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Avian Behavior, Ecology, and Evolution

Long-distance dispersal in a recovering endangered shorebird population facilitates recolonization of historical nesting sites following decades of extirpation

Dispersión de larga distancia en una población amenazada en recuperación de aves playeras facilita la recolonización de sitios de anidación históricos luego de décadas de haber sido extirpada.

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ABSTRACT. After extirpation from most of the Great Lakes by the 1980s, the Piping Plover (*Charadrius melodus circumcinctus*) did not nest again outside Michigan until 1998. The number of Plovers breeding in the region has gradually increased, with nesting locations expanding from Michigan. We studied the pattern of dispersers recolonizing their historical range after near extirpation using data from individually identifiable banded birds. Objectives were to determine if: (1) the origin of the first recolonizing individuals was Michigan; (2) dispersers remained within the Great Lakes population boundaries; (3) colonizing individuals were mainly natal dispersers; and (4) dispersal distances differed between the sexes and between natal and breeding dispersers. Finally, we tested the effects of time (year), yearly average Great Lakes water-level anomalies, and number of breeding pairs per year in Michigan on the rate of colonization outside Michigan. Plovers recolonized the Great Lakes primarily via recruits from Michigan. Additionally, six individuals were recorded leaving the Great Lakes and colonizing locations within Northern Great Plains and Atlantic Coast population boundaries. Colonizers dispersed on average 489.0 ± 55.0 km with no significant differences in distances between males and females or between natal and breeding dispersal events. No significant effect was found of water-level anomalies or number of breeding pairs in Michigan on the number of colonizers, but there was a positive effect of year. Our findings demonstrate that birds will return to sites unused for decades if the habitat is still suitable. The results also identify key locations that can support the continued growth of the endangered Great Lakes Piping Plover population as it increases toward recovery goals.

RESUMEN. Después de la extirpación de la mayor parte de los grandes lagos para la década de 1980, el chorlito, *Charadrius melodus circumcinctus* no volvió a anidar fuera de Michigan hasta 1998. El número de Chorlitos reproduciéndose en la región ha incrementado gradualmente, con localidades de anidación expandiéndose desde Michigan. Estudiamos los patrones de individuos que se dispersan y recolonizan su rango histórico, luego de la casi extirpación, usando datos de individuos identificados mediante anillos. Los objetivos fueron: determinar si, (1) Michigan era el origen de los primeros individuos en recolonizar; (2) los individuos que se dispersan se mantienen en la población de los Grandes Lagos; (3) los individuos colonizadores fueron principalmente dispersores recién nacidos; y (4) las distancias de dispersión fueron diferentes entre sexos y entre individuos recién nacidos y reproductores. Finalmente evaluamos los efectos del tiempo (año), promedio en la anomalía anual en el nivel del agua de los Grandes Lagos y el número de parejas reproductivas por año en Michigan sobre la tasa de colonización fuera de Michigan. Los chorlitos recolonizaron los grandes lagos principalmente por medio de reclutas de Michigan. Adicionalmente, registramos seis individuos que abandonaron los Grandes Lagos y colonizaron localidades dentro de los límites de las poblaciones de las Grandes Planicies Norteñas y la Costa Atlántica. Los colonizadores se dispersaron en promedio 489.0 ± 55.0 km y no encontramos diferencias significativas en las distancias de los eventos de dispersión entre los machos y las hembras ni entre los individuos recién nacidos y los individuos reproductivos. No hubo un efecto significativo de las anomalías en el nivel del agua, ni del número de individuos reproduciéndose en Michigan sobre el número de eventos de colonización, pero si encontramos un efecto positivo del año. Nuestros resultados demuestran que las aves pueden retornar a los sitios que no han sido utilizados por décadas si el hábitat todavía es adecuado. Los resultados también identificaron localidades clave para soportar el crecimiento continuado de la población amenazada de *Charadrius melodus circumcinctus* a medida que incrementa hacia las metas de recuperación.

Key Words: *Charadrius melodus circumcinctus; distribution patterns; Great Lakes; Michigan; water levels.*

INTRODUCTION

Piping Plovers (*Charadrius melodus*) are small, cryptically colored shorebirds found along marine and freshwater shorelines in North America. The species is divided into two subspecies: *C. m. melodus*, which breeds on the Atlantic Coast from Eastern Canada as far south as North Carolina in the USA (Miller et al. 2010), and *C. m. circumcinctus*, the inland subspecies, which nests in the Great Lakes, the U.S. Great Plains, and the Canadian Prairies (Elliot-Smith and Haig 2020). These two subspecies comprise three populations; *C. m. melodus* Plovers represent the Atlantic Coast population, whereas *C. m. circumcinctus* is divided into two populations, the Great Lakes and the Northern Great

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Plains/Prairie Canada (U.S. Fish and Wildlife Service (USFWS) 2003). The Great Lakes population is listed as "Endangered" under Ontario's Endangered Species Act (ESA), Canada's Species at Risk Act (SARA), and the United States' Endangered Species Act (USFWS 1985). The other two populations are listed as "Threatened" under the United States' Endangered Species Act and "Endangered" under Canada's Species at Risk Act.

Prior to listing, a review of the Great Lakes breeding population (Russell 1983) indicated that of the eight states and one province bordering the five lakes, the species was extirpated from four units (Indiana, Ohio, Pennsylvania, Ontario). In four additional states (Illinois, Minnesota, New York, Wisconsin), the population had been reduced to such low numbers (<2–3 individuals) as to be effectively extirpated. Finally, at the time of listing (USFWS 1985, 2003) in 1985, an estimated 12–17 pairs were nesting in Michigan. Population size and distribution at listing was a significant reduction from an historical estimate of up to approximately 800 breeding pairs (Russell 1983). The greatly reduced population by the 1980s was likely a result of many factors that continue to threaten Piping Plovers today, including increased human presence (e.g., beach recreation, off-road vehicles), high predation rates, habitat degradation associated with shoreline development, climate change, and disease (Russell 1983, Committee on the Status of Endangered Wildlife in Canada (COSEWIC) 2013). With intensive recovery efforts (e.g., predator management, nest monitoring and protections, captive rearing), Piping Plovers nesting in Michigan increased sufficiently to result in dispersal from that state to the Apostle Islands National Lakeshore on Lake Superior, Wisconsin, in 1998 and Seagull Bar, Wisconsin, in 2001, on Lake Michigan. Subsequently, the first single nest in the province of Ontario was discovered at well-monitored Sauble Beach on Lake Huron in 2007 (COSEWIC 2013).

Since initial records of colonization in Wisconsin and Ontario, the Great Lakes population has expanded to include records of Piping Plovers nesting in Illinois, Pennsylvania, New York, and Ohio. The population has also slowly increased to 60–76 breeding pairs between 2007 and 2021. Plovers have been intensively monitored across the Great Lakes since the late 1990s, and birds are consistently banded with individual markers allowing them to be tracked over time (Saunders et al. 2014). Banding, in combination with the small population size and significant public interest in the species, has provided the information needed to track the dispersal and reoccupation of many historical nesting sites that were unused by this species for decades.

Key factors that can affect dispersal probability and distance in birds include sex (Greenwood 1980, Haig and Oring 1988, Mabry et al. 2013), previous nest success (Flynn et al. 1999, Swift et al. 2021), age (Skrade and Dinsmore 2010, Pakanen et al. 2015), habitat stability (McNicholl 1975), and habitat suitability and availability (Swift et al. 2021). In general, in birds, females disperse further than males, natal dispersal distances exceed those of experienced breeding adults (Oring and Lank 1984), and habitat instability and nest failure promote dispersal away from previous sites (Catlin et al. 2016). Spatiotemporal variation in habitat suitability (e.g., elevation, precipitation, wetland type) or availability lead to dispersal in Northern Great Plains Piping Plovers, with birds dispersing both to and from previously used sites depending on the conditions in a given year (Swift et al. 2021). Male-biased return rates and shorter interannual distances between breeding sites also result from greater sensitivity of females to changes in their local environment (Clarke et al. 1997).

Information regarding colonization of rare species to new breeding sites is sparse in the literature due to the infrequency with which this phenomenon occurs and challenges in tracking individuals outside their typical nesting range (Probst et al. 2003). Long-standing collaborations among many university, governmental, NGO, and volunteer organizations involved in the recovery of Great Lakes Piping Plovers, both in banding adults and chicks, and in resighting individuals across their range, provide a unique opportunity to examine colonization of this species in the region over the last 25 years (LeDee et al. 2010). Here, we report on the origins of Piping Plovers that recolonized (hereafter "colonizers") historical habitat in the Great Lakes and the timeline over which this occurred. We expected, based on the proximity of the Michigan population, that the first colonizing Piping Plovers in the Great Lakes following extirpation would initially be from the shorelines of the State of Michigan, and not from either of the other two populations, as this state held the core of the remaining Piping Plovers breeding in the region. Additionally, active and intensive management of this population (Saunders et al. 2018) demonstrated that it had grown from 17 pairs in 1977 to 51 by the early 2000s (USFWS 2003).

We also expected that dispersal distances of Great Lakes colonizers would differ from distances recorded in other populations of Piping Plovers (e.g., birds nesting in the Great Plains and on the Atlantic coast), because of the greater fragmentation of potential breeding habitat in this region (Wemmer et al. 2001). We also expected females to disperse further than males because this was reported in other studies on this species (Haig and Oring 1988, Roche et al. 2012, Swift et al. 2021). As with many other bird species, we expected that natal dispersal distances would exceed breeding dispersal distances (Greenwood and Harvey 1982, Wiens and Cuthbert 1988, Paradis et al. 1998). Finally, we tested the significance of three potential covariates in explaining the annual number of colonizers outside the state of Michigan, including the size of the Michigan breeding population, the Great Lakes water levels in the current year, and the year, assuming that colonizers would gradually increase over time. We expected colonizers would increase outside Michigan with an increase in nesting pairs and/or higher than average water levels as Plovers sought suitable unoccupied habitat when habitat availability was redistributed (Haig and Oring 1988, Swift et al. 2021).

METHODS

Study Area

The Great Lakes population of Piping Plovers nests on wide, sparsely vegetated sand and cobble beaches along the shoreline of all five lakes (Superior, Michigan, Huron, Erie, and Ontario). This distribution is also documented in historical records (Russell 1983, USFWS 2003). Nests are constructed on the open beach and are highly vulnerable to flooding, predation, and destruction by humans and their pets (USFWS 2003, Brudney et al. 2013). Breeding sites can be described as discrete stretches of shoreline delineated by natural or artificial features, or as concentrations of nest sites within more homogeneous stretches of beach habitat;

they occur on lands under public, private, and multiple ownership (Wemmer et al. 2001). The entire shoreline of the Great Lakes is extensive (ca. 17,000 km), but potential nesting habitat for Piping Plovers is fragmented by natural as well as anthropogenic processes and is very limited. Our study used data from all known nesting locations during 1997–2021.

Data Sources

Data were obtained from the University of Minnesota, which hosts the banding records for Piping Plovers that have hatched and nested in Michigan and other midwestern U.S. states and from the Canadian Wildlife Service (CWS), which has maintained records in Ontario since the first recolonization in 2007. Data were typically collected when nests were initiated in May or June of each year and include band combinations, sex, GPS coordinates of each nest, and unique nest site ID codes. Sex of individuals was determined by behavior during courtship and plumage comparisons. For the purposes of this paper, we defined colonization events as the first one to five nesting attempts in a given U.S. state (excluding Michigan), Canadian province, or outside the Great Lakes population boundary. After the first five, there was movement within colonization jurisdictions, and we were primarily interested in dispersal arising from the population growth in Michigan. Because some band combinations were re-used by the CWS and the USFWS over the years, and, initially, only broods (i.e., chicks hatched from the same parents) were given unique combinations, rather than individual hatchlings, not all individuals could be assigned to their brood or a general geographic location. Using these databases, we identified 39 nesting attempts after the Great Lakes population was listed as Endangered (USFWS 2003) that we defined as colonization events for different political jurisdictions. These nesting attempts included 36 individual birds that we included in this analysis, three of which were involved in more than one colonization event. For some analyses, some information was missing regarding origin, hatch year, sex, or whether dispersal was breeding or natal. For these, we used subsets of the data.

Great Lakes water-level data for the years 1998–2020 were obtained from the National Oceanic and Atmospheric Administration (NOAA) website (NOAA 2021), and yearly water anomaly data (in meters) for each lake were averaged for each year prior to analysis.

Statistical Methods

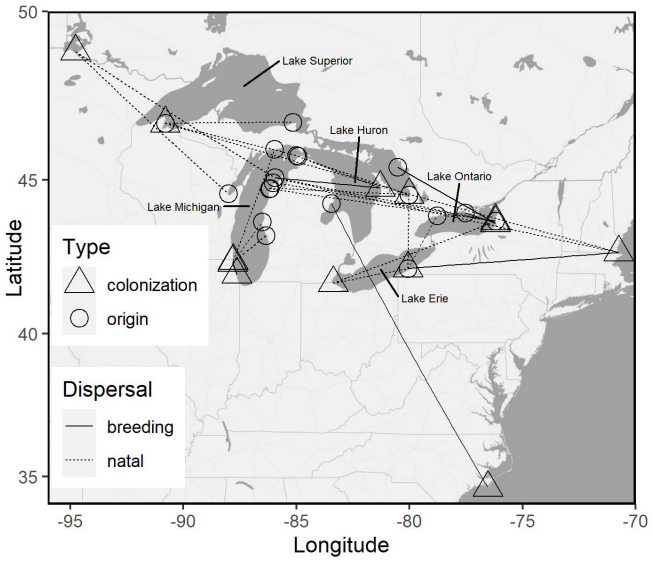
Beginning in 1997, we obtained UTM coordinates for natal sites for all Piping Plover colonizers for which there was information and used the R package "geosphere" (Hijman 2019) to calculate the distance between UTM coordinates for natal and nest sites. We selected the year 1997 because the first reported recolonization event occurred in Wisconsin in 1998. For nest sites in Ontario, we had coordinates for the exact nest locations. However, for sites in the USA, we categorized data into general locations instead of using specific coordinates of nests. We used a Wilcoxon Rank-Sum test to determine if significant differences existed in colonization dispersal distance between dispersal types as these data were non-normal. Also, we used a Welch's two-sample t-test to determine if significant differences in dispersal distance existed between sexes, as we found the variances for males and females to be unequal. We used the R package "gam" (Hastie 2020) to create a generalized additive model (GAM) to test the relationships between our response variable, the number of colonization events per year, and average annual Great Lakes water level, annual number of breeding Piping Plover pairs in Michigan, and year. Generalized additive models have relaxed assumptions about linearity, normality, and homoscedasticity of residuals (Ulanicki et al. 1999). We used a restricted maximum likelihood (REML) smoothing parameter to include the effect of year because the relationship between this variable and the response variable was non-linear. To assess the fit of our candidate models, we selected the model with the highest adjusted R^2 value (Li et al. 2017). We used the packages "ggplot2" and "ggmap" (Kahle and Wickham 2013, Wickham 2016) to create the dispersal trajectory map, and plots to visualize the results of the GAM.

RESULTS

Origin of Dispersing Individuals

Most colonization events recorded represented birds dispersing from Michigan to other jurisdictions (Fig. 1). Out of a total 39 colonizations, we document, 23 (59.0%) birds originated in Michigan, 8 (20.5%) in Ontario, 3 (7.7%) in Illinois, 2 (5.1%) in Pennsylvania, 2 (5.1%) in Wisconsin, and 1 (2.6%) in New York. These colonizers expanded into the historical range by reoccupying habitat in Wisconsin (4), Illinois (5), New York (9), Ohio (2), Pennsylvania (5), and Ontario (8). All sites reoccupied were the same sections of shoreline reported as former Plover general nest locations at last occupancy before the mid-1980s (Russell 1983, USFWS 2003).

Fig. 1. Map of dispersal routes for all Piping Plovers with confirmed origin and colonization sites.



Dispersal outside the Great Lakes Population Boundaries

In addition to dispersal of Great Lakes origin Plovers within the Great Lakes region, we document six cases of transboundary Plovers that dispersed, after their natal year, to the Atlantic Coast and Northern Great Plains populations (Fig. 1). These include three birds that were recorded nesting in Massachusetts (Cuthbert, *unpublished data*) and one bird nesting in North

Table 1. Origins, colonizations, and dispersal distances of the 22 Piping Plovers with confirmed year, sex, and dispersal types.

Sex	Type	Origin Site	Colonization Site	Distance (km)
F	Breeding	Sleeping Bear, Michigan	Oliphant Beach, Ontario	371
F	Breeding	Tawas, Michigan	Cape Lookout, North Carolina	1224
M	Breeding	Limestone Islands, Ontario	SIBSP, New York	396
F	Natal	Presque Isle State Park, Pennsylvania	Maumee, Ohio	280
F	Natal	Sleeping Bear, Michigan	Montario Point, New York	792
F	Natal	Sleeping Bear, Michigan	Montario Point, New York	796
F	Natal	Wasaga Beach, Ontario	Presque Isle State Park, Pennsylvania	262
F	Natal	Wasaga Beach, Ontario	Presque Isle State Park, Pennsylvania	262
F	Natal	Muskegon, Michigan	Waukegan, Illinois	155
F	Natal	Sturgeon Bay, Michigan	Wasaga Beach, Ontario	409
F	Natal	Sleeping Bear, Michigan	Wasaga Beach, Ontario	487
F	Natal	Apostle Islands, Wisconsin	Crane Beach, Massachusetts	1646
F	Natal	Sleeping Bear, Michigan	Lake of the Woods, Minnesota	791
F	Natal	Cat Island, Wisconsin	Lake of the Woods, Minnesota	703
M	Natal	Vermillion, Michigan	Apostle Islands, Wisconsin	432
M	Natal	Wilderness State Park, Michigan	Apostle Islands, Wisconsin	461
M	Natal	Gulliver, Michigan	Illinois Beach State Park, Illinois	418
M	Natal	Montrose Beach, Illinois	Maumee, Ohio	629
M	Natal	Sleeping Bear, Michigan	Montario Point, New York	806
M	Natal	Sturgeon Bay, Michigan	Oliphant Beach, Ontario	307
M	Natal	Darlington Prov. Park, Ontario	Presque Isle State Park, Pennsylvania	216
M	Natal	Silver Lake State Park, Michigan	Waukegan, Illinois	180

Carolina (Hillman et al. 2012). Additionally, two individuals were documented nesting just inside the eastern border of the Northern Great Plains population at Lake of the Woods, Minnesota (Cuthbert et al., *unpublished manuscript*). The Atlantic Coast Plovers originated from Michigan (2), Wisconsin (1) and Pennsylvania (1). The origins of the two individuals confirmed nesting in the Northern Great Plains population boundary were Michigan and Wisconsin.

Breeding and Natal Dispersal

Of the 39 dispersal events (Fig. 1) that we attempted to classify as breeding or natal dispersal, eight were attributed to breeding dispersal and 11 were unknown; the other 20 were natal dispersal events. The average natal dispersal distance of these colonizers was 564.0 km ± 84.7 SE whereas the average breeding dispersal distance from this sample was 371.5 km ± 152.1 SE, with no significant difference in the distances between the two dispersal types (t = 1.170, P = 0.25). Eleven colonization events as we defined from our sample were the result of dispersal with distances >500 km. Of these 11 events, we knew for eight of them the year of dispersal, sex, and whether it was a natal or breeding dispersal event (Table 1).

Male and Female Dispersing Colonizers and Their Distances

There was no statistically significant difference in the dispersal distances between male and female colonizers with confirmed sexes, although the average of female distances was slightly greater than the average of males (male: 431.7 km ± 54.4 SE, N = 15; female: 480.9 km ± 82.7 SE, N = 22; t = 0.497, P = 0.62).

Factors Explaining Number of Colonizers

We assessed the performance of seven competing models with combinations of the three potential predictor variables including year, number of breeding pairs in Michigan, and Great Lakes average water-level anomaly to explain the number of colonizations per year. Our best performing model included both year and water-level anomaly (R_{adj}^2 = 0.69, P = Table 2). This model found a significant positive effect of year (X^2 = 17. 7, P = 0.013; Fig. 2), and no significant effect of water-level anomaly on the number of colonizers per year (number of colonizers = 1.02 × water-level anomaly - 0.16 m, z = 1.01, P = 0.32).

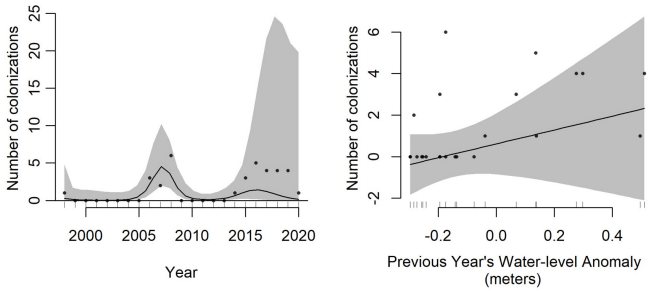
Table 2. Comparison of linear and generalized additive models using adjusted R^2 and percent deviance explained (GAM only).

Model	Type	Number of Parameters	$R^2_{adj.}$	% Deviance Explained
Colonizations ~ Pairs	LM	2	0.050	NA
Colonizations ~ Water	LM	2	0.232	NA
Colonizations ~ s(Year)	GAM	2	0.211	21.5
Colonizations ~ Water + s(Year)	GAM	3	0.691	83.5
Colonizations ~ Pairs + s(Year)	GAM	3	0.246	24.8
Colonizations ~ Water + Pairs	GAM	3	0.233	34.1
Colonizations ~ Water + Pairs + s(Year)	GAM	4	0.084	36.3

DISCUSSION

We studied dispersal by Piping Plovers in the Great Lakes population to determine if the origin of the first recolonizing individuals in the Great Lakes following extirpation initially was from Michigan vs. the other two populations, and to determine if dispersers remained within the Great Lakes population boundaries. Although the origin of dispersers initially was Michigan, as the Piping Plover population increased, individuals colonizing other Great Lakes jurisdictions were also birds from other Great Lakes locations where they had hatched or previously nested. We also confirmed reports of population-transboundary dispersal of Great Lakes Plovers to the Atlantic and Great Plains populations. We found that the majority of colonization events

Fig. 2. Effect of year and average water-level anomalies on the annual number of colonizations of Piping Plovers in the Great Lakes region between 1998–2020. Black lines show the predicted value of the number of colonizations, and the gray shading represents the confidence intervals of the predictions. The year data were smoothed using a spline, and the water-level anomaly data were linear.



were from natal dispersers and that dispersal distances were not significantly different between breeding and natal dispersers or the sexes in this sample of birds. Finally, we tested the effects of three covariates (e.g., year, number of breeding pairs/year, yearly mean Great Lakes water-level anomaly) on the rate of colonization outside of Michigan and found a significant positive effect of year and no significant effect of water-level anomaly on the number of colonizers per year. Except for a 5-yr period (2009–2013) where we have no records of colonization, between one to six colonizers were recorded outside of Michigan each year through 2020.

The Lake Michigan shoreline was and is an especially important source of recruits, likely because the highest number of nests and fledging success for the entire population is typically recorded from this coastal region. For example, in 2006, 91.8% of breeding Piping Plovers in the Great Lakes were found along Lake Michigan (Elliott-Smith et al. 2009; Cuthbert, *unpublished data*). During the period of time of our dispersal study, the peak number of nesting Plovers has always been located at Sleeping Bear Dunes National Lakeshore, Lake Michigan.

In 2009 and 2014, we recorded two Northern Great Plains Plovers nesting in Michigan, within the Great Lakes population boundaries. Their natal origins were Manitoba (Grand Beach Village) and South Dakota (Gavins Point), respectively. Genetic evidence of an Atlantic Coast Plover breeding in Michigan was also discovered by Miller et al. (2010), but no details are known for this individual as the sample came from an abandoned egg found in a nest in Michigan; the identity of the parents was not recorded (F. Cuthbert, *personal observation*). Therefore, when we received reports of four Great Lakes Plovers confirmed to nest within the Atlantic Coast boundary in Massachusetts (Cuthbert, *unpublished data*) and North Carolina (Hillman et al. 2010), the rare observations were not unexpected. These were followed by additional records in the Minnesota portion of the Northern Great Plains population boundary (Cuthbert et al., *unpublished manuscript*). These transboundary reports are of particular interest because they suggest that when the Great Lakes population was larger in the early 1900s (Russell 1983), genetic exchange likely occurred with greater frequency. The decline of the Great Lakes population to as low as a dozen pairs at listing may have eliminated or greatly reduced the likelihood of transboundary dispersal. Miller and colleagues (2010) reported that the Great Lakes population went through a bottleneck but they were unable to identify a specific time range. However, by the time of listing in the mid-1980s, the population was estimated at 12–17 pairs (USFWS 2003), and Miller and colleagues (2010) hypothesized that a bottleneck occurred around this time. Miller and colleagues also found the Great Lakes birds had the lowest genetic diversity of the three populations when sampled between 1991–2001 (Miller et al. 2010) when the population ranged from 17 to 32 nesting pairs. The dispersal records that we report also suggest that, as the Great Lakes population continues to increase, more mixing of the populations will occur, ultimately increasing the genetic diversity of the small Great Lakes population.

The natal dispersal distances that we report in this study for colonizing Piping Plovers were, on average, much longer (i.e., approximately 550 km, up to ca. 1600 km) than estimates reported in earlier studies for Northern Great Plains Plovers. However, our sample was restricted to birds that dispersed outside of Michigan, and to the first five colonizers in a jurisdiction, so is positively biased. Nonetheless, a study on natal dispersal of this species by Haig and Oring (1988), which reviewed natal dispersal distances from multiple studies of Piping Plovers in a variety of locations, found only three out of 39 individuals dispersed more than 250 km. Additionally, compared with *Charadrius* Plover species, this natal dispersal distance is long. For example, Nol et al. (2010) found that Semipalmated Plovers (*Charadrius semipalmatus*) that returned to the study site in Churchill, Manitoba, dispersed an average of 5 km between hatching and first breeding sites. Additionally, a study on Kentish (*C. alexandrinus*) and Little Ringed (*C. dubius*) Plovers found median natal dispersal distances between 10–15 km (Foppen et al. 2006), considerably shorter than what was reported in our study. In most studies, including these on other *Charadrius* Plovers, shorter natal dispersal distances are largely due to the low likelihood of detection for birds that dispersed out of the study area. This contrasts with studies of Piping Plovers. At the end of a typical breeding season, 92–98% of adult Piping Plovers and 99–100% of chicks in the Great Lakes population are individually recognizable from their band combinations. Because our study involves an intensively managed and monitored species, often in areas of relatively high human population densities, detection rates of birds dispersing greater distances are likely higher than in other studies and may explain the much longer distances recorded in this study. This comment is supported by the high detection rates of breeding Great Lakes Piping Plovers previously reported (LeDee et al. 2010).

Adult Piping Plovers generally disperse further between successive breeding seasons after nest failure in the previous year (Swift et al. 2021). This finding may suggest that years with low nest success associated with factors such as high predator abundance and high water levels could also be driving these colonization events (Catlin et al. 2016). Insufficient data were available for the few breeding dispersers that we recorded to assess the influence of nest success on dispersal.

In examining factors that may have influenced the rate of colonization through our study period, we found a significant

effect of time (year) on the number of colonizations. This means that as the Michigan population has grown, the number of colonizers to other jurisdictions has also increased. Recently fledged and post-breeding Piping Plovers are often sighted exploring other beaches in the Great Lakes before continuing south on their fall migrations (Van Zoeren, *personal communication*), which suggests that they start their dispersal decision process while still in their natal area (Rioux et al. 2011). Many beaches in the Great Lakes appear to have lost habitat as a result of vegetation encroachment and high water levels (Cuthbert, *unpublished data*). Our model was improved by the inclusion of a metric describing extreme water levels, although its parameter estimate was not significantly different from zero. This lack of significance may have been due to our small sample size. In combination with the larger number of breeding pairs in Michigan over time, and their corresponding greater production of young (Cuthbert, *unpublished data*), habitat limitation along the shores of the Great Lakes may also be influencing colonization rates. Similarly, in one of the few published examples of factors influencing expansion of an endangered species, Probst et al. (2003) suggested that aggressive habitat creation and management during the period 1990–2000 resulted in tripling of the Michigan Kirtland's Warbler (*Setophaga kirtlandii*) population and at least six occurrences of dispersal to and colonization of newly created habitat that were associated with habitat saturation in the Warbler's core range.

Although the re-use of some band combinations over the years led to uncertainty in the individual identity, hatch/breeding location, or hatch/breeding years of some birds, these issues became less prevalent in more recent years of the study after we began to use individually coded band combinations for plastic bands as standard practice in 2007. Thus, the increase in the number of colonizers since 2014 is not due to problems with identifying individuals across destination locations. Piping Plover dispersal in the Northern Great Plains population was associated with habitat type and availability, with the most dispersal skewed toward short-distance (>1 km) movements (Swift et al. 2021). Individuals in the Great Plains generally moved shorter distances when more habitat was available near their natal/previous breeding sites. Average dispersal distances for both natal and interannual breeding dispersers were consistently lower than those reported in our study. The results of Swift and colleagues' study suggested that these short-distance dispersal events comprising most of the movement in this region were due to the very large area (84,000 km^2) of semi-continuous habitat available for birds to select for nesting. In contrast, we observed many long-distance dispersal events in colonizers, which may suggest that these birds are limited by lack of suitable habitat in their previous breeding/natal sites, although the bias in our sample is acknowledged. Haig and Oring (1988) reported that first-year Piping Plovers were typically found in the vicinity of their natal sites when habitat was available. Thus, as the observation that most of our colonizers were first-time nesting birds. this further supports limited nesting habitat in the Great Lakes. Additionally, because much of the suitable Piping Plover nesting habitat in the Great Lakes is fragmented by shoreline development, generally unsuitable nesting habitat, and periodic high water levels, colonization in this population may be driven by habitat conditions causing birds to move further than expected in this species to find a location to nest. Although habitat availability is a compelling argument for the dispersal events that we recorded here, dispersal to avoid intraspecific competition mediated through habitat availability and as an adaptation for increasing gene flow (Greenwood and Harvey 1982) are also factors that may affect dispersal.

CONCLUSION

This study determined that recruits originating around Lake Huron and Lake Michigan have been critical for increasing the population of Great Lakes Piping Plovers in Ontario and five of the seven U.S. Great Lakes states that were occupied by Plovers prior to near extirpation of this population. Additionally, we characterized patterns of dispersal during a recolonization event, where Plovers dispersed farther than what is generally reported in this species, possibly a result of the bias in detection of long-distance dispersal events in other populations, or a result of the ephemeral nature (Wemmer et al. 2001) of Piping Plover breeding habitat. Future research should focus on characterizing the true amount of available habitat over this period to determine if habitat availability and local densities of breeding Piping Plovers may play a role in dispersal distances in Great Lakes population birds over time. Both the impetus and consequences of dispersal to reproductive success are worthy of a follow-up study. Finally, our results confirm the importance of the east coast of Lake Michigan as an area of extremely high conservation value for the continued growth of the Great Lakes Piping Plover population.

Responses to this article can be read online at:
https://journal.afonet.org/issues/responses.php/122

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Data Availability:

The data/code that support the findings of this study are available on request from the corresponding author, [AB]. None of the data/code are publicly available because Great Lakes Piping Plovers are of the status "Endangered," and our data include specific locations for a significant number of breeding sites, which if made public could put their success at risk.

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