

CONTRIBUTED PAPER

Five-year assessment of wolf translocation to Isle Royale National Park, 2018–2023

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Abstract

Gray wolf (*Canis lupus*) translocation is a common approach for restoring ecological function through top-down regulation. Understanding the processes that contribute to successful wolf translocations is essential for planning future restorations. We investigated the Isle Royale National Park (IRNP) wolf restoration project 5 years post-translocation (September 24, 2018–September 1, 2023) to evaluate whether the management goal to establish a wolf population that would persist for 20 years was achieved. We used Global Positioning System (GPS) radio collar location data, remote cameras, howl surveys, and population viability analysis (PVA) to determine (1) if wolf demographics, including cause-specific mortality, survival, pack formation, reproduction, and population size resembled long-term averages and (2) whether observed wolf demographics would result in a self-sustaining population for 20 years. The National Park Service released 19 wolves captured from populations in the Grand Portage Reservation, Minnesota, USA; the Upper Peninsula, Michigan, USA; Jostle Lake, Ontario, Canada; and Michipicoten Island, Ontario, Canada onto IRNP during September 2018–September 2019. The primary cause of wolf mortality was intraspecific aggression, with five of 11 confirmed mortalities

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attributed to other wolves. Average annual wolf survival was 0.74 (95% CI = 0.58–0.94), and across years the wolf population increased or remained stable with an estimated population of 27 wolves in April 2023. Wolves reproduced each year including the year of initial translocations. Population viability analysis simulations suggest an >80% chance of wolf population persistence for 20 years, despite high levels of inbreeding. We found that releasing socially bonded wolves facilitated pack formation; however, the numerical and social dominance of a family group may complicate the long-term genetic health of the population.

KEYWORDS

camera trap, cause specific mortality, ecological restoration, LoCoH home range, predator–prey, reproduction, survival

1 | INTRODUCTION

Translocating species is a common conservation and management practice (Seddon et al., 2012). Translocations serve diverse purposes including preserving endangered populations (Bolam et al., 2021), restoring ecosystem function and services (Hayward & Somers, 2009), mitigating human-wildlife conflicts (Bradley et al., 2005; Massei et al., 2010), supporting indigenous resources and food security (Hoffmann & Cliburn, 2021), facilitating biocontrol (Marshall, 2019), and enabling genetic rescue or augmentation of isolated populations (Johnson et al., 2010; Whiteley et al., 2015). Translocating carnivores has been used to restore predation to ecosystems, but the success of these programs is difficult to measure and context dependent (Alston et al., 2019; Svenning et al., 2016), and up to one-third of large carnivore reintroductions fail (Thomas et al., 2023). Evaluating the ecological consequences and success of translocation programs has historically received limited attention (Pérez et al., 2012; Palmer et al., 2020) though exceptions exist (Beschta & Ripple, 2016).

Gray wolf (*Canis lupus*) translocation is a controversial approach to restoring ecological function through top-down regulation (Niemic et al., 2020; Smith & Bangs, 2009). Wolf predation can have ecosystem effects by directly altering ungulate abundance and reducing pressure on competitors and preferred browse (Beschta & Ripple, 2016; Hebblewhite et al., 2002). Additionally, wolves influence ecological communities by suppressing meso-predators, facilitating smaller mammals and bird populations (Berger & Conner, 2008; Ripple et al., 2013). Wolves can also create a “landscape of fear,” altering prey behavior and redistributing browsing pressure to different areas or less palatable, but safer, food sources (Flagel et al., 2016; Laundré et al., 2001). However, wolf

restoration remains controversial, with competing interests across agencies and stakeholders. Thus, it is crucial to establish clear objectives and closely monitor the outcomes of translocations.

Although wolves were once abundant in North America, eradication programs led to their near extirpation in the contiguous United States by 1930 (Mech & Boitani, 2003). Since the 1970s, various jurisdictions have conducted reintroduction projects to support recovery of the species (Varley & Brewster, 1990), restore predation and top-down regulation in ecosystems (Mech & Boitani, 2003), or to address public demand (Niemic et al., 2020). Wolf (*Canis* spp.) reintroductions have had mixed success, from the challenges of establishing a self-sustaining red wolf (*Canis rufus*) population in the southeastern United States (Hinton et al., 2013) to the restoration of the Yellowstone wolf population (Smith & Bangs, 2009). Colorado reintroduced wolves to the Western Slope of the Rocky Mountains in 2023 after a voter-mandated ballot initiative (Schmelzer, 2023), and conservation groups continue to advocate for wolf restoration around the world, including New York, USA (Enck & Brown, 2000), Scotland (Nilsen et al., 2007), and Japan (Sakurai et al., 2020). Understanding the factors and processes that contribute to translocated wolf population persistence and how wolves reintegrate into ecosystems is critical for planning and managing future restoration projects.

The translocation of wolves to Isle Royale National Park (IRNP), Michigan, USA (Figure 1) provided an opportunity to characterize the process of translocating wolves to establish a self-sustaining population and restore predation as an ecosystem process. Wolves likely arrived on IRNP by crossing an ice bridge from mainland Canada sometime in the 1940s (Mech, 1966). During 1960–2000, the wolf population averaged 22 individuals with a high of 50 in 1980 and a low of 11 in 1989 (Hoy

FIGURE 1 Isle Royale National Park, Michigan, USA and wolf capture locations: Grand Portage, Minnesota, USA; Upper Peninsula, Michigan, USA; Jostle Lake, Ontario, Canada; and Michipicoten Island, Ontario, Canada. Inset: Shaded box overlays project area located within the United States and Canada.

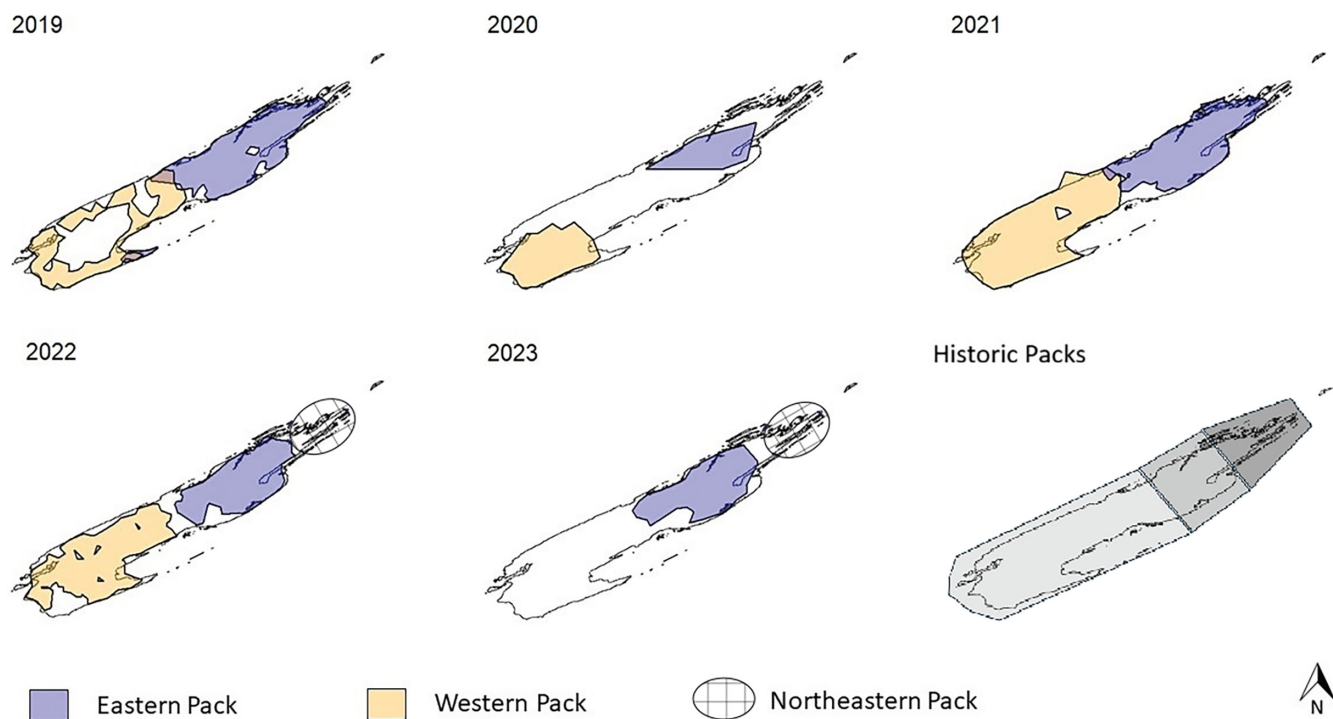
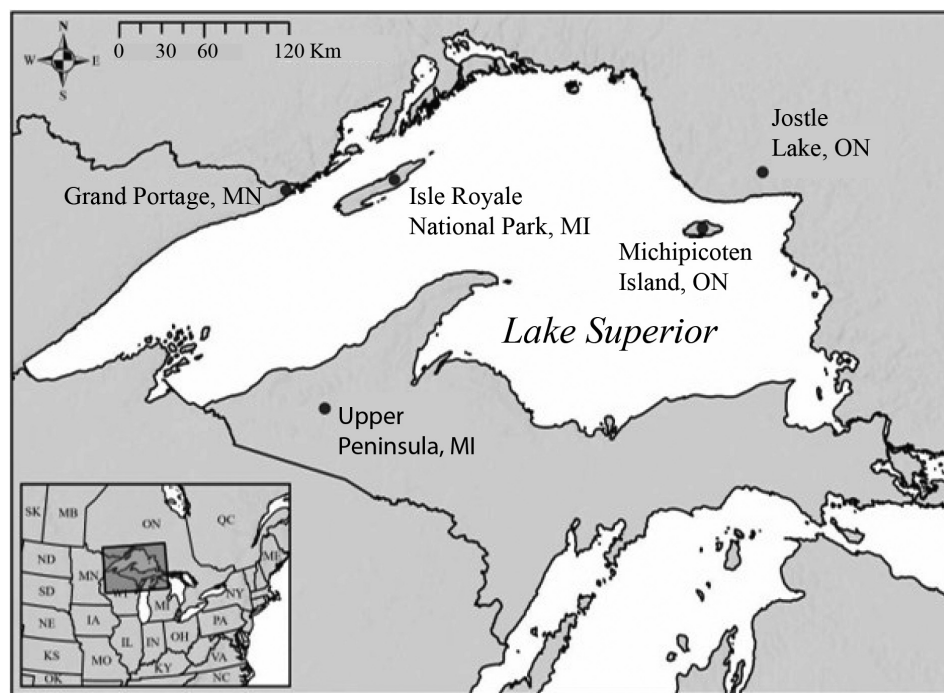


FIGURE 2 Annual (April 15–April 15) 95% LoCoH home ranges of wolf packs in Isle Royale National Park, Michigan, USA. Eastern pack 2019 home range estimated from GPS data collected October 15, 2019–April 15, 2020 following consistent association. Home ranges in 2023 estimated from GPS data collected April 15–September 1 (end of study period). We did not detect breeding activity in the Western Pack in 2023. Northeastern group home ranges estimated using remote camera data. Historic pack boundaries adapted from Vucetich and Peterson (2009).

et al., 2022; Romanski et al., 2020). The number of packs in IRNP ranged from one to five (Räikkönen et al., 2009), but wolves typically organized into three packs that

occupied the western, central, and eastern areas of the island (Figure 2, Vucetich & Peterson, 2009). Limited genetic exchange between the mainland and IRNP may

have been maintained through the formation of ice bridges (Hedrick et al., 2014). However, the yearly probability of ice bridge formation declined steadily through the 1900s (Licht et al., 2015). The IRNP wolf population entered a steady decline from 2009 to a non-reproducing, highly inbred pair by 2016 (Hedrick et al., 2017). The causes of this decline are unclear but potential reductions in fitness related to inbreeding depression (Hedrick et al., 2014; Rääkkönen et al., 2009), malnutrition (Peterson et al., 1998), disease (Peterson et al., 1998), and accidents (Vucetich & Peterson, 2013) in addition to kin avoidance and demographic stochasticity contributed to the population entering an “extinction vortex” (Fagan & Holmes, 2006).

Moose (*Alces alces*) were the primary component of the wolf diet in IRNP during 1940–2000 (85%–95%; Thurber & Peterson, 1993), with American beaver (*Castor canadensis*), an important secondary prey (Gable et al., 2018). The park has consistently supported high moose densities, with a long-term average of about 1000 individuals (1.84 moose/km²) (Hoy et al., 2023). During the wolf population decline (2012–2017), moose numbers increased to 1600 individuals [90% CI = 1077–2238, 2.95 moose/km²] (Peterson & Vucetich, 2017). Responding to deteriorating environmental conditions caused by persistent intense moose herbivory, and the likely extirpation of wolves, the US National Park Service (NPS) translocated wolves to IRNP to restore the ecological services they provide (NPS, 2018a; Romanski et al., 2020).

The broad objectives of the wolf translocation were to establish a genetically viable population that would persist for at least 20 years and to restore predation as a top-down influence on moose and beavers (NPS, 2018a, 2018b). Here, we report our examination of the wolf translocation project in relation to the first objective over its first 5 years (September 24, 2018–September 1, 2023). Specifically, we evaluated whether wolf demographics and behavior, including mortality sources, survival, reproduction, pack formation, and population size, resembled values observed during 1960–2000 (when the wolf population was considered stable) and if the population is likely to persist for 20 years (Figure 1).

2 | METHODS

2.1 | Study area

Located 24 km east of Thunder Bay, Ontario, Canada in Lake Superior IRNP is an archipelago with a land area of 542 km² (Figure 1). Over 99% of IRNP is federally designated wilderness (National Park Service, 2023). Due to its isolation, IRNP supports few terrestrial vertebrates

compared to the nearby mainland. Mammal species include moose, wolves, red foxes (*Vulpes vulpes*), short-tailed weasels (*Mustela erminea*), river otters (*Lontra canadensis*), beavers, muskrats (*Ondatra zibethicus*), snowshoe hares (*Lepus americanus*), American martens (*Martes americana*), American mink (*Neogale vison*), deer mice (*Peromyscus maniculatus*), red squirrels (*Tamiasciurus hudsonicus*), and several bat species (Manlick et al., 2018; Peterson, 1977; Romanski & Belant, 2008). The best-known wildlife species associated with IRNP are wolves and moose, whose predator–prey relationship is well-studied (Mech, 1966; Peterson, 1977; Vucetich et al., 2012). At the time of wolf translocation, a related non-breeding pair of wolves inhabited IRNP (Robinson et al., 2019).

2.2 | Selection of source populations

The NPS selected wolf source populations with advice from subject experts (NPS, 2018a) and in partnership with other federal, tribal, state, and provincial agencies. Wolves were translocated from multiple populations geographically close to IRNP (Figure 1) to maximize genetic diversity, locally adapted genotypes, and familiarity with prey species on IRNP (NPS, 2018a).

Minnesota, USA—Wolves were captured from the Grand Portage Indian Reservation (193 km²) in North-eastern Minnesota. Moose occur at 0.27 individuals/km² throughout the reservation, while white-tailed deer (*Odocoileus virginianus*) and beavers are common (S.A. Moore, unpublished data).

Michigan, USA—Wolves were captured from the western Upper Peninsula of Michigan, including Baraga (2769 km²), Gogebic (3823 km²), Houghton (3890 km²), and Ontonagon (9689 km²) counties. White-tailed deer are the primary prey of wolves in the Upper Peninsula, comprising 70%–78% of their diet (Petroelje et al., 2019). Moose abundance is low and wolf predation has a negligible effect on moose population dynamics in the Upper Peninsula (Beyer et al., 2011).

Michipicoten Island, Ontario—Wolves were captured on Michipicoten Island (184 km²) in northeastern Lake Superior, about 16 km from mainland Ontario. After wolves colonized the island in winter 2014–2015, the resident woodland caribou (*Rangifer tarandus caribou*) population decreased from about 450 individuals to near extirpation in 2018. This decline prompted managers to translocate the surviving caribou to predator-free islands (Fletcher, 2022). After the removal of caribou, wolves primarily preyed on beavers, and managers did not expect the wolf population to persist (Richardson, 2019; B. Patterson, personal communication).

Mainland Ontario—Wolves were captured from Jostle Lake, Ontario, about 20 km west of Wawa, Ontario, and east of Pukaskwa National Park. Moose are the primary prey of wolves in this region (Forshner et al., 2003).

2.3 | Wolf capture and translocation

Wolves were captured using foothold traps (Olsen et al., 1988) in Minnesota during September 24–October 5, 2018 and in Michigan during September 4–14, 2019. Wolves were captured using net guns from helicopters in both Ontario sites during February 24–March 1 and March 23–24, 2019 (Romanski et al., 2020). The NPS desired to release an equal number of male and female wolves with some from the same packs to facilitate social bonds. Wolves selected for translocation were adults (1–5 years old; estimated using tooth wear [Gipson et al., 2000] and body size), in good body condition (i.e., not emaciated or with mange and/or lice), with no physical abnormalities (no fractures or missing limbs, both eyes present and apparently functional, at least three canine teeth), potential to reproduce, not habituated to humans, not infected with heartworm (*Dirofilaria immitis*), and without apparent disease. Each wolf identified for translocation was transported to a facility for veterinarian evaluation or was evaluated in situ by a veterinarian. Based on a disease risk analysis (Verant et al., 2022), each wolf was tested for heartworm before translocation and blood and feces were collected for retrospective analyses for multiple pathogens of interest. All wolves were vaccinated with core canine vaccines and treated for parasites; wolves with capture-related or pre-existing injuries also received antibiotics (Verant et al., 2022). Each wolf was fit with a Global Positioning System (GPS) telemetry collar (Vertex Plus; VECTRONIC Aerospace, Berlin, Germany, or TGW-4470-4; Telonics, Mesa, AZ, USA) programmed to attempt a location every 4–5 h and emit a mortality signal when stationary for 24 h. Each wolf received ear tags and a passive integrated transponder between their shoulder blades for individual identification. Wolves were transported to IRNP via helicopter, fixed-wing aircraft, or boat and released within 36 h of capture. Wolves were released when IRNP was closed (February–March) or had low visitation (September–October). Each jurisdiction followed their agencies' respective animal care and use procedures and translocation protocols were approved by the NPS Institutional Animal Care and Use Committee (IACUC; MWR_ISRO_Romanski_Wolves_2018.A3). Protocols for capture of wolves in Ontario were approved by the Ontario Ministry of Natural Resources Animal Use and Care Committee (Permit No. 19-441). See Romanski et al. (2020) for detailed permitting information.

To improve long-term monitoring we captured previously marked and unmarked wolves on IRNP in May 2021 using foothold traps and in February 2022 and 2023 using darting and net guns from helicopters (e.g., Kreeger & Arnemo, 1996; Nelson et al., 2006). Each unmarked wolf received a GPS collar (Vertex Plus; VECTRONIC Aerospace, Berlin Germany), ear tags, and a passive integrated transponder between their shoulder blades. The NPS IACUC approved capture protocols in IRNP (MWR_ISRO_Romanski_Wolves_2018 and MI_ISRO_Romanski_Wolf_2022 with associated amendments). Capture and translocation related injuries are reported in the results.

2.4 | Cause specific mortality, survival, and minimum wolf count

We monitored GPS-collared wolves and investigated any mortality signal as soon as possible to determine cause of death. When practical, we submitted wolf carcasses to the US Geological Survey (USGS) National Wildlife Health Center, Madison, WI, USA or the Veterinarian Diagnostics Lab at the University of Minnesota, St. Paul, Minnesota, MN, USA for necropsy.

We used the Kaplan–Meier product limit estimator (Kaplan & Meier, 1958) to estimate annual survival and a Cox proportional hazards model (Andersen & Gill, 1982) to compare survival between sexes, among source locations, and release time. We censored animals when their radio collar failed or if they emigrated from the island. We conducted analyses in R version 4.2.2 (R Core Team, 2022) using the `surv()` and `coxph()` functions in the Survival package (Fox & Weisberg, 2002).

We estimated the minimum wolf count using territory mapping (e.g., Burch et al., 2005) and data from 156 remote cameras (Stealth Cam DS4K; Irving, Texas) deployed September 15, 2019–April 15, 2023. We placed cameras 300–1600 m apart along or about 50 m from hiking trails throughout IRNP (Supporting Information S1). Cameras were positioned 1.5 m above ground and oriented to detect wolves at 4–15 m. We programmed cameras to take five images of each detection with a trigger speed of ≤ 0.5 s and no delay between detections. We grouped images into 10-min sequences and at least two observers identified the minimum number of individuals in each sequence. We identified wolves to age class (adult or young of the year, i.e., <10 months) from images obtained during October 15–November 14 based on known collared individuals, body size, and morphology (Figure 4). We selected this period because pups are more likely to travel with adults yet remain morphologically distinct. We plotted the maximum wolf count per camera October 15–April 14 using a 24–48-h moving window. We estimated the wolf count during the period between park closure (October 15), when wolf detectability

on remote cameras increased (NPS unpublished data), and the approximate start of denning season (April 15). We selected sequences based on pack home ranges estimated from GPS locational data and distance between cameras. For each pack home range and moving window, we selected the camera and sequence with the highest count and censored all sequences within the home range and/or within 10 km. We selected a 10 km buffer because GPS data indicated wolves rarely moved >10 km in 36 h in our study system (<1.6% of observed movements). To estimate the number of wolves living outside of established pack home ranges, we identified the sequence with the highest wolf count and censored cameras within 10 km. Each year, we identified the 36-h interval with the greatest wolf count. We consider our count a minimum estimate because, while pack cohesion is higher in winter, some wolves may not travel with the larger pack or trail the larger group by >10 min. Also, as we could not confidently identify all individuals, minimum counts do not include singles and lone pairs that used areas within or near established pack territories. Our methods could double count the rare instances where wolves traversed distances >10 km in 36 h (<1.6% of observed movements), however these movements are likely compensated by undercounting pack size and loners.

2.5 | Pack formation and reproduction

To infer social organization, we used GPS location data to estimate proximity among individuals (Silk et al., 2017). We defined a pack as two or more wolves associating, establishing a territory, and producing pups (Mech & Boitani, 2003). For each biological year (April 15–April 14), we estimated the boundaries of each pack's territory using the 95% adaptive local convex hull method (Adaptive LoCoH; Getz et al., 2007) for all GPS locations of wolves associated with the pack. The adaptive LoCoH method constructs convex hulls for each point such that the distance to the nearest neighbors is less than or equal to d . We selected d as the distance where most pack home range size estimates stabilized. LoCoH uses polygons instead of kernels and is more appropriate in our island system. We conducted the analysis in R using the LoCoH.a() function in the adehabitat package (Calenge, 2006).

We used radio telemetry, howl surveys, and remote camera data to estimate the number of litters produced yearly. We monitored the movements of collared wolves for evidence of denning behavior during April–July using GPS clusters (Cluff & Mech, 2023). In addition, we inferred a female denned if their daily movements declined to near 0 and the frequency of satellite uplink failures increased (Walsh et al., 2016) or if we observed

evidence of lactation (enlarged mammary glands) in remote camera images (Galaverni et al., 2012). We inferred a pack member was provisioning pups if their GPS locations indicated they made short forays from a central location (i.e., presumed den site) during April–July (Picardi et al., 2020; Ylitalo et al., 2021). When GPS location data indicated that wolves shifted their central location at least 2 km away (i.e., pups were moved to rendezvous sites), we visited suspected den sites to verify. We also conducted howl surveys to detect pups at potential wolf rendezvous sites. We traversed within 250 m of a potential rendezvous site and performed three sets of howls. One observer simulated wolf howls by howling three times with 10–15 s between each howl and waiting 10 min between sets for a wolf response (Harrington & Mech, 1982). We identified pups by their high-pitched howls (Palacios et al., 2016). We also placed remote cameras (Stealth Cam DS4K, GSM Outdoors, Irving, TX; HyperFire 2, Reconyx, Holmen, WI, or Bushnell Trophy Cam, Bushnell, Overland Park, KS) on and off hiking trails and near known den or rendezvous sites April 15–October 15 each year and identified the number of pups (based on morphology) detected in images and videos.

2.6 | Population persistence

To determine the likelihood that the restored wolf population would persist for 20 years without additional translocations, we conducted a population viability analysis (PVA) using the program Vortex (Lacy & Pollak, 2025). Population viability analysis integrates biological parameters while simulating environmental variation and stochasticity to estimate population trends (Brook et al., 2000). We parameterized the model using demographic information derived from GPS tracking and demographic monitoring of IRNP wolves and published sources (detailed model specifications are described in Supporting Information). We considered scenarios with and without inbreeding depression and ran models over a 20-year period for 1000 iterations.

3 | RESULTS

3.1 | Original population

Based on aerial surveys, we estimated a bonded, non-breeding related pair occupied IRNP when translocations began in September 2018 (Robinson et al., 2019). The male was killed by other wolves in October 2019, and the fate of the female is unknown. There is no evidence, genetic or otherwise, that either wolf integrated into the

newly established packs. We censored these wolves from further analysis.

3.2 | Captures and translocation

We captured 36 wolves and translocated 19 to IRNP during September 2018–September 2019. We captured 22 wolves in Minnesota and selected 5 for translocation; however, one wolf died from adverse reaction to anesthesia before translocation resulting in four animals (three females and one male) being moved to IRNP. We translocated all individuals captured from all other sites: two females and two males from Michigan, three females and five males from Michipicoten Island (a breeding pair and their offspring; Hervey et al., 2021), and one female and two males from Jostle Lake, Ontario (Romanski et al., 2020). We conducted additional trapping and radio-collaring in IRNP May 2021, February 2022, and February 2023. In May 2021, we captured four unmarked (i.e., animals we did not release) wolves (three yearling males, one yearling female) and recaptured two translocated males. In February 2022, we captured three unmarked wolves (two yearling males, one yearling female) and recaptured one adult female tagged the prior year and a translocated adult male. In February 2023, we captured two unmarked yearling males and recaptured a 2-year-old female tagged the year prior. Considering their ages (<2 years old) and social associations (captured near or with known translocated animals), unmarked animals were likely the offspring of translocated wolves. Alternatively, unmarked wolves may have been offspring of undetected animals present in IRNP before translocation or recent immigrants from the mainland. Further genetic analysis will elucidate the source of these animals.

3.3 | Cause-specific mortality, survival and minimum wolf count

One wolf captured in Michigan and selected for translocation died of an adverse reaction to anesthesia before translocation; we censored this animal from analysis. Of the 28 collared wolves, we documented 11 mortalities during September 24, 2018–September 1, 2023. Two wolves died shortly after release from apparent capture or translocation-related stress or injuries. Necropsies performed by the USGS indicated the first wolf died of cellulitis secondary to a foot-hold trap wound and the other died of pneumonia. We excluded these wolves from survival analysis. Five wolves died from confirmed or suspected intraspecific strife and four died of unknown

causes. Of the four wolves with unknown mortality cause, two died after their radio collars failed and we did not find the carcass until several months later. The remaining two wolves died in winter, and we could not investigate the mortality sites until spring. One wolf emigrated across an ice bridge in January 2019 (Orning et al., 2020), we censored that animal from survival analysis at the time of departure. The radio collars of 11 wolves failed before their deaths.

For survival analysis, we monitored 26 wolves for a total of 11,988 days. Monitoring period ranged from 31 to 1349 days, with one known founder alive at the end of our reporting period. Fourteen of the 19 translocated wolves (74%) survived at least 6 months. For wolves with a known date of death, the average survival time was 405 days. Average annual survival of wolves during September 24, 2018–September 1, 2023 was 0.74 (95% CI = 0.58–0.94, Supporting Information S3). We did not have sufficient sample sizes to estimate year-specific survival. We did not detect a difference in survival among wolves across sex, source population, or release period, likely due to small sample sizes. Wolves translocated from Michipicoten Island had the greatest absolute annual survival among translocated wolves (Figure 3; Supporting Information S3). The estimated minimum number of wolves during October 15–April 14 was 10 in 2019–2020, 23 in 2020–2021, 23 in 2021–2022, and 27 in 2022–2023. The minimum number of pups detected during October 15–November 14 was 2 in 2019, 11 in 2020, 9 in 2021, and 7 in 2022.

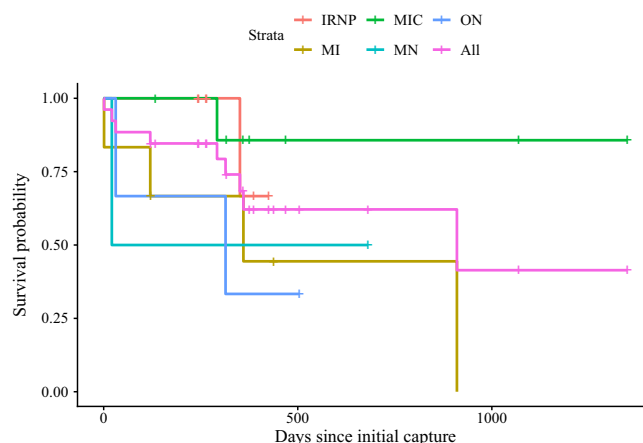


FIGURE 3 Kaplan–Meier survival estimates for wolves introduced to Isle Royale National Park, Michigan, USA, 24 September 2018–September 2023. Colored lines represent source populations: IRNP, unmarked animals captured in Isle Royale National Park, Michigan, USA; MI, Upper Peninsula, Michigan, USA; MN, Grand Portage Reservation, Minnesota, USA; JOS, Jostle Lake, Ontario, Canada; MIC, Michipicoten Island, Ontario, Canada; All, all wolves combined regardless of source population.

3.4 | Pack formation and breeding

We confirmed the formation of three packs and documented 10 litters during September 24, 2018–September 1, 2023. Two packs formed during spring–fall 2019 and produced pups in spring 2020. The breeding pairs in these packs and the boundaries of their home ranges appeared stable from formation in 2019 through winter 2023 (Figure 2). A third pack developed at the northeast end of IRNP in 2022 and produced pups in 2022 and 2023 (Figure 2). The estimated annual proportion of pups in the population ranged from 0.15 to 0.33.

We documented a single litter produced by the Michipicoten breeding female shortly after her translocation in March 2019. GPS data indicated she denned in south-central IRNP in April 2019; the timing of this behavior indicated she was pregnant during translocation. Location data from the Michipicoten breeding male indicated he visited the den site multiple times in April 2019 but ceased associating with the female in May. We detected two pups on remote cameras near the den area in September and October 2019. The breeding female's radio collar failed in April 2020, and we did not detect evidence

of her denning or pups in this area thereafter. Because this female did not appear to establish a bond with another wolf or reproduce in successive years, we consider this a breeding event but not the formation of a pack.

A female from Minnesota and two males from Michipicoten Island formed a pack in the western end of IRNP in March 2019 (Figure 2). The female of this group displayed denning behavior (based on GPS clustering) in March 2020; we collected pup scat from this den site in July 2020 and documented four pups on cameras in the pack's core area in October 2020. Due to radio collar failure, we were unable to track the breeding pair to confirm denning in 2021. However, we detected a pup on a remote camera in the pack's range in November 2021. We re-collared the suspected breeding male from this pack in winter 2022, and he began to display provisioning behavior in April 2022. In July 2022, we collected pup scat from the same den site used in 2020 and observed three pups during a howl survey of a rendezvous site in August 2022. The breeding male's radio collar failed in early March 2023, and we did not detect evidence of breeding activity by this pack in 2023 (Figure 2).

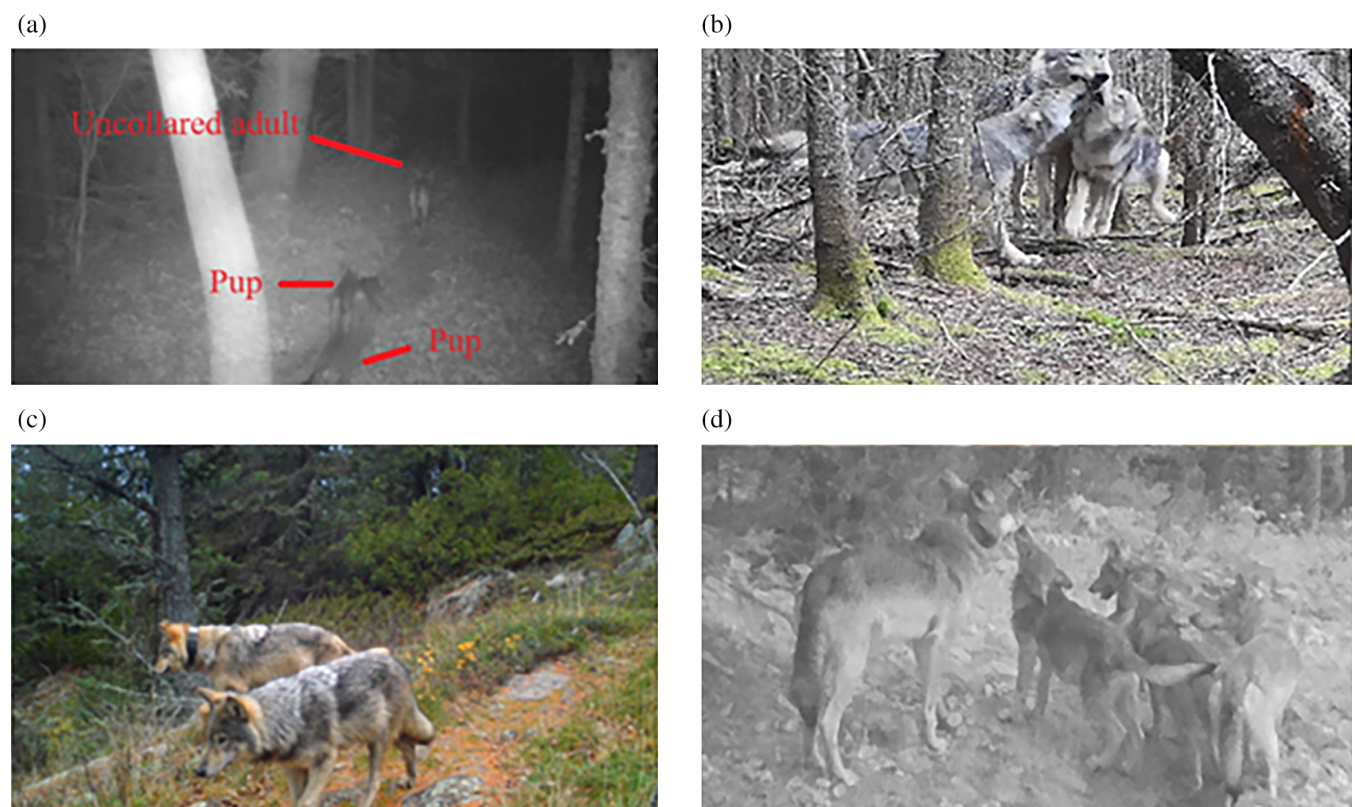


FIGURE 4 Examples of camera images used to estimate the minimum number of wolves alive. Isle Royal National Park, Michigan, USA. (A) Uncollared adult and two pups July 2022. (B) Two pups and an adult at a rendezvous site August 2022. (C) A collared and uncollared member of the eastern pack November 2021. (D) Three pups with a collared and uncollared adult in the northeastern group August 2022.

A full-sibling pair from Michipicoten Island (Hervey et al., 2021) formed a pack in the Eastern portion of the island in October 2019. This pack occupied an area in central IRNP (Figure 2). We confirmed this pack produced litters each year during 2020–2023. While neither breeding adult had a functional radio collar during 2020, we detected four pups on cameras in the pack's territory in October 2020. In 2021, we re-collared the breeding

male and this wolf began displaying provisioning behavior in May 2021. We detected three pups during a rendezvous site howl survey in August 2021, and three pups on cameras in November 2021. In February 2022, we radio collared a non-breeding male that displayed provisioning behavior in May 2022. We detected four pups on cameras near this pack's rendezvous site in July 2022 and during a howl survey in August 2022. In 2023, we collared a suspected non-breeding male who displayed provisioning behavior in May 2023. We detected four pups on a camera placed near the pack's rendezvous site in July 2023.

A pack formed in northeast IRNP in 2022 and reproduced in 2022 and 2023 (Figure 2). Remote cameras detected two adults traveling with three pups in northeastern IRNP in August 2022 (>20 km from the nearest known rendezvous site associated with the eastern pack). This group likely reproduced in 2023 as remote cameras detected an uncollared female in the area with enlarged mammary glands indicative of lactation in June 2023.

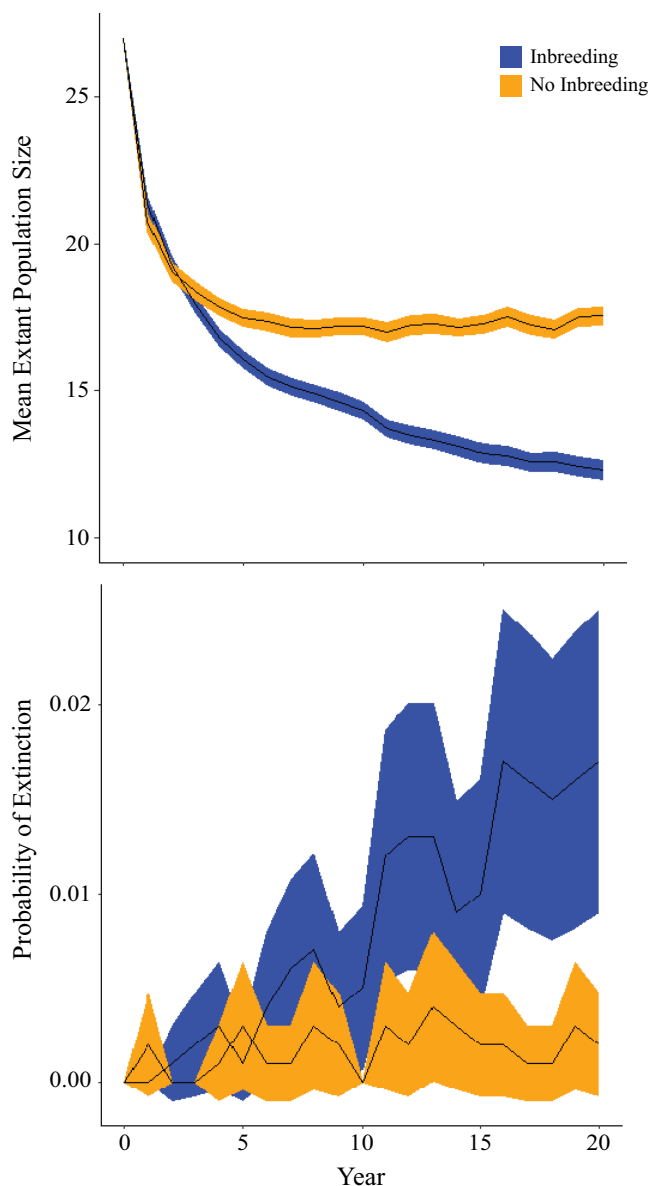


FIGURE 5 Population viability analysis (PVA) simulation results for wolf population size (top panel) and probability of extinction (bottom panel) in Isle Royale National Park, Michigan, USA. Solid lines represent mean values from 1000 simulations, filled area represent 95% confidence intervals, and color represents inbreeding scenario (orange—inbreeding over first 20 years post-reintroduction does not affect first year survival or fecundity; blue—inbreeding over first 20 years post-reintroduction affects first year survival and fecundity).

3.5 | PVA results

3.5.1 | No inbreeding depression scenario

Over a 20-year period the probability of wolf extinction in IRNP was 0.04 (SE 0.006), with a growth rate of 0.11 (SE 0.002). The expected mean population size for extant populations after 20 years was 17.07 (SE 0.15) individuals (Figure 5).

3.5.2 | Inbreeding depression scenario

Over a 20-year period, the probability of wolf extinction in IRNP was 0.18 (SE 0.01), with a growth rate of -0.02 (SE 0.002). The expected mean population size for extant populations after 20 years was 12.19 (SE 0.29) individuals (Figure 5). Final genetic diversity was 0.67 (SE 0.004).

4 | DISCUSSION

Wolf demographics 5 years post-introduction, including cause-specific mortality, survival, reproduction, pack formation, and wolf counts were within historic ranges. Given the trends in reproduction, recruitment, counts, and population viability we anticipate that the IRNP wolf translocation project will meet its objectives of restoring a wolf population persisting over 20 years. However, the population could experience declines in genetic diversity due to isolation (Hervey et al., 2021). Continued monitoring of demographic parameters linked to inbreeding

TABLE 1 Comparison of wolf demographics during the 5-year post-translocation period (2018–2023) to demographic rates prior to wolf decline (1960–2000).

Demographic metric	Current	Historic	Reference period	Source
Wolf count				
Max	27	50	1960–2000	Romanski et al. (2020); Hoy et al. (2022)
Min	10	11	1960–2000	Romanski et al. (2020); Hoy et al. (2022)
Mean	21	22	1960–2000	Romanski et al. (2020); Hoy et al. (2022)
Survival	0.74	0.84–0.87	1974–1975	Peterson and Page (1988)
		0.49	1980–1982	Peterson and Page (1988)
		0.66–0.67	1983–1986	Peterson and Page (1988)
		0.60–0.74	1999–2008	Marucco et al. (2012)
Pup proportion ^a	0.15–0.33	0.2–0.4	1975–1980	Peterson et al. (1998)
Strife ^b	1.0	0.66	1975–1986	Peterson and Page (1988)

^aProportion of the wolf population comprised of young of the year.^bProportion of known cause mortalities attributed to intraspecific strife.

depression (first-year survival and fecundity) will be necessary to guide management decisions.

Translocated wolves had mortality causes and survival rates similar to historic periods of population growth or stability (Peterson & Page, 1988). We observed three capture/translocation related mortalities, one associated with a foot-hold trap injury. Foot-hold traps have higher injury rates than aerial darting and netting due to longer restraint times (Van Ballenberghe, 1984). Despite these early mortalities, 74% of the released wolves survived >6 months, similar to the 73% average success rate of other canid translocations (Thomas et al., 2023), indicating our methods were safe and practical to capture, transport, and release wolves. The only identified non-capture related cause of wolf mortality in IRNP was intraspecific aggression. Our locational data indicated that intraspecific mortalities involved solitary wolves traveling in areas used by packs. This observation supports previous research that dispersing and lone wolves have lower survival rates due to crossing unfamiliar terrain and the risk of encountering packs (Mech & Boitani, 2003). We did not detect any mortalities of known pack-associated wolves within or at the periphery of another pack's territory, evidence of a lack of inter-pack conflict. Wolf packs engage in complex behaviors to reduce encounters (Harrington & Mech, 1982; Peters & Mech, 1975) and when interacting, mortality is relatively rare. Less than 10% of aggressive pack-to-pack interactions resulted in mortality in Yellowstone National Park (Cassidy et al., 2015). Intraspecific aggression is linked to population density (Cubaynes et al., 2014) and seasonality (Mech & Barber-Meyer, 2017) and will likely continue to be a leading cause of mortality for IRNP wolves, especially for young dispersers (Peterson & Page, 1988), given the

island's small size, dense wolf population, and limited dispersal opportunities. Other sources of mortality historically common on IRNP include starvation and accidents (Peterson & Page, 1988; Vucetich & Peterson, 2013). These sources of mortality may increase in frequency as prey populations decline and wolves experience more nutritional stress.

Adult survival is a key factor influencing large mammal population growth rates (Gaillard et al., 1998). Post-release annual survival for wolves was greater than annual survival during many periods of population growth and stability in IRNP (Table 1). The high survival of translocated wolves was likely a result of abundant prey and a lack of anthropogenic mortality in IRNP. Wolf survival may decline in IRNP in the near future due to density-dependent factors including intraspecific aggression (Cubaynes et al., 2014). Wolves translocated from Michipicoten Island had the greatest absolute survival and founded two of the packs on the island. This supports results from reintroductions of social animals, where translocated family groups had greater survival than animals translocated without family members (Garai et al., 2004; Shier, 2006).

Translocated wolves reproduced each year post-translocation, producing at least 10 litters and 29 pups. Pup production on IRNP is similar to previous estimates where pups comprised 20%–40% of the population (Peterson et al., 1998). The presence of unmarked adults in IRNP suggests successful pup recruitment or immigration. Continued genetic monitoring of the population can elucidate the origin of unmarked animals and the frequency of genetic exchange with the mainland. Translocated wolves formed two packs in late 2019. The boundaries of these territories were relatively stable

during 2019–2023 and reflect historic territories on IRNP (Figure 2; Mech, 1966; Vucetich & Peterson, 2009). We elected to use a LoCoH estimator because it is well suited to systems with hard geographic boundaries such as IRNP; however, LoCoH does not address autocorrelation and may underestimate home-range area (Noonan et al., 2019). Future research may consider alternative approaches that explicitly account for autocorrelation (e.g., autocorrelated kernel density estimation [AKDE]) or occurrence distributions (e.g., Brownian bridge or correlated random walk models) to better evaluate how animals respond to linear features or specific landscape elements (Alston et al., 2026).

Social bonds and familiarity with an island ecosystem could have facilitated the Michipicoten wolves' success. A full-sibling pair from Michipicoten founded the eastern pack in 2020 and produced at least 12 pups 2020–2023. Full-sibling breeding is rare in wolves (Smith et al., 1997) but is more likely to occur between siblings from different litters (Geffen et al., 2011), which these individuals likely were (B. Patterson personal communication). Given the availability of unrelated wolves, it is notable and unanticipated that these animals bonded shortly after translocation. For social animals, establishing new social bonds is stressful and familiarity likely reduces stress when acclimating to a new environment (Goldenberg et al., 2019). Two male Michipicoten siblings (Hervey et al., 2021) began traveling with a female from Minnesota shortly after translocation. These wolves formed the western pack and were associated as a trio for >1 year. This may be an example of paired dispersal or a coalition, which is rare in wolves (Mech & Boitani, 2003) but can occur in high-density populations and may function as a strategy to increase success in the event of aggressive interactions (Cassidy & McIntyre, 2016). In addition to pre-existing social bonds, wolves translocated from Michipicoten had experience living in an island environment. Individuals translocated to areas ecologically close to their source location tend to have higher success rates (Letty et al., 2007).

Interestingly, the only bonded pair we released (the breeding pair from Michipicoten Island) did not form a lasting association once on IRNP. “Divorce” is rare in wolves (Mech & Boitani, 2003; Milleret et al., 2017) and may have been a result of social disruption due to translocation. However, there is some evidence that the pair had disbanded before translocation. On Michipicoten, the male was captured via aerial netting traveling without the female in late February 2019. Due to logistical challenges, the female was not captured and translocated to IRNP until a month later. In addition, preliminary genetic analysis suggests the pups born on IRNP in April 2019 were not sired by her long-term mate (S. Hervey,

unpublished data, personal communication). We failed to detect either animal after winter 2020 and did not obtain data, genetic or otherwise, to suggest either integrated into new packs.

Pack disruption and the loss of social cohesion can increase the likelihood of incestuous pairings (Rutledge et al., 2010). We know of no other wolf translocation project that hard-released a free-ranging family group in the manner we did. The Yellowstone reintroduction project used acclimatization pens and soft-released breeding pairs and their pups-of-the-year together (Fritts et al., 1997). Only two of the first 30 matings of this population involved related individuals (VonHoldt et al., 2008). In contrast, the Idaho wolf translocation project hard-released older pack members together (2–3 individuals). These wolves periodically associated but did not form packs or breed with relatives (Fritts et al., 1997). In addition to release strategy, translocations in Yellowstone and Idaho differed from ours in the prevalence of vacant available habitat and existence of dispersal opportunities. IRNP has hard, nearly impassable boundaries and very few wolves are known to have dispersed from the island (Orning et al., 2020). This restricted movement can limit mate choice and increase kin encounter rates (Geffen et al., 2011; Stevens & Wiley, 1995). In addition, low wolf numbers and high prey density may reduce the pressure to disperse (Morales-González et al., 2022). Dispersal functions as an inbreeding-avoidance behavior in canids (Geffen et al., 2011; Randall et al., 2007). Potentially, the social disruption caused by hard releasing the Michipicoten Island group and the lack of dispersal options within IRNP interrupted the typical inbreeding avoidance behavior of these wolves.

Using a soft release strategy could have maintained social cohesion in the Michipicoten group or allowed for bonding between non-related wolves. However, the benefits of using soft releases to maintain or create bonds in social species are unclear. For example, pre-release penning appeared to facilitate bonding in translocated red wolves compared to solitary releases (McLellan & Rabon, 2006). Reintroduction programs for African wild dogs (*Lycaon pictus*) frequently introduce unrelated individuals in pre-release enclosures, yet social integration occasionally fails, resulting in aggression or pack breakdown (Marneweck et al., 2019). Similarly, despite efforts to form a single cohesive group using soft-release, translocated lions (*Panthera leo*) in South Africa reformed into prides based on relatedness (Kilian & Bothma, 2003). Bangs et al. (1998), Fritts et al. (2001), and the Interagency Field Team (2005) each noted that release method did not affect individual wolf success, but hard-released wolves traveled farther and had lower pack cohesion. The primary benefit of using soft release strategies in

canid reintroduction is the elimination of long-distance roaming behavior (Moehrenschrager & Somers, 2004), which is effectively mitigated by the hard boundaries and limited area of IRNP. Soft releases require considerable resources and may expose wolves to additional stress, disease, and habituation to humans (Resende et al., 2021; Teixeira et al., 2007). Based on our results and previous translocations, for areas with conditions like IRNP (difficult access and limited dispersal opportunities), we recommend hard-releasing bonded pairs, unrelated wolves, or same-sex packmates to facilitate pack formation and mitigate potential inbreeding.

The IRNP wolf count has increased during the 5 years since translocation. By 2019, wolves had formed packs and successfully reproduced. In three of 5 years during 2018–2023, the minimum wolf count exceeded the 50-year (1960–2009) average of 22 individuals (Romanski et al., 2020; Vucetich & Peterson, 2016). Our minimum wolf counts derived from remote cameras are similar to, but slightly lower than, estimates derived from aerial counts conducted during the same years (Hoy et al., 2023). Our minimum counts may be enhanced by including genetic mark-recapture (Caniglia et al., 2012) or time to detection models (Ausband et al., 2022). In addition, using remote cameras, we documented breeding events that were not identified using GPS monitoring and howl surveys. These results indicate that remote cameras are a useful non-invasive tool for monitoring wolf abundance and reproduction in IRNP.

Finally, our Population Viability Analysis indicates that even with high levels of inbreeding depression, the IRNP wolf population will meet the NPS's goal of establishing a wolf population that will persist for 20 years. Both of our scenarios indicated a low probability (<0.2) of population extinction in the next 20 years. However, the PVA scenario with inbreeding depression had a negative population growth rate, indicating the wolf population will decline if there is a marked decline in first-year survival and fecundity in successive generations due to inbreeding depression. Population Viability Analysis outputs are sensitive to model assumptions, specifically carrying capacity, and should be interpreted cautiously. Alternative process models including spatially explicit individual-based modeling (Atzeni et al., 2026; Letcher et al., 1998) may be useful to model population persistence in a spatially constrained population.

While inbreeding and homozygosity is likely to increase in the population (Hervey et al., 2021) it is unclear how quickly the negative effects of inbreeding depression will become evident. Some small wolf populations persist despite low levels of genetic diversity and inbreeding (Mooney et al., 2023). The effects of inbreeding depression will likely depend on the presence of

deleterious recessive mutations in the founding population (Robinson et al., 2019). All IRNP wolf founders are from large, outbred populations that may have high rates of heterozygosity for deleterious recessive traits. Future monitoring of indicators of inbreeding depression including key demographic rates (e.g., fecundity and first year survival) and physical characteristics (e.g., spinal malformities) could further inform management decisions to ensure the wolf population persists beyond the scope of the original recovery plan.

5 | CONCLUSIONS

During the first 5 years post-translocation, the IRNP wolf restoration project has met its objective to restore a self-sustaining wolf population. The population will likely persist without additional translocations over the next 20 years. Translocating wolves, specifically family units, from nearby source populations with experience preying on large ungulates and beaver facilitated pack formation on IRNP. However, the social and numerical dominance of a family unit could complicate the long-term genetic viability of the IRNP wolf population, as we suspect all pups born on the island share common parents/grandparents from Michipicoten Island. Inbreeding depression likely contributed to the decline of the previous wolf population, and reduced connectivity with the mainland due to warmer winters could limit future genetic exchange. Monitoring the population's genetic health can help inform future management decisions including the need for additional translocations.

AUTHOR CONTRIBUTIONS

Adia R. Sovie: Formal analysis; investigation; data curation; writing—original draft; visualization; supervision. **Mark C. Romanski:** Conceptualization; methodology; validation; investigation; resources; writing—review and editing; supervision; project administration; funding acquisition. **Dean E. Beyer Jr:** Conceptualization; methodology; validation; investigation; resources; review and editing; supervision; project administration; funding acquisition. **Hailey M. Boone:** Formal analysis; investigation; data curation; writing—review and editing. **Edmund J. Isaac:** Investigation; supervision; project administration. **Kenneth F. Kellner:** Methodology; data curation; writing—review and editing. **David Marneweck:** Investigation; data curation; writing—review and editing; supervision. **Seth A. Moore:** Conceptualization; methodology; validation; investigation; resources; review and editing; supervision; project administration; funding acquisition. **Elizabeth K. Orning:** Investigation; data curation; writing—review and editing, supervision.

Brent R. Patterson: Conceptualization; methodology; validation; investigation; resources; review and editing; supervision; project administration; funding acquisition. **Lynette R. Potvin:** Investigation; supervision; project administration. **Michelle L. Verant:** Conceptualization; methodology; validation; investigation; resources; review and editing. **Jerrold L. Belant:** Conceptualization; methodology; validation; investigation; resources; writing—review and editing; supervision; project administration; funding acquisition.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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DATA AVAILABILITY STATEMENT

Non-sensitive data used in this manuscript will be publicly available in Dryad.

ETHICS STATEMENT

The NPS Institutional Animal Care and Use Committee approved translocation and capture protocols in IRNP. Each jurisdiction followed their agencies' respective animal care and use procedures.

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