinformatics/bti803>

- Binding, C. E., T. A. Greenberg, G. McCullough, S. B. Watson, and E. Page. 2018. An analysis of satellite-derived chlorophyll and algal bloom indices on Lake Winnipeg. *Journal of Great Lakes Research* 44(3):436-446. <https://doi.org/10.1016/j.jglr.2018.04.001>
- Bracey, A., S. Lisovski, D. Moore, A. McKellar, E. Craig, S. Matteson, F. Strand, J. Costa, C. Pekarik, P. Curtis, G. Niemi, and F. Cuthbert. 2018. Migratory routes and wintering locations of declining inland North American Common Terns. *Auk* 135(3):385-399. <https://doi.org/10.1642/auk-17-210.1>
- Bunting, L., P. R. Leavitt, G. L. Simpson, B. Wissel, K. R. Laird, B. F. Cumming, A. St. Amand, and D. R. Engstrom. 2016. Increased variability and sudden ecosystem state change in Lake Winnipeg, Canada, caused by 20th century agriculture. *Limnology and Oceanography* 61(6):2090-2107. <https://doi.org/10.1002/lno.10355>
- Burson, S. L. 1990. Population genetics and gene flow of the Common Tern. *Condor* 92(1):182-192. <https://doi.org/10.2307/1368397>
- Collar, S., D. D. Roby, and D. E. Lyons. 2017. Top-down and bottom-up interactions influence fledging success at North America's largest colony of Caspian Terns (*Hydroprogne caspia*). *Estuaries and Coasts* 40:1808-1818. <https://doi.org/10.1007/s12237-017-0238-x>
- Corcoran, R. M., S. Studebaker, and R. A. Macintosh. 2018. Aleutian Tern *Onychoprion aleuticus* colony abandonment in response to Bald Eagle *Haliaeetus leucocephalus* nest predation. *Marine Ornithology* 46:113-115. [online] URL: [http://www.marineornithology.org/PDF/46\\_2/46\\_2\\_113-115.pdf](http://www.marineornithology.org/PDF/46_2/46_2_113-115.pdf)
- Courtney, P. A., and H. Blokpoel. 1983. Distribution and numbers of Common Terns on the lower Great Lakes during 1900-1980: a review. *Colonial Waterbirds* 6:107-120. <https://doi.org/10.2307/1520977>
- Cuthbert, F. J., L. R. Wires, and K. Timmerman. 2003. Status assessment and conservation recommendations for the Common Tern (*Sterna hirundo*) in the Great Lakes Region. U.S. Department of the Interior, Fish and Wildlife Service, Ft. Snelling, Minnesota, USA. [online] URL: <https://www.fws.gov/midwest/es/soc/birds/pdf/cote-sa03.pdf>
- Depew, D. C., E. Krutzemann, K. E. Watchorn, A. Caskenette, and E. C. Enders. 2021. The distribution, density, and biomass of the zebra mussel (*Dreissena polymorpha*) on natural substrates in Lake Winnipeg 2017-2019. *Journal of Great Lakes Research* 47(3):556-566. <https://doi.org/10.1016/j.jglr.2020.12.005>
- Duffy, D. C. 1995. Apparent river otter predation at an Aleutian tern colony. *Colonial Waterbirds* 18(1):91-92. <https://doi.org/10.2307/1521402>
- Fox, G. A. 1976. Eggshell quality: its ecological and physiological significance in a DDE-contaminated common tern population. *Wilson Bulletin* 88:459-477. <https://sora.unm.edu/sites/default/files/journals/wilson/v088n03/p0459-p0477.pdf>
- Gilbertson, M., R. D. Morris, and R. A. Hunter. 1976. Abnormal chicks and PCB residue levels in eggs of colonial birds on the Lower Great Lakes (1971-73). *Auk* 93:434-442. [online] URL: <https://sora.unm.edu/sites/default/files/journals/auk/v093n03/p0434-p0442.pdf>
- Given, A. D., J. A. Mills, and A. J. Baker. 2002. Isolation of polymorphic microsatellite loci from the Red-billed Gull (*Larus novaehollandiae scopulinus*) and amplification in related species. *Molecular Ecology Notes* 2(4):416-418. <https://doi.org/10.1046/j.1471-8286.2002.00261.x>
- Government of Canada. 2021. Canada's nature legacy: protecting our nature. Government of Canada, Ottawa, Canada. [online] URL: <https://www.canada.ca/en/services/environment/conservation/nature-legacy.html>
- Green, M. C., M. C. Luent, T. C. Michot, C. W. Jeske, and P. L. Leberg. 2008. Comparison and assessment of aerial and ground estimates of waterbird colonies. *Journal of Wildlife Management* 72(3):697-706. <https://doi.org/10.2193/2006-391>
- Hale, M. L., T. M., Burg, and T. E. Steeves. 2012. Sampling for microsatellite-based population genetic studies: 25 to 30 individuals per population is enough to accurately estimate allele frequencies. *PLoS ONE* 7(9):e45170. <https://doi.org/10.1371/journal.pone.0045170>
- Hall, C. S., and S. W. Kress. 2004. Comparison of Common Tern reproductive performance at four restored colonies along the Maine coast, 1991-2002. *Waterbirds* 27:424-433. [online] URL: [https://bioone.org/journals/waterbirds/volume-27/issue-4/1524-4695\\_2004\\_027\\_0424\\_COCTRP\\_2.0.CO\\_2/Comparison-of-Common-Tern-Reproductive-Performance-at-Four-Restored-Colonies/10.1675/1524-4695\(2004\)027\[0424:COCTRP\]2.0.CO;2.full](https://bioone.org/journals/waterbirds/volume-27/issue-4/1524-4695_2004_027_0424_COCTRP_2.0.CO_2/Comparison-of-Common-Tern-Reproductive-Performance-at-Four-Restored-Colonies/10.1675/1524-4695(2004)027[0424:COCTRP]2.0.CO;2.full)
- Haymes, G. T., and H. Blokpoel. 1978. Seasonal distribution and site tenacity of the Great Lakes Common Tern. *Bird-Banding* 49(2):142-151. <https://doi.org/10.2307/4512344>
- Hays, H., and M. LeCroy. 1971. Field criteria for determining incubation stage in eggs of the Common Tern. *Wilson Bulletin* 83:425-429. [online] URL: <https://sora.unm.edu/sites/default/files/journals/wilson/v083n04/p0425-p0429.pdf>
- Hébert, P. N. 1985. Breeding failure and decline of a Common Tern colony in southern Manitoba. *Colonial Waterbirds* 8(2):183-185. <https://doi.org/10.2307/1521070>
- Hoban S., J. A. Arntzen, M. W. Bruford, J. A. Godoy, A. Rus Hoelzel, G. Segelbacher, C. Vilà, and G. Bertorelle. 2014. Comparative evaluation of potential indicators and temporal sampling protocols for monitoring genetic erosion. *Evolutionary Applications* 7(9):984-998. <https://doi.org/10.1111/eva.12197>
- Hunter, R. A., and R. D. Morris. 1976. Nocturnal predation by a Black-crowned Night-Heron at a Common Tern colony. *Auk* 93:629-633. [online] URL: <https://sora.unm.edu/sites/default/files/journals/auk/v093n03/p0629-p0633.pdf>
- King, D. T., and D. W. Anderson. 2005. Recent population status of the American White Pelican: a continental perspective. *Waterbirds* 28:48-54. [online] URL: [https://bioone.org/journals/waterbirds/volume-28/issue-sp1/1524-4695\\_2005\\_28\\_48\\_RPSOTA\\_2.0.CO\\_2/Recent-Population-Status-of-the-American-White-Pelican--A/10.1675/1524-4695\(2005\)28\[48:RPSOTA\]2.0.CO;2.full](https://bioone.org/journals/waterbirds/volume-28/issue-sp1/1524-4695_2005_28_48_RPSOTA_2.0.CO_2/Recent-Population-Status-of-the-American-White-Pelican--A/10.1675/1524-4695(2005)28[48:RPSOTA]2.0.CO;2.full)
- Kling, H. J., S. B. Watson, G. K. McCullough, and M. P. Stainton. 2011. Bloom development and phytoplankton succession in Lake Winnipeg: a comparison of historical records with recent data.

- Aquatic Ecosystem Health & Management 14(2):219-224. <https://doi.org/10.1080/14634988.2011.577722>
- McGowan, P. C., K. M. Reinstma, J. D. Sullivan, K. P. Devoss, J. L. Wall, M. D. Zimnik, C. R. Callahan, B. Schultz, and D. J. Prosser. 2018. Use of Bank Swallow (*Riparia riparia*) burrows as shelter by Common Tern (*Sterna hirundo*) chicks. *Waterbirds* 41:179-182. <https://doi.org/10.1675/063.041.0210>
- McKellar, A. E., S. E. Simpson, and S. Wilson. 2021. Abundance, population trends, and negative associations with lake water levels for six colonial waterbird species over five decades in southern Manitoba. *Avian Conservation and Ecology* 16(1):7. <https://doi.org/https://doi.org/10.5751/ACE-01789-160107>
- Meirmans, P. G. 2019. Subsampling reveals that unbalanced sampling affects Structure results in a multi-species dataset. *Heredity* 122:276-287. <https://doi.org/10.1038/s41437-018-0124-8>
- Morris, R. D., C. Pekarik, and D. J. Moore. 2012. Current status and abundance trends of Common Terns breeding at known coastal and inland nesting regions in Canada. *Waterbirds* 35(2):194-207. <https://doi.org/10.1675/063.035.0202>
- Morris, R. D., D. V. Weseloh, F. J. Cuthbert, C. Pekarik, L. R. Wires, and L. Harper. 2010. Distribution and abundance of nesting Common and Caspian Terns on the North American Great Lakes, 1976 to 1999. *Journal of Great Lakes Research* 36(1):44-56. <https://doi.org/10.1016/j.jglr.2009.09.008>
- Nisbet, I. C. T. 2002. Common tern (*Sterna hirundo*), version 2.0. In A. Poole and F. Gill, editors. *The birds of North America*. Cornell Lab of Ornithology, Ithaca, New York, USA. <https://doi.org/10.2173/bna.618>
- Nisbet, I. C. T., and W. H. Drury. 1972. Measuring Breeding Success in Common and Roseate Terns. *Bird Banding* 43(2):97-106. <https://doi.org/10.2307/4511853>
- Nisbet, I. C. T., C. S. Mostello, R. R. Veit, and W. Fox James. 2011. Migrations and winter quarters of five Common Terns tracked using geolocators. *Waterbirds* 34(1):32-39. <https://doi.org/10.1675/063.034.0104>
- Pinkowski, B. C. 1980. Adaptations of Common Terns nesting on an inland reservoir. *Prairie Naturalist* 12:111-113.
- Pritchard, J. K., M. Stephens, and P. J. Donnelly. 2000. Inference of population structure using multilocus genotype data. *Genetics* 155(2):945-949. <https://doi.org/10.1093/genetics/155.2.945>
- R Development Core Team. 2021. R: A language and environment for statistical computing. Foundation for Statistical Computing, Vienna, Austria. [online] URL: <http://www.r-project.org/>
- Sæther, B. E., T. Coulson, V. Grøtan, S. Engen, R. Altwegg, K. B. Armitage, C. Barbraud, P. H. Becker, D. T. Blumstein, F. S. Dobson, M. Festa-Bianchet, J. M. Gaillard, A. Jenkins, C. Jones, M. A. C. Nicoll, K. Norris, M. K. Oli, A. Ozgul, and H. Weimerskirch. 2013. How life history influences population dynamics in fluctuating environments. *American Naturalist* 182(6):743-759. <https://doi.org/10.1086/673497>
- Schindler, D. W., R. E. Hecky, and G. K. McCullough. 2012. The rapid eutrophication of Lake Winnipeg: greening under global change. *Journal of Great Lakes Research* 38(3):6-13. <https://doi.org/10.1016/j.jglr.2012.04.003>
- Schindler, D. W., and P. G. Lee. 2010. Comprehensive conservation planning to protect biodiversity and ecosystem services in Canadian boreal regions under a warming climate and increasing exploitation. *Biological Conservation* 143(7):1571-1586. <https://doi.org/10.1016/j.biocon.2010.04.003>
- Shrestha, R. R., Y. B. Dibike, and T. D. Prowse. 2012. Modelling of climate-induced hydrologic changes in the Lake Winnipeg watershed. *Journal of Great Lakes Research* 38(3):83-94. <https://doi.org/10.1016/j.jglr.2011.02.004>
- Sirois, J., M. Fournier, and M. Kay. 1995. The colonial waterbirds of Great Slave Lake, Northwest Territories: an annotated atlas. Canadian Wildlife Service Occasional Papers 89. Environment Canada, Yellowknife, Canada. [online] URL: [https://publications.gc.ca/collections/collection\\_2018/eccc/CW69-1-89-eng.pdf](https://publications.gc.ca/collections/collection_2018/eccc/CW69-1-89-eng.pdf)
- Stelfox, H. A., and G. J. Brewster. 1979. Colonial-nesting Herring Gulls and Common Terns in northeastern Saskatchewan. *Canadian Field Naturalist* 93:132-138.
- Szczys, P., C. R. Hughes, and R. V. Kesseli. 2005. Novel microsatellite markers used to determine the population genetic structure of the endangered Roseate Tern, *Sterna dougallii*, in Northwest Atlantic and Western Australia. *Conservation Genetics* 6:461-466. <https://doi.org/10.1007/s10592-004-4975-6>
- Szczys, P., I. C. T. Nisbet, and D. B. Wingate. 2012. Conservation genetics of the Common Tern (*Sterna hirundo*) in the North Atlantic region; implications for the critically endangered population at Bermuda. *Conservation Genetics* 13:1039-1043. <https://doi.org/10.1007/s10592-012-0351-0>
- Szczys, P., S. A. Oswald, and J. M. Arnold. 2017. Conservation implications of long-distance migration routes: regional metapopulation structure, asymmetrical dispersal, and population declines. *Biological Conservation* 209:263-272. <https://doi.org/10.1016/j.biocon.2017.02.012>
- Taylor, P. D., T. L. Crewe, S. A. Mackenzie, D. Lepage, Y. Aubry, Z. Crysler, G. Finney, C. M. Francis, C. G. Guglielmo, D. J. Hamilton, R. L. Holberton, P. H. Loring, G. W. Mitchell, D. Norris, J. Paquet, R. A. Ronconi, J. Smetzer, P. A. Smith, L. J. Welch, and B. K. Woodworth. 2017. The Motus Wildlife Tracking System: a collaborative research network to enhance the understanding of wildlife movement. *Avian Conservation and Ecology* 12(1):8. <https://doi.org/10.5751/ACE-00953-120108>
- United States Geological Survey (USGS) Bird Banding Laboratory. 2021. North American bird banding program data set. Patuxent Wildlife Research Center, Laurel, Maryland, USA. [online] URL: <https://www.usgs.gov/labs/bird-banding-laboratory/data>
- Wails, C. N., S. A. Oswald, and J. M. Arnold. 2014. Are morphometrics sufficient for estimating age of pre-fledging birds in the field? A test using Common Terns (*Sterna hirundo*). *PLOS ONE* 9(11):e111987. <https://doi.org/10.1371/journal.pone.0111987>
- Weseloh, D. V., and B. M. Braune. 1989. DDE: PCB ratios in eggs of fish-eating birds from the Great Lakes. *Colonial Waterbirds Society Newsletter* 13:21.

Wilson, S. 2013. Abundance, distribution, and species assemblages of colonial waterbirds in the boreal region of west-central Manitoba and east-central Saskatchewan. *Canadian Field-Naturalist* 127(3):203-210. <https://doi.org/10.22621/cfn.v127i3.1483>

Wilson, S., R. Bazin, W. Calvert, T. J. Doyle, S. D. Earsom, S. A. Oswald, and J. M. Arnold. 2014. Abundance and trends of colonial waterbirds on the large lakes of southern Manitoba. *Waterbirds* 37(3):233-244. <https://doi.org/10.1675/063.037.0302>

Wilson, G. A., and B. Rannala. 2003. Bayesian inference of recent migration rates using multilocus genotypes. *Genetics* 163(3):1177-1191. <https://doi.org/10.1093/genetics/163.3.1177>

Wires, L. R., and F. J. Cuthbert. 2006. Historic populations of the Double-crested Cormorant (*Phalacrocorax auritus*): implications for conservation and management in the 21st century. *Waterbirds* 29(1):9-37. [online] URL: [https://bioone.org/journals/waterbirds/volume-29/issue-1/1524-4695\\_2006\\_29\\_9\\_HPOTDC\\_2.0.CO\\_2/Historic-Populations-of-the-Double-crested-Cormorant-Phalacrocorax-auritus/10.1675/1524-4695\(2006\)29\[9:HPOTDC\]2.0.CO;2.full](https://bioone.org/journals/waterbirds/volume-29/issue-1/1524-4695_2006_29_9_HPOTDC_2.0.CO_2/Historic-Populations-of-the-Double-crested-Cormorant-Phalacrocorax-auritus/10.1675/1524-4695(2006)29[9:HPOTDC]2.0.CO;2.full)



**Appendix 1:** Supplementary Material from Arnold et al. “Understanding widespread declines for Common Terns across inland North America: Productivity estimates, causes of reproductive failure, and movement of Common Terns breeding in the large lakes of Manitoba” Avian Conservation and Ecology.

**Table A1.1.** Genetic diversity estimates for Common Terns breeding in the large lakes of Manitoba. Number of individuals genotyped, mean number of alleles, effective number of alleles, observed and expected Heterozygosity, inbreeding coefficient (GenAIEx; Peakall and Smouse, 2012).

Colony Site	N	N <sub>A</sub>	N <sub>E</sub>	H <sub>O</sub>	H <sub>E</sub>	F
Mexico	26	5.4	3.52	0.61	0.67	0.16
Egg	28	6.2	3.30	0.69	0.68	0.01
Mcleods	23	5.6	3.20	0.50	0.63	0.25
Riverton	17	5.4	3.45	0.60	0.70	0.14
Shoals	27	6.4	3.03	0.59	0.62	0.06

**Table A1.2.**  $F_{ST}$  values below the diagonal and  $D_{EST}$  levels above the diagonal. All values are significant ( $P < 0.0011$ ) based on 9999 permutations implemented in GenAIEx (Peakall and Smouse, 2012).

	Manitoba	Inland	Coast
Manitoba	-	0.044	0.061
Inland	0.010	-	0.063
Coast	0.015	0.013	-

**Table A1.3.** Estimates of migration rates among regions. BAYESASS 3.0 (Wilson and Rannala, 2003) was implemented to estimate *contemporary migration rates* (A). Acceptance rates for parameters, -m0.1 -a0.2 -f 0.3, were 20-60% with a burn-in of  $1 \times 10^6$  iterations and  $3 \times 10^6$  iterations of MCMC sampled every 3000 iterations. The results of ten replicates were consistent; log-probability for each sub-region run ranged from -1403.75 to -1411.82. We report  $m$  values (fraction of individuals with recent migrant ancestry) from the run with the highest log probability (-1403.75); 95% CI overlapping 0.00 supports no migration. To estimate *historical migration rates* (B) Migrate-n (Beerli 2006) was implemented using the Brownian-motion model for microsatellite genotypes using 10000 recorded every 100 steps over 2 concurrent chains to sample 2000000 trees. We converted  $M$  (the mutation-scaled migration rate) to  $m$  (fraction of individuals with recent migrant ancestry) for ease of comparison to contemporary migration rate estimates from BayesAss ( $m = M * \mu$ ) where  $\mu = 0.00054$ ).

<b>A</b>		Migration From								
Migr	Manitoba + BOR			Great Lakes			Coast			
To	$m$	95% CI		$m$	95% CI		$m$	95% CI		
Man + Bor	0.849	0.732	0.965	<b>0.146</b>	<b>0.029</b>	<b>0.262</b>	0.006	-0.005	0.017	
Gr. Lakes	0.038	-0.039	0.115	0.954	0.876	1.031	0.009	-0.006	0.023	
Coast	0.048	-0.027	0.123	<b>0.157</b>	<b>0.033</b>	<b>0.280</b>	0.796	0.693	0.899	
<b>B</b>		Manitoba + BOR			Great Lakes			Coast		
Migr	$m$	95% CI		$m$	95% CI		$m$	95% CI		
Man + Bor				0.001	0.001	0.002	0.002	0.000	0.002	
Gr. Lakes	0.003	0.002	0.003				0.002	0.002	0.003	
Coast	0.003	0.002	0.003	0.003	0.002	0.003				

**Table A1.4.**  $F_{ST}$  values below the diagonal and  $D_{EST}$  levels above the diagonal. Significant values after B-Y Correction ( $P < 0.017$ ) based on 9999 permutations implemented in GenAIE<sub>x</sub> (Peakall and Smouse, 2012) are in bold.

	Mexico	Egg	McLeods	Riverton	Shoals
Mexico	x	<b>0.054</b>	<b>0.048</b>	<b>0.097</b>	<b>0.107</b>
Egg	<b>0.022</b>	x	<b>0.092</b>	<b>0.183</b>	<b>0.064</b>
McLeods	<b>0.024</b>	<b>0.033</b>	x	<b>0.188</b>	0.018
Riverton	<b>0.034</b>	<b>0.049</b>	<b>0.057</b>	x	<b>0.230</b>
Shoals	<b>0.037</b>	<b>0.025</b>	0.017	<b>0.066</b>	x

**Table A1.5.** Estimates of migration rates among colonies within the Manitoba Lakes. BAYESASS 3.0 (Wilson and Rannala, 2003) was implemented to estimate *contemporary migration rates* (A). As above in Table A3 with modification: -m0.3 -a0.5 -f0.99. We report values from the run with the highest log probability, -1338.85. To estimate *historical migration rates* (B) among sites within Manitoba we used Migrate-n (Beerli 2006) as above in Table A3 with modifications: 1000 recorded every 100 steps over 5 concurrent chains to sample 5000000 trees. The number of migrants per generation ( $N_m$ ) =  $\theta \times M/4$  so estimates range from  $N_m = 1.2$  (where  $m = 0.001$ ) to 4.5 (where  $m = 0.005$ ).

		MIGRATION FROM														
A.		Mexico			Egg			McLeod			Riverton			Shoals		
TO	<i>m</i>	~95% CI	~95% CI	<i>m</i>	~95% CI	~95% CI	<i>m</i>	~95% CI	~95% CI	<i>m</i>	~95% CI	~95% CI	<i>m</i>	~95% CI	~95% CI	
Mexico	0.720	0.633	0.808	0.033	-0.021	0.087	<b>0.170</b>	<b>0.028</b>	<b>0.312</b>	0.044	-0.014	0.102	0.033	-0.069	0.134	
Egg	0.050	-0.033	0.133	0.689	0.635	0.742	<b>0.193</b>	<b>0.042</b>	<b>0.343</b>	0.020	-0.017	0.057	0.049	-0.069	0.166	
McLeod	0.035	-0.034	0.105	0.016	-0.015	0.046	0.813	0.698	0.928	0.015	-0.014	0.043	<b>0.121</b>	<b>0.002</b>	<b>0.241</b>	
Riverton	0.032	-0.042	0.105	0.020	-0.018	0.059	0.062	-0.012	0.136	0.854	0.766	0.943	0.032	-0.024	0.087	
Shoals	0.023	-0.021	0.067	0.037	-0.023	0.096	<b>0.175</b>	<b>0.035</b>	<b>0.316</b>	0.014	-0.012	0.040	0.751	0.637	0.865	
B.		Mexico			Egg			McLeod			Riverton			Shoals		
TO	Median (m)	~95% CI	~95% CI	Median (m)	~95% CI	~95% CI	Median (m)	~95% CI	~95% CI	Median (m)	~95% CI	~95% CI	Median (m)	~95% CI	~95% CI	
Mexico				0.002	0.001	0.004	0.002	0.001	0.003	0.002	0.001	0.003	0.002	0.001	0.003	
Egg	0.003	0.001	0.004				0.002	0.001	0.003	0.002	0.001	0.003	0.002	0.001	0.003	
McLeod	0.002	0.001	0.003	0.003	0.002	0.004				0.003	0.001	0.004	0.002	0.001	0.003	
Riverton	0.003	0.002	0.004	0.002	0.001	0.002	0.002	0.001	0.004				0.002	0.001	0.003	
Shoals	0.002	0.001	0.005	0.002	0.001	0.003	0.002	0.001	0.003	0.001	0.000	0.003				

## Literature Cited

Beerli, P. 2006. Comparison of Bayesian and maximum-likelihood of population genetic parameters. *Bioinformatics* 22: 341–345.

Peakall, R., and Smouse, P. E. 2012. GenALEX 6.5: Genetic analysis in Excel. Population genetic software for teaching and research—an update. *Bioinformatics*. 28: 2537-2539.

Wilson, G.A. and B. Rannala. 2003. Bayesian inference of recent migration rates using multilocus genotypes. *Genetics* 163: 1177–1191.