

DEMOGRAPHICS AND MOVEMENTS OF MUTE SWANS IN MICHIGAN, USA

By

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ABSTRACT

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Mute swans (*Cygnus olor*) were introduced by humans to Michigan with translocation of one pair from Iowa into Michigan's Charlevoix County in 1919. Michigan's mute swan population peaked in 2013 with an estimated abundance of 17,520 individuals. This coincided with the Michigan Department of Natural Resources drafting a policy which sought fewer than 2,000 wild mute swans present in Michigan by 2030. However, uncertainty in life stage-specific demographic rates and movements did not allow for robust analyses of levels and types of management needed to achieve the long-term goal. A pilot project was launched in 2014 to investigate inter- and intrastate movements of mute swans within the Great Lakes region. This effort spawned a formal research partnership between Michigan State University, the Michigan Department of Natural Resources, and the Wildlife Services division of the U.S. Department of Agriculture Animal and Plant Health Inspection Service. The goals of this research were to refine mute swan management strategies in Michigan by incorporating region-specific parameters into demographic models and to understand seasonal movements of mute swans.

We investigated nesting ecology and life stage-specific survival and movements for mute swans located in the Lower Peninsula of Michigan. We used aerial surveys to locate nests and fledged young within site boundaries. We used boats to neck collar individuals and visit nests. Estimated nest survival ($\hat{S} = 0.701$), mean egg volume ($328.2 \pm \text{SD } 26.6 \text{ cm}^3$), and mean incubation initiation date (8 April) were comparable to estimates from other portions of mute swan range. Mean clutch size ($7.0 \pm \text{SE } 0.15$) was slightly higher than in areas of their native

range, but comparable to estimates from the introduced range in North America. Apparent cygnet survival (i.e., hatch to estimated fledge; 0.27 ± 0.01), brood survival (0.58 ± 0.03), overall productivity (1.2 fledglings/pair), and percentage of gray young in newly hatched broods (36.9% gray plumage) were slightly lower compared to portions of native range. Observed breeding productivity related to saturation of characteristic nesting habitat ($\hat{\beta} = -0.9792$, $p = 0.04$). Seven-month survival estimates for fledged young ($\hat{S} = 0.526$, 95% CI = $0.342 - 0.703$) were slightly lower than areas of their native range and may be related to ratio of gray and leucistic morph individuals in our population ($\hat{\beta}_{\text{leucistic}} = -0.908$, 95% CI = $-2.086 - 0.269$). Estimated annual survival for non-breeding ($\hat{S} = 0.698$, 95% CI = $0.419 - 0.881$) and breeding swans ($\hat{S} = 0.850$, 95% CI = $0.686 - 0.936$) was slightly less but near reported values for native range. Breeding female mute swans remained on or close to nesting territories year-round and were furthest from territories during winter ($\bar{x} = 11.3$ km). Juvenile-marked female swans tended to move farther from natal areas than juvenile-marked males during their first 2 years of life; however, juvenile-marked females were closer to natal territories than juvenile-marked males at the end of the study.

We parameterized a density-dependent matrix population model for Michigan using estimated values from this research. This model suggests that survival rates for juvenile, non-breeding, and breeding swans should be reduced by 26% annually to achieve the long-term goal of fewer than 2,000 mute swans statewide by 2030. This requires a 17% removal of the annual population to reach the long-term goal (12,760 swans removed 2018 – 2029). Importantly, removals must be spread evenly across all life stages. Targeting removal across all adult population segments is the most efficient control strategy, as 94% of mute swan nests would need to be destroyed annually (15,748 nests destroyed 2018 – 2029) to achieve the same goal.

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CHAPTER 1: INTRODUCTION

Mute swans (*Cygnus olor*) are a large swan species native to northern and central Eurasia (Allin et al. 1987), but became established in North America during the 20th century. Concerns regarding overabundance of mute swans exist throughout their native (Wood et al. 2014) and introduced ranges (Reese 1975, Petrie and Francis 2003). Population expansion in their native range resulted from milder winters, protection from harvest, banning of lead fishing weights in portions of their range, and creation of artificial nesting habitat through urban and agricultural expansion (Kirby et al. 1994, Fouque et al. 2007). Expansion in their introduced range resulted from abundant submerged aquatic vegetation (SAV), protection from harvest, supplemental feeding (Gelston and Wood 1982), and translocation of mute swans by humans. Early records indicate that mute swans were brought to North America in the late 1800s to adorn city parks and estates (Baldassarre 2014). The first reports of feral breeding populations in North America occurred in the Atlantic flyway along the Hudson river in 1910 (Baldassarre 2014). Mute swans first established in Michigan in 1919 when a breeding pair was transferred from a private estate in Iowa to Round Lake in Charlevoix County, Michigan, amid concerns of aggression toward children at the Iowa estate (Gelston and Wood 1982). Populations along the Atlantic coast and throughout the Great Lakes region continued to increase throughout the 20th century. Population estimates in the Atlantic flyway indicate that the population of feral mute swans reached 14,000 in 2002 (Atlantic Flyway Council 2003). Estimates of mute swan populations in Michigan indicate that the population grew rapidly through 2010 with a long-term annual growth rate of 9.3% but peaked near 2013 ($n = 17,520$) with onset of heightened control efforts (D. R. Luukkonen, Michigan Department of Natural Resources, unpublished data).

Management in North America

Management of mute swans in North America is implemented to alleviate conflicts with native wildlife, aquatic ecosystems, and humans; however, reductions of mute swans is often met with opposition from segments of the public (Allin and Husband 2004, Blackburn et al. 2010, Jager et al. 2016). However, management of mute swans is supported by a broad variety of environmental organizations (U. S. Department of Agriculture 2012). Opposition to culling mute swans and subsequent litigation led to the United States Court of Appeals for the D.C. Circuit granting mute swans federal protection under the Migratory Bird Treaty Act on 28 December 2001. Congress passed the Migratory Bird Treaty Reform Act of 2004 which requires the U. S. Fish and Wildlife Service to publish an official list of bird species to which the Migratory Bird Treaty Act did not apply (U. S. Department of Agriculture 2012). This list, which included mute swans, was published in the federal register on 15 March 2005 (U. S. Fish and Wildlife Service 2005). This clarification removed ambiguity in federal protection of nonnative birds and relegated mute swan management to individual states.

Migratory bird populations in North America, specifically those with consumptive use, are managed cooperatively across political borders to ensure equitable access and biological sustainability. This manifests in a system with 4 administrative flyway regions (i.e., Atlantic Flyway, Mississippi Flyway, Central Flyway, and Pacific Flyway; Nichols et al. 1995; Figure 1.1). Mute swans can be found in all administrative flyways; however, highest abundance of mute swans has historically occurred in the Atlantic and Mississippi Flyways (Mississippi Flyway Council 2012).

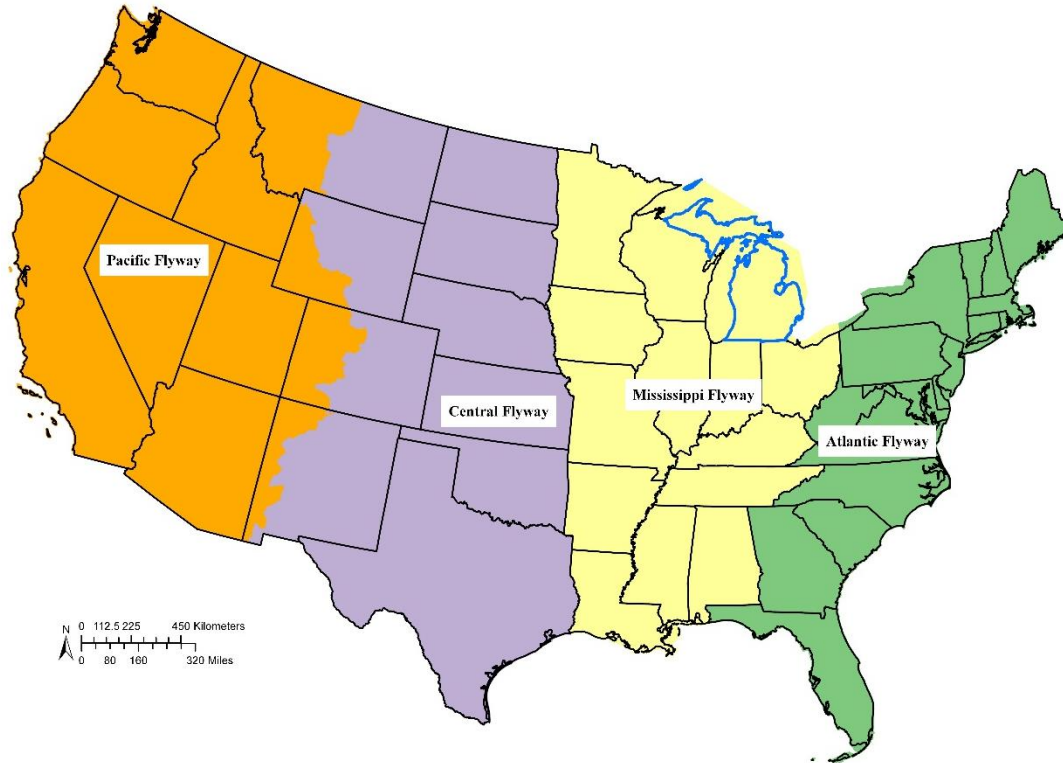


Figure 1.1. Location of Michigan (highlighted in blue) within the 4 administrative flyways of the conterminous United States of America.

Coordination of management goals is partially accomplished through administrative flyway councils that establish flyway-wide population objectives. However, state-level management of mute swans in the United States varies in scope and urgency. The Atlantic Flyway Council established their first formal mute swan management plan in 2003 that sought to reduce abundance of mute swans in the Chesapeake Bay area to fewer than 3,000 individuals by 2011 (Atlantic Flyway Council 2003). This plan was revised in 2015 after initial control efforts by partner states failed to achieve the flyway-wide reduction goal set in 2003 (Costanzo et al. 2015) despite localized success in some regions such as Chesapeake Bay (L. Hindman, unpublished data). The Michigan DNR established a policy for managing mute swans in 2006 with a short-term goal of reducing the mute swan population to 3,500 individuals by 2010 and a long-term goal of no more than 2,000 mute swans in Michigan by 2030 (Michigan Department

of Natural Resources 2006). The Mississippi Flyway Council formally established a mute swan management plan in 2012 with a goal of no more than 4,000 mute swans in the flyway by 2030. Concomitantly, the Michigan DNR updated their mute swan management policy with revised short- and long-term goals which, respectively, were to: 1) remove all mute swans on DNR-administered lands and reduce statewide population growth to zero, and 2) maintain fewer than 2,000 mute swans statewide by 2030 (Michigan Department of Natural Resources 2012). The Wildlife Services section of the U. S. Department of Agriculture Animal and Plant Health Inspection Service conducted an environmental assessment to review management options and potential environmental impacts of their involvement in mute swan damage management activities in Michigan in 2012 (U. S. Department of Agriculture 2012) which culminated in a finding of no significant impact (FONSI) of mute swan damage management in Michigan. The revised policy program and procedures published by the Michigan DNR in 2012 and FONSI in the environmental assessment by USDA-APHIS Wildlife Services established a foundation for mute swan management in Michigan. However, the level of removal needed to achieve the short- and long-term goals was uncertain due to ambiguity in mute swan demographics and particularly the sub-adult life cycle of mute swans in Michigan.

Demographic and life history comparison

Stochastic population models developed by Ellis and Elphick (2007) demonstrated that reduction in adult survival was likely the most socially acceptable and biologically efficient strategy to reduce mute swan populations in the short term; however, the model structure assumed absence of density-dependence in vital rates and was parameterized using research conducted in the native range of mute swans. An attempt to use the Ellis and Elphick (2007) model structure to predict observed abundance estimates of mute swans in Michigan suggested

that the mute swan population should have experienced exponential growth in the 1970s and 1980s; however, exponential growth of the mute swan population was not observed until the 1990s and 2000s (D. R. Luukkonen, unpublished data). Basing management scenarios on ill-fitting population models lead to unrealistic projections of population abundance under management scenarios; therefore, a need to understand variation in demographics across the geographic range of mute swans exists.

Vital rates likely differ for a species between native range where evolutionary forces shaped life-history traits and an introduced range where the species is subject to varying resource availability, different climatic factors, different interspecies interactions, and changing interplay between human and natural systems. Conover and Kania (1999) estimated clutch sizes in mute swans of Chesapeake Bay as slightly higher (6.6 ± 0.1 eggs/clutch) than estimates from native range (5.9 ± 2.2 eggs/clutch; Perrins and Reynolds 1967), although Wood and Gelston (1972) found lower (4.5 eggs/clutch) clutch sizes in a semi-captive flock in northern Michigan when swan abundance was below current levels. Reese (1980) estimated cygnet survival at 82% in Maryland while Brown and Brown (2002) estimated survival of cygnets at 69% in the United Kingdom. Conover et al. (2000) found cygnet survival varied from 53% to 87% on the Atlantic Coast and depended on cygnet color morph.

Two color morphs of mute swan cygnets exist in varying proportions throughout introduced and native ranges. Variation exists due to preferential selection of the recessive white color morph in swan propagation programs (Munro et al. 1968, Nelson 1976, Enright 1994). Historically, white color morph individuals made up only 1% of the population in Britain, but nearly 20% of the sub-populations in eastern Europe are composed of white morphs (Bacon 1980). Leucistic cygnets have lower survival rates than those exhibiting gray juvenile plumage

(Conover et al. 2000). Conover et al. (2000) also found white plumage males and females more likely nested earlier than gray morph individuals of the same age. Ratio of color morphs in Michigan was unknown at the initiation of this study; however, leucistic morph individuals were prevalent in populations nearby in Ontario (Lumsden 2016).

Vital rates also exhibit temporal variation within a geographic extent due to biotic and abiotic factors. Interannual variation in survival and reproductive productivity may result from factors such as winter severity (i.e., ice coverage) or seasonal food availability. Birkhead et al. (1983) found egg laying date and clutch size related to mean winter temperature (i.e., December - March) prior to the breeding season although the preceding mean winter temperature was not ultimately related to number of cygnets fledged. Czapulak and Wieloch (1991) and Czapulak (2002) found that clutches initiated later in the nest season were smaller and contained smaller eggs (i.e., egg volume) while also finding that mean egg size in clutches influenced cygnet survival to 100 days. Scott and Birkhead (1983) determined that mute swans with high quality territories (i.e., abundant aquatic vegetation) laid earlier clutches and had larger clutch sizes compared to swans in other territories; however, they did not find a relationship between territory quality and number of fledged young per pair or cygnet weight.

These findings along with potential for density dependence in reproductive parameters of mute swans (McCleery et al. 2002, Nummi and Saari 2003) suggest that vital rates and life history strategies for mute swans vary between native and introduced ranges as well as among populations originated through discrete origins (i.e., translocation of a few individuals). Interannual, genetic, and geographic variation must be accounted for when implementing control strategies for invasive species, such as mute swans. Much is known about demographics, movement, and population trends in the native range of mute swans; however, comparatively

little is known about vital rates and movements in North America, especially in the Great Lakes region.

This study was implemented in Michigan with the expressed goals to 1) estimate survival rates for breeding, non-breeding, and immature swans, 2) document reproductive parameters and breeding productivity, 3) understand natal and seasonal movements of juvenile and adult swans, 4) develop population projection models using derived demographic parameters, and 5) provide strategies to achieve short- and long-term mute swan management goals (Figure 1.2).

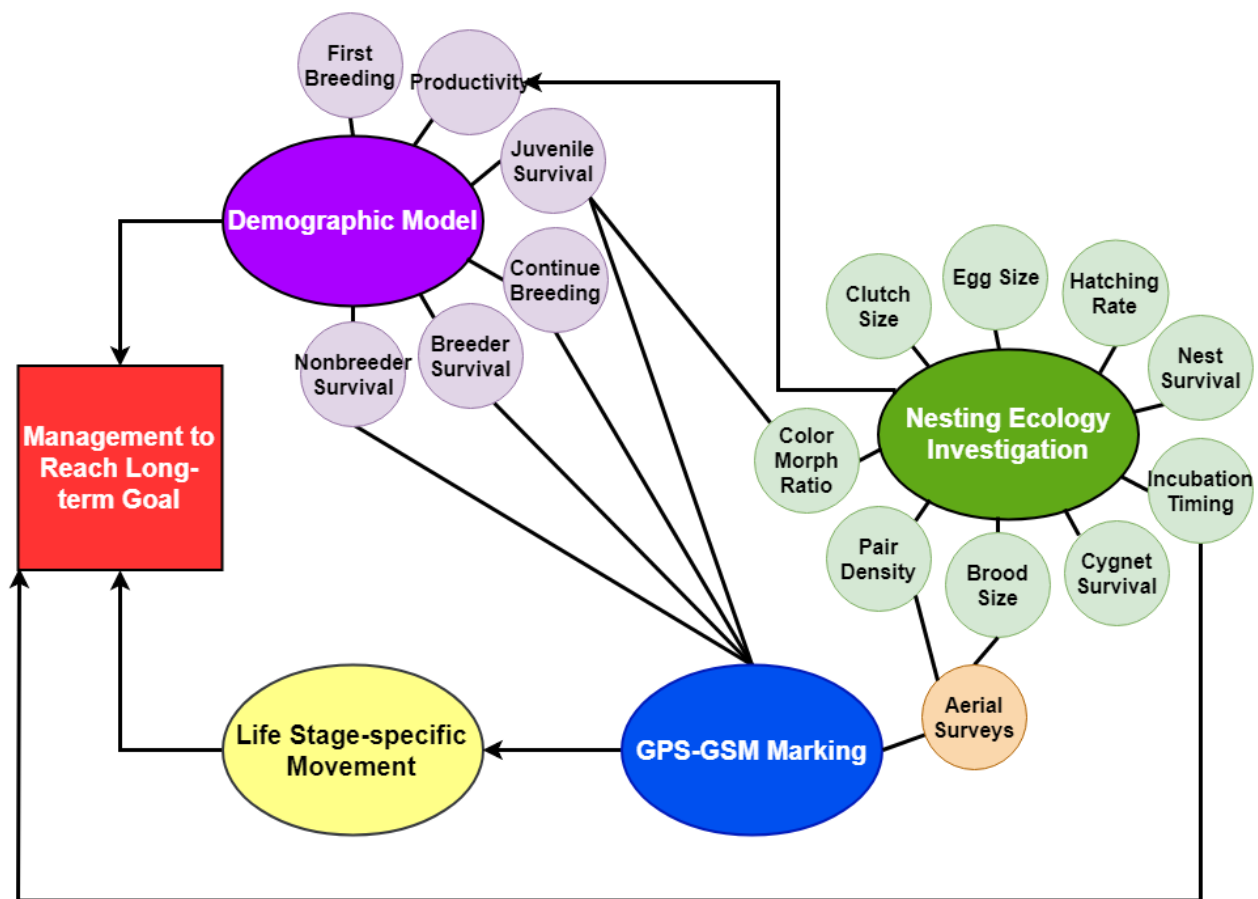


Figure 1.2. Conceptual flow diagram showing integrated nature of research methods and how they were used to refine mute swan management in Michigan, USA.

STUDY DESIGN

Study Area

Michigan is biologically and administratively located in the Mississippi Flyway (Figure 1.1; U. S. Fish and Wildlife Service 1959, Boere and Stroud 2006) and the Upper Mississippi River and Great Lakes Region Joint Venture (NAWMP Committee 1999). We focused research in the Lower Peninsula of Michigan (centroid 43° 29' 19.2", -84° 37' 34.2") where most mute swan detections recently occurred during breeding waterfowl surveys (Michigan DNR, unpublished data). Land cover in Michigan's Lower Peninsula represents a south to north gradient of deciduous hardwoods (i.e., oak [*Quercus* spp.], beech [*Fagus grandifolia*], and maple [*Acer* spp.]) interspersed with agriculture to mixed forest (i.e., pines [*Pinus* spp.], spruces [*Picea* spp.], firs [*Abies* spp.], maples, oaks, and aspen [*Populus* spp.]; Pugh et al. 2017). There are over 26,000 individual lakes in Michigan ≥ 0.4 hectares in size with just over 18,000 occurring in the Lower Peninsula (Breck 2004).

Focal site selection

Annual surveys of breeding and wintering waterfowl by the Michigan Department of Natural Resources (DNR), surveillance efforts by U.S. Department of Agriculture Wildlife Services, and broad-scale habitat suitability guidelines by Weaver et al. (2012) helped guide selection of focal study sites. We used a geographic information system (GIS; ArcGIS 10.3.1, ESRI, Redlands, CA, USA) to stratify the Lower Peninsula into physiographic regions (Schaetzl et al. 2013). We overlaid hydrologic and public land survey system (PLSS) township shapefiles (Center for Shared Solutions and Technology Partnerships 2015) to further stratify physiographic regions. We summarized total area (ha) and shoreline length (km) of lakes within each township. We linked locations where ≥ 1 mute swan per square mile was estimated during the breeding

season of 2015 via Michigan DNR spring waterfowl surveys to PLSS townships. We used mean amount of shoreline in PLSS townships where estimated spring density was ≥ 1 mute swan per square mile was 2011 – 2015 (≥ 40 km) to identify townships where adequate shoreline edge existed to likely have multiple nesting mute swan pairs during the first breeding season of this research (2016; Figure 1.3).

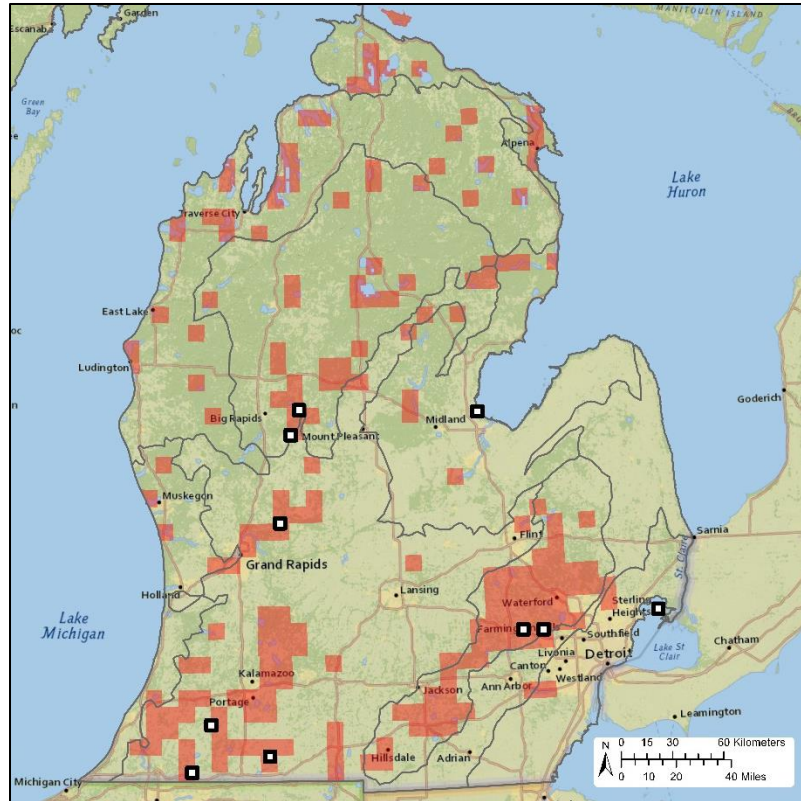


Figure 1.3. Ten preliminary study sites (white squares outlined in black) located within 5 of the 8 physiographic regions (gray outline) found in Michigan's Lower Peninsula with inland sites occurring within townships with ≥ 40 km of shoreline (areas shaded red).

We selected 10 sites (6 km x 6 km) in areas with potential concentrated nesting habitat (Figure 1.3). All 10 sites included publicly-accessible and privately-owned waterbodies. These sites, located in 5 of the 8 physiographic regions of the Lower Peninsula, were surveyed 11 December 2015 via fixed-wing aircraft (Cessna 185; Northwoods Aviation Inc, Cadillac, MI, USA) to record the amount of suitable nesting habitat for nesting pairs the following spring (i.e.,

emergent aquatic vegetation along shorelines) and number of mute swans within proposed boundaries to aid in study site determination. We detected 1,111 mute swans within site boundaries with mute swan counts among the 10 sites ranging from 9 to 286. We surveyed 5 of 10 preliminary sites and 3 additional areas with fixed-wing aircraft on 12 and 14 April 2016 to count breeding pairs, approximate nest locations, and estimate number of non-breeding mute swans within site boundaries. We chose 5 of these sites for studying nesting ecology 2016-18. We added an additional study site in the northern Lower Peninsula in 2017; therefore, 6 sites had nest monitoring in 2017 and 2018 (Figure 1.4).



Figure 1.4. Six study sites (each 36 km²) located in Antrim, Bay, Cass, Kent, Oakland, and St. Clair Counties of Michigan's Lower Peninsula where intensive nest monitoring was conducted for mute swans 2016 – 2018.

Focal site descriptions

We chose 6 equal-sized (36 km²) study sites of varying land cover composition for intensive nest monitoring (Figures 1.4 and 1.5). Study sites occurred in 6 counties (Antrim, Cass, Bay, Kent, Oakland, and St. Clair) across 5 of 8 physiographic regions of the Lower Peninsula (Schaetzl et al. 2013). We summarized land cover data within study sites using data from the 2011 National Land Cover Database (2011 NLCD; Homer et al. 2015). The 2011 NLCD classified layer recognizes 16 land cover classes (Homer et al. 2015). We found 15 cover classes within ≥ 1 study site. We consolidated the 15 cover classes into 7 cover classes (i.e., agriculture, developed, early successional, emergent herbaceous wetlands, forest, open water, and woody wetlands). Open water contained areas of water with $\leq 25\%$ soil or vegetation (Homer et al. 2015). Developed included areas with residential or commercial development designated as either developed, open space; developed, low intensity; developed, medium intensity; or developed, high intensity (Homer et al. 2015). Forest included deciduous forest, evergreen forest, or mixed forest. Early successional included shrub/scrub or grassland/herbaceous. Agriculture included pasture/hay or cultivated crops. Woody wetlands included seasonally wet or flooded areas with $\geq 20\%$ forest or shrub cover whereas emergent herbaceous wetlands were seasonally wet or flooded areas with $\geq 80\%$ coverage in perennial herbaceous vegetation (Homer et al. 2015).

Study sites (Figure 1.4) contained areas of open water ($\bar{x} = 29.0\%$, [range: 9.6 - 85.3%]) varying between chains of inland lakes and a portion of freshwater delta, St. Clair Flats (Figure 1.5). Human influences were prevalent across the study sites with areas dominated by agriculture ($\bar{x} = 21.3\%$, [range: 0 – 45.9%]) and development ($\bar{x} = 14.7\%$, [range: 2.0 - 41.7%]). Much of the developed areas were adjacent to open water (Figure 1.6). Percentage of emergent herbaceous

wetlands ($\bar{x}$ = 4.2%, [range: 0.6 – 12.0%]) and woody wetlands ($\bar{x}$ = 11.9%, [range: 0.6 – 16.1%]) also varied among study sites; however, waterbodies on all sites contained areas of developed and natural shoreline.

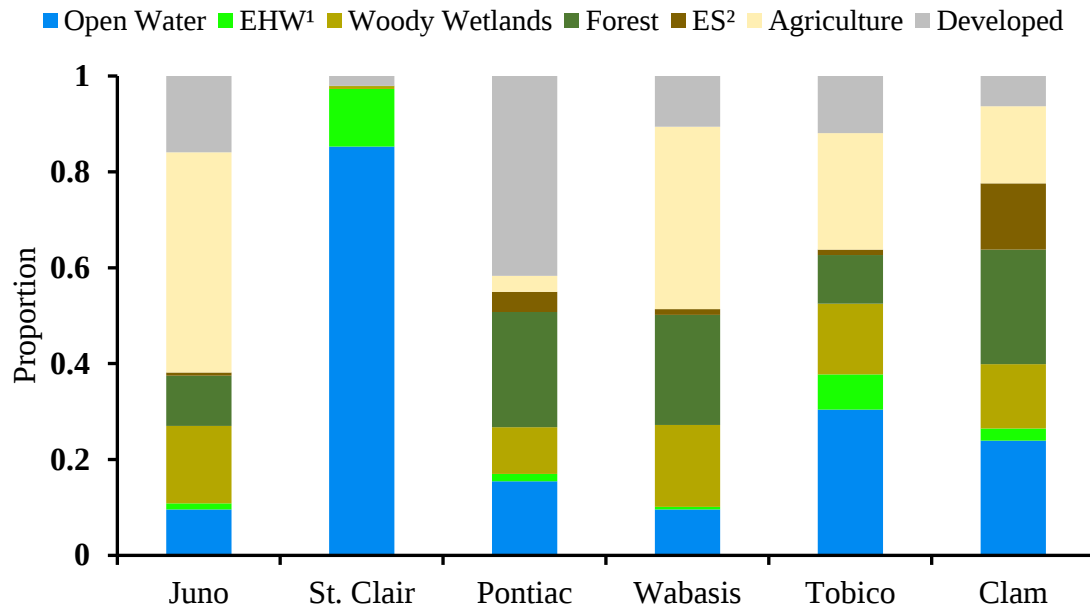


Figure 1.5. Cover type composition of study sites in the Lower Peninsula of Michigan, USA, where intensive nest monitoring occurred for mute swans 2016 – 2018.

¹EHW = emergent herbaceous wetlands; ²ES = early successional

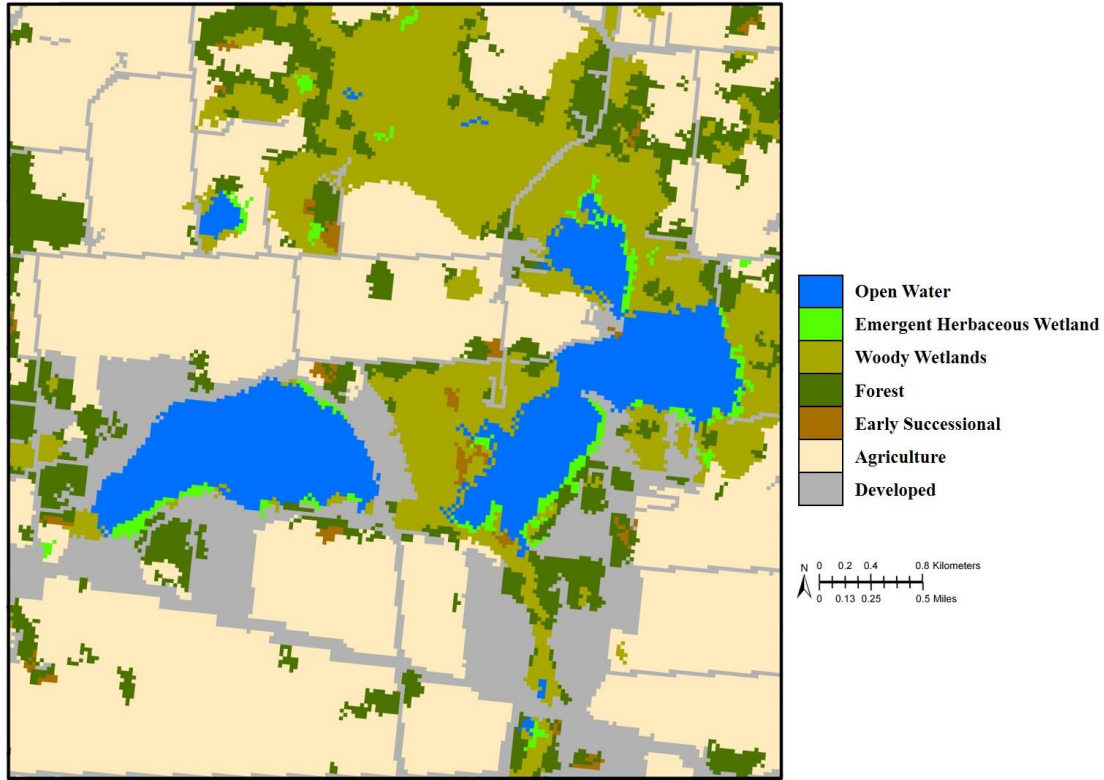


Figure 1.6. Land cover map for Juno study site in Cass County Michigan, USA, showing consolidated NLCD 2011 cover classes.

Emergent herbaceous wetlands were dominated by narrow-leaved cattail (*Typha angustifolia*), broad-leaved cattail (*T. latifolia*), and their hybrid (*T. glauca*). Monotypic stands of phragmites (*Phragmites australis*) occurred across all sites; however, they were especially abundant on the St. Clair study site. Many other aquatic plant species (e.g., American lotus [*Nelumbo lutea*], bulrush [*Schoenoplectus* spp.], sweet-scented water lily [*Nymphaea odorata*], yellow pond-lily [*Nuphar* spp.]) also occurred within and alongside areas designated emergent herbaceous wetlands. Shallow open water areas contained beds of submerged aquatic vegetation (SAV) with coontail (*Ceratophyllum demersum*), Eurasian watermilfoil (*Myriophyllum spicatum*), Sago pondweed (*Stuckenia pectinatus*), slender naiad (*Najas flexilis*), and other pondweeds (*Potamogeton* spp.). Woody wetlands contained buttonbush (*Cephalanthus*

occidentalis), dogwoods (*Cornus* spp.), willows (*Salix* spp.), and alders (*Alnus* spp.) in addition to emergent herbaceous plants like cattail, phragmites, and reed canary grass (*Phalaris arundinacea*). Agriculture was primarily row crop cultivation of corn (*Zea mays*) and soybean (*Glycine max*) with wheat (*Triticum* spp.) occasionally planted as a cover crop or for harvest.

DISSERTATION CONTENT

This dissertation is organized into this introductory chapter, four primary research chapters, and a concluding chapter. I intend to submit individual chapters for publication in the scientific literature with coauthors; therefore, I wrote these chapters using plural pronouns even though I take full responsibility for the work presented herein. In Chapter 2 I report on nest survival, cygnet survival, brood survival, cygnet color morph ratios, and mean clutch size for mute swans in Michigan's Lower Peninsula. This was accomplished by 1) counting number of eggs per clutch, 2) estimating incubation initiation and hatch dates, 3) tracking individual egg survival, and 4) examining number of hatched and fledged cygnets of both color morphs. In Chapter 3 I examined influence of nest density on breeding productivity. This was completed by 1) counting nesting pairs and estimating breeding productivity with fixed-wing aircraft, 2) estimating total available nesting cover using aerial imagery and boat surveys, and 3) by comparing current nesting density to a theoretical maximum density derived through spatial optimization procedures. In Chapter 4 I document seasonal movements and generate life stage-specific survival estimates for use in demographic modeling. I accomplished this by 1) affixing GPS-GSM transmitters to breeding females, 2) GPS-marking cygnets of known origin, and 3) monitoring swan movements in relation to their annual cycle (e.g., brood rearing, molting, etc.) and abiotic factors such as winter severity or disturbance. In Chapter 5 I incorporated derived demographic parameters and density-dependent influences on breeding productivity into a matrix

population model that guides future management of mute swan populations in Michigan. The four primary research chapters, collectively, will advance mute swan management within the Great Lakes region of the United States while also contributing to general understanding of mute swan biology. Finally, in Chapter 6, I offer data-driven strategies to help state and federal agencies achieve management goals for managing this charismatic invasive species.

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CHAPTER 2: NESTING ECOLOGY OF MUTE SWANS IN MICHIGAN, USA

INTRODUCTION

Mute swans (*Cygnus olor*) expanded their geographic distribution in North American since their introduction by humans in the late 1800s (Baldassarre 2014). This expansion occurred through natural dispersal and human-assisted translocations. The first recorded breeding pairs in North America occurred in the early 1900s along the Hudson river in the eastern United States (Baldassarre 2014). Feral populations were first noted in the Great Lakes region in 1919 following introduction of a breeding pair to an inlet waterbody of Lake Michigan, Round Lake, that connects the Boyne River to Lake Michigan in Charlevoix County, Michigan (Wood and Gelston 1972). Mute swans in northern Michigan originated as a semidomesticated flock under the care of employees of the Chicago Club and local citizens (Gelston and Wood 1982). Cold winters of northern Michigan coupled with lack of an established migratory pattern necessitated human assistance through supplemental feeding and ice clearing to ensure mute swan survival through winter months. Gelston and Wood (1982) documented distribution, nesting ecology, movement, and mortality during the early years of mute swan establishment in Michigan; however, no such formal effort occurred since the statewide expansion of mute swans.

Nesting ecology for mute swans has been investigated throughout their native range (Perrins and Reynolds 1967, Birkhead et al. 1983, Czapulak 2002) and in areas of introduced range (Nummi and Saari 2003), including the United States (Willey and Halla 1972, Reese 1975, Conover and Kania 1999). Breeding parameters likely differ between introduced and native ranges due to variation in nest predator communities, food availability, human disturbance, and varying levels of intra- and interspecific competition. Characteristic nesting cover in native range consists of emergent vegetation with 46% of nests placed adjacent to flowing water (Campbell

1960). Small waterbodies (<25 ha) used in aquaculture (i.e., fish ponds) are also colonized by breeding pairs due to emergent nesting cover along the banks and shallow (<1 m) water (Czapulak 2002). Breeding in the Atlantic coastal states of the United States were generally limited to estuaries and tidal rivers early during mute swan invasion; however, pairs began nesting on inland waterbodies in the late 1970s (Conover and Kania 1999). Wieloch (1991) and Gayet et al. (2011) suggested that mute swans exhibit plasticity in nest site selection which could contribute to range expansion.

Variability in nest site composition, intraspecific competition, physical geography, and genetic lineage could also result in differing clutch sizes, egg size, nest survival, and overall productivity. Reese (1975) and Conover and Kania (1999) estimated mean clutch sizes as slightly higher (6.1 [Chesapeake Bay] and $6.6 \pm \text{SE } 0.1$ eggs [Connecticut], respectively) than reported values within native range (5.9 eggs, Perrins and Reynolds [1967]); however, Gelston and Wood (1982) documented lower mean clutch size (4.3 eggs) in a northern Michigan mute swan sub-population. Conover and Kania (1999) documented higher nest survival, egg survival, and overall breeding productivity compared to areas of their native range. Reese (1975) found a Chesapeake Bay sub-population exhibited higher cygnet survival and more young fledged per pair compared to other populations in native (Eltringham 1966, Perrins and Reynolds 1967) and introduced ranges (Willey 1968, Gelston and Wood 1982). Additionally, Conover et al. (2000) found varying cygnet survival rates among the two cygnet color morphs (i.e., white or leucistic [Polish] and gray [royal]) controlled by a sex-linked recessive gene (Munro et al. 1968).

Variation in nesting parameters across the geographic range of mute swans and potential for differences related to genetic composition underscores need for regional estimation of nesting ecology parameters. This is especially true if those parameters are being incorporated into

modeling for future population management. We conducted this study to estimate region-specific nesting ecology parameters of mute swans while also investigating phenotypic distribution and demographic consequences of leucistic and gray morph individuals.

STUDY AREA

Study Site Selection

We studied nesting ecology for mute swans in Michigan's Lower Peninsula (Figure 2.1). To ensure that study sites captured geographic and physiographic variability within the nesting range of mute swans in the Lower Peninsula, we used physiographic regions (Schaetzl et al. 2013) and a geographic information system (GIS; ArcGIS 10.3.1, ESRI, Redlands, CA, USA) to delineate potential study sites based on waterbody availability and topography. We overlaid results from a 2015 survey of breeding waterfowl (Michigan Department of Natural Resources, unpublished data) with hydrography and public land survey system data (PLSS; Center for Shared Solutions and Technology Partnerships 2015) to further separate the Lower Peninsula into discrete blocks. PLSS townships with estimated spring density ≥ 1 mute swan per square mile during the 2011 – 2015 waterfowl breeding season had mean shoreline distance of 40 km for inland lakes and rivers; therefore, we used this as a threshold to identify PLSS townships where mute swan presence was likely during the 2016 breeding season (Figure 2.1). We subsequently flew 14 6 by 6 km study sites with fixed-wing aircraft (Cessna 185; Northwoods Aviation Inc, Cadillac, MI, USA) in December of 2015 or April 2016 to estimate mute swan abundance and determine suitability as study sites (Figure 2.1). We chose 5 study sites in Bay, Cass, Kent, Oakland, and St. Clair Counties for investigation of nesting ecology in 2016 – 2018 and added 1 site in Antrim County in 2017 – 2018 (Figure 2.1).

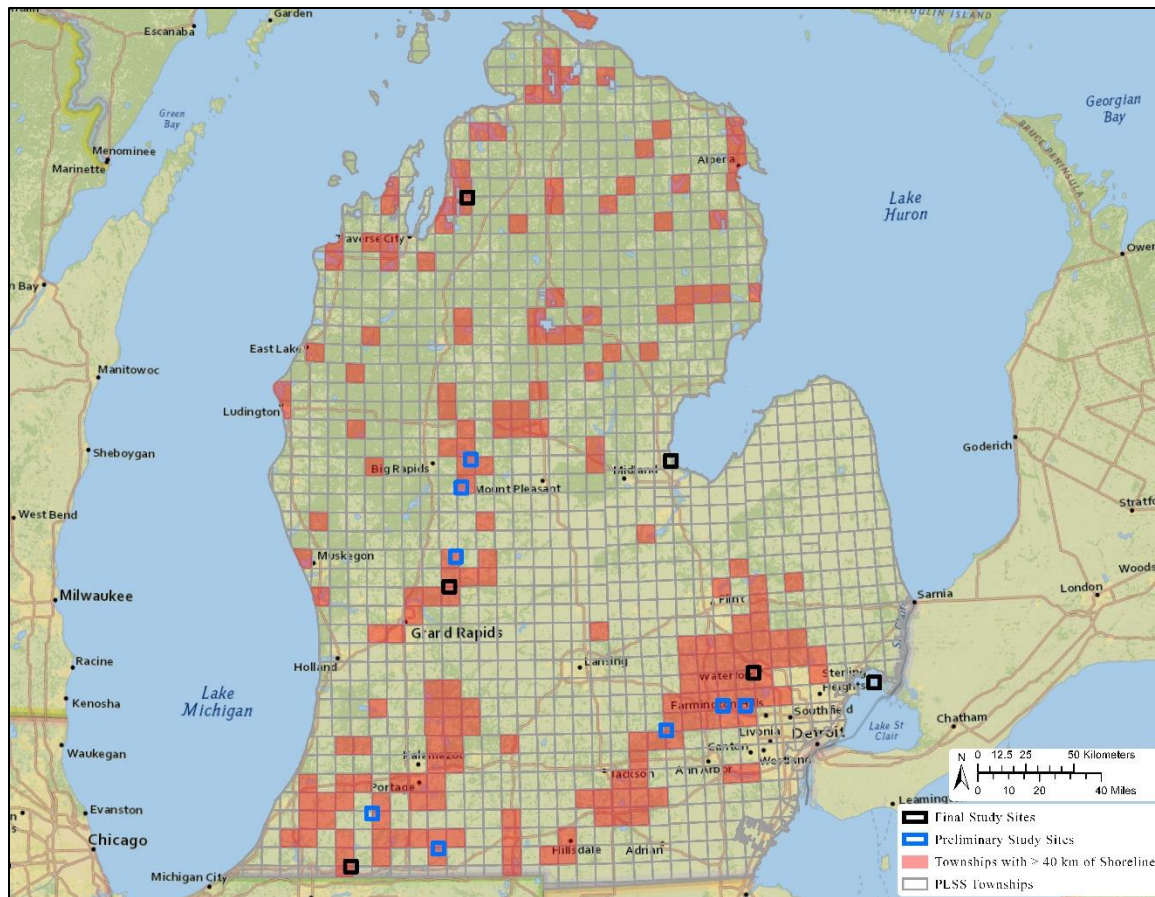


Figure 2.1. Preliminary and final study sites were located throughout Michigan’s Lower Peninsula within public land survey system (PLSS) townships with ≥ 40 km of shoreline.

Study Site Descriptions

Six study sites were located in 5 of the 8 physiographic regions (Schaetzl et al. 2013). Land cover composition varies latitudinally across the Lower Peninsula of Michigan (Homer et al. 2015) and, therefore, varied among our four inland and two coastal-oriented sites. Inland sites contained a mix of private and publicly-accessible waterbodies with moderate to heavily developed shorelines. Inland waterbodies contained areas of developed and undeveloped shoreline with permanently-flooded open water (cover type L1UBH based on the National Wetland Inventory Classification System; U. S. Fish and Wildlife Service 2015). Inland sites also contained areas of freshwater emergent wetland (PEM) adjacent to open water areas (U. S.

Fish and Wildlife Service 2015). The coastal-oriented sites varied in composition. One contained the Tobico Marsh wetland complex in Bay County with areas of persistent emergent vegetation that was semi-permanently flooded (PEM1F) and open water (PABG; U. S. Fish and Wildlife Service 2015) among areas of agriculture, human development, and forest cover (Homer et al. 2015). The second coastal study site contained a portion of a freshwater delta, St. Clair Flats, in St. Clair County. This site was primarily open water (L1UBH and L2UBH) with large areas of freshwater emergent wetlands (PEM) that consisted of native emergent vegetation (e.g., broad-leaved cattail [*Typha latifolia*], bulrushes [*Schoenoplectus* spp.], etc.) and nonnative emergent vegetation (narrow-leaved cattail [*Typha angustifolia*], phragmites [*Phragmites australis*]; U. S. Fish and Wildlife Service 2015). Small (< 5 ha each) developed islands are also interspersed within this study area.

METHODS

Field Techniques

We conducted aerial surveys annually during incubation (12 April – 1 May) to locate nesting pairs within each study site ($n = 5$ sites, 2016; $n = 6$ sites, 2017 – 2018). Incubating females on nests are easily identifiable from aerial surveys due to conspicuous plumage and large (≥ 1 m) nest structure against a backdrop of senesced emergent vegetation and open water (Conover and Kania 1999). Two observers worked together to detect nests on either side of the aircraft. All detected nests were marked on orthophotographs and later transferred to digital format through a GIS (ArcGIS Pro, ESRI, Redlands, CA, USA). We logged flight paths using a cellphone application that records GPS coordinates at 1 second intervals (Strava, Inc., San Francisco, CA USA). Flights were recorded using wing strut-mounted high-definition video camera systems in 2016 – 2017 (MotoCam 360, Bothell, WA, USA) and 2018 (GoPro Hero 4

Silver, San Mateo, California, USA). We assumed that detection probability of mute swan nests was near 1 as reliable detection of nests and determination of nesting locations was possible by using 2 aerial observers, recording a detailed flight path, and use of flight video.

GPS-marking

Uniquely identifiable alphanumeric neck collars were placed on a subset of nesting females (≤ 5 per site) to aid in detection of broods throughout the brood-rearing cycle, estimate between-year nesting constancy, and estimate survival and movement (Chapter 4). Nesting females were captured during incubation or brood-rearing using a modified shepherd's crook (Coleman and Minton 1979) or shoulder-fired netgun (CODA Enterprises Inc. Mesa, AZ, USA). We fit nesting female mute swans with green and white plastic neck collars (56 mm diameter; Spinner Plastics, Inc., Springfield, Illinois, USA) that included a GPS-GSM transmitter (CTT-1070 BT3; Cellular Tracking Technologies, Inc., Rio Grande, New Jersey, USA) and weighed 117 - 121.5 g when deployed ($< 1.4\%$ of body weight). Select male mute swans paired with GPS-collared females were also captured and fit with uniquely-coded plastic neck collars that did not include a GPS-GSM transmitter. All captured swans were weighed, sexed, and fitted with rivet-lock aluminum leg bands (28.5 mm diameter (9C); National Band and Tag Co., Newport, KY, USA) and we measured tarsus, wing, and skull length using dial Vernier calipers or a stopped wing ruler. Capture and handling of live mute swans was led by staff of the U.S. Department of Agriculture Wildlife Services section of the Animal Plant Health Inspection Service (USDA APHIS WS). Michigan State University (MSU) Institutional Animal Care and Use Committee (IACUC) granted an animal-use exemption for MSU personnel throughout this project since capture and marking efforts were led by staff of USDA APHIS Wildlife Services.

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Pre-hatch nest monitoring

We visited a subset of nests (≤ 12 annually per site; $n = 110$) detected via aerial surveys ($n = 251$) to intensively monitor aspects of mute swan nesting ecology. We used a flat-bottomed boat with longtail mud motor (S.W.O.M.P. 26.5, Backwater, Inc., Freeport, MN, USA) to approach mute swan nests which were typically located adjacent to shallow (< 1 m) water. Nests with completed clutches (i.e., warm eggs and/or an actively incubating female) had incubation stage determined by floating all eggs using methods outlined by Westerskov (1950) and Walter and Rusch (1997) adjusted for mean incubation length of mute swans (36 days; Reese 1975, Baldassarre 2014). We estimated incubation initiation date for each nest by averaging estimated egg age across the entire clutch and subtracting mean egg age (in days) from date of observation. Laying order was estimated for all eggs in each clutch based on variation in egg staining (dirtiest eggs were assumed laid earliest and cleanest eggs last), and eggs were numbered uniquely using colored markers (Sharpie, Newell Brands, Inc., Atlanta, GA, USA). All eggs had the number corresponding to laying order marked on their shells in ~ 10 locations due to the large size of mute swan eggs. Nests that were encountered during the laying stage were subsequently revisited to mark newly laid eggs, obtain estimated hatch dates, and determine clutch size. We measured length and width of all eggs ($n = 748$) using a dial Vernier caliper (Flexbar Machine Corporation, Islandia, NY USA) to the nearest tenth of mm. We placed coated (Plasti Dip, Plasti Dip International, Blaine, MN, USA) temperature logging iButtons (DS1921G-F5#; Maxim Integrated San Jose, CA, USA) beneath each clutch of eggs to monitor nest fate by comparing in-nest temperature to ambient temperatures recorded by an auxiliary iButton placed on the edge of

or in cover near a representative nest. Temperature logging technology has successfully determined hatching and nest failure dates with ground nesting avifauna (Hartman and Oring 2006, O'Connor and Ritchison 2013), especially when ambient temperatures during the nesting cycle are $\leq 29^{\circ}\text{C}$ (Schneider and McWilliams 2007). Mute swans incubate nests constantly (Conover and Kania 1999); therefore, changes in nest temperature relative to ambient temperature indicates nest failure or hatching of young. We coated iButtons in clear Plasti Dip which safely waterproofs the devices to prevent data loss with minimal influence on temperature readings (Roznik and Alford 2012, MacNeil and Williams 2014). iButtons were programmed to turn on at a predetermined date prior to nesting season and were set to record temperature readings every 60 minutes so that onboard memory storage ($n = 2,048$ readings) would not be full before termination of the nesting season.

Post-hatch investigation

We visited nests near estimated hatching dates to recover iButtons, ascertain nest status, count hatched or depredated eggs, and count cygnets hatched and color morph, if successful. Hatched and depredated eggs were distinguished by status of egg shell membranes (Klett et al. 1986). We determined fate of individual eggs in 2017 and 2018 based on presence of eggshells with uniquely identifiable markings (i.e., colored numbers). Marked eggs absent in eggshell fragments upon nest hatch were assumed to have failed through predation or removal from nest. We located the nesting pair and broods near the nest site and counted cygnets in each color morph. The time needed for mute swans to fledge varies with environmental factors, but is typically 120 – 154 days (Willey and Halla 1972, Reese 1975). We added 120 days to actual hatching dates of monitored nests to conservatively estimate fledging date for all hatched cygnets.

Boat and aerial surveys were conducted near estimated fledging dates to again count cygnets in each color morph for intensively monitored and non-monitored nests. Aerial surveys were flown in fixed-wing aircraft with flight paths and flight video recorded in the same manner as during the spring nest detection surveys. We counted white (i.e., adult or white-morph cygnets) and gray swans and recorded approximate location of broods on aerial photos. We used boats to locate pairs detected through aerial surveys and confirm brood size and color morph ratio (i.e., count white-morph cygnets separately from adults) when necessary.

Data analysis methods

Nesting parameters

Nesting ecology parameters and use of terminology varies widely within the scientific literature; therefore, we felt it useful to clarify our terminology and methods for ease in comparing these estimates with those in the published literature. We defined apparent nest survival as proportion of all nests under observation with eggs that were successful (i.e., hatched ≥ 1 egg; Conover and Kania 1999). Modeled nest survival (see below) was estimated through program MARK (White and Burnham 1999). Further, nest survival has been reported in multiple ways which either includes survival of the nest through the egg laying period (Conover and Kania 1999), excludes the egg laying period, or does not note the technique used (King et al. 2013). We reported modeled nest survival both ways. Daily survival rate follows Dinsmore et al. (2002) as the probability a nest survives 1 day. Hatching rate was defined as proportion of eggs that hatched from all eggs laid including those from nests that did not hatch 1 egg (i.e., failed). Apparent egg survival was defined as the proportion of eggs that hatched from successful nests (Johnson and Shaffer 1990). Estimates of hatched young per nest are typically based on an initial brood size at first re-sighting of the brood post-hatch; however, this may be biased low if hatched

cygnets die or disappear before the first nest check after hatch. Further, estimates of apparent cygnet survival will be biased high if initial young observed is used rather than number of eggs that hatched from each nest. We reported number of eggs that hatched (i.e., true initial brood size) and observed initial brood sizes (i.e., number of young at first brood re-sighting) for comparison among studies in the literature. Additionally, cygnet survival was calculated using both estimates of initial brood size. Cygnet survival was defined as proportion of cygnets that survived from hatch or first brood re-sighting (see above) to estimated fledge for successful nests. Apparent brood survival was estimated by taking number of nests that fledged young and dividing it by total number of nests that hatched young based off the “true initial brood size.” Brood size at fledging or productivity is also reported in multiple ways which may or may not account for pairs that failed to hatch or fledge young. We followed Conover and Kania (1999) by reporting number of young per pair for pairs with young at fledging (i.e., mean brood size at fledging), and number of young fledged per nesting pair (i.e., overall productivity). Nesting ecology parameters were summarized by year and then used as sampling units to obtain a grand mean and standard error with sites pooled unless otherwise noted.

Modeled nest survival

We used the nest survival approach (Dinsmore et al. 2002) in Program MARK (ver. 8.1; White and Burnham 1999) to estimate annual nest survival across study sites. Use of iButton temperature loggers allowed us to summarize nest fate using daily intervals during the nesting season without regular nest checks thereby avoiding disturbance that accompanies those activities (Boellstorff et al. 1988, Sedinger 1990). However, nests were typically visited once during incubation to assess status of the clutch and to ensure iButtons remained just below eggs in the nest bowl. We included terms for temporal and spatial variability in nest survival analyses

based on *a priori* models of variation in nest survival between year, site, and an additive model of year and site.

Egg survival

We used a generalized linear mixed-effects model (GLMM) within Program R (R Development Core Team 2018) to understand the relationship between egg hatching and its size. We used logistic regression to estimate the probability of survival for eggs ($n = 603$) in successful nests as a function of egg volume. Egg volume was calculated using the formula $V = K_v \times L \times B^2$ following (Hoyt 1979) where K_v is a shape constant (0.512), L = egg length, and B = egg breadth. Egg volume and site were included in the logistic regression models as fixed effects while nest was included as a random effect. We ranked models using Akaike's Information Criterion corrected for small sample sizes (AICc; Anderson and Burnham 2002).

RESULTS

Two-hundred twenty-nine pairs with nests were detected within study site boundaries from 2016 – 2018 (Table 2.1) using aerial and boat surveys. We intensively monitored 109 nests (Juno = 25, St. Clair = 24, Pontiac = 28, Wabasis = 17, Tobico = 7, and Clam = 8) for clutch sizes, nest survival, egg survival, initial brood sizes, and cygnet survival. This total includes nests of two GPS-marked females that nested beyond study site boundaries in 2018 but were captured and nested within site boundaries in previous study years. We documented 10 instances where territories in typical nesting cover (i.e., residual cattails, reed, or phragmites) were filled with new individuals following dissolution of a mating pair through death of one or both members. Mean incubation initiation date was 8 April and mean hatch date was 12 May; however, we noted eggs in nests as early as 16 March and as late as 7 June. Earliest recorded hatch occurred on 20 April 2017 and latest observed hatch occurred on 4 June in 2016 and 2017.

Ninety-three percent of all successful nests with known hatch dates ($n = 81$) had eggs throughout the period of 20 – 30 April (Figure 2.2). Mean clutch size pooled across years and sites was 7.0 ± 0.15 eggs per clutch (range 1 - 10). One GPS-marked female renested 172 m from the original nest and began incubation on a new clutch ($n = 4$ eggs) 25 days after failure of the first clutch ($n = 5$ eggs; failed on 13 April). Two failed nests with small clutches of infertile eggs were incubated beyond estimated hatch dates. One nest containing one infertile egg was incubated 22 days past its estimated hatch date. A second nest containing 2 eggs was incubated an additional 20 days. Neither female renested following these failed nesting attempts. Hatch date was typically estimated to within 1 day (0.93 ± 4.22 days) of actual hatch date for nests ($n = 82$) using flotation methods (Westerskov 1950, Walter and Rusch 1997) although flotation slightly overestimated nest age early and late in the incubation period and underestimated age at median incubation (Table 2.2).

Table 2.1. Number of detected nesting pairs and number of fledglings per pair 2016 – 2018 for 6 study sites located in the Lower Peninsula of Michigan, USA.

	2016		2017		2018		Pooled Mean	
	Pairs	Fledged per Pair	Pairs	Fledged per Pair	Pairs	Fledged per Pair	Pairs	Fledged per Pair
Juno	21	1.6	20	1.3	10*	1.5	17.0	1.5
St. Clair	25	0.9	19	1.2	6*	2.4	16.7	1.0
Pontiac	31	1.0	25	0.9	22	0.4	26.0	0.8
Wabasis	9	2.6	9	2.1	7	1.0	8.3	2.3
Tobico	7	2.7	5*	1.8	5	2.6	5.7	2.3
Clam	.	.	5	0.6	2	1.0	3.5	0.6
All Sites	93	1.4	84	1.2	52	1.1	77.5	1.2

*Total does not include nests that were influenced by investigators or nests of pairs culled during incubation in official removal efforts.

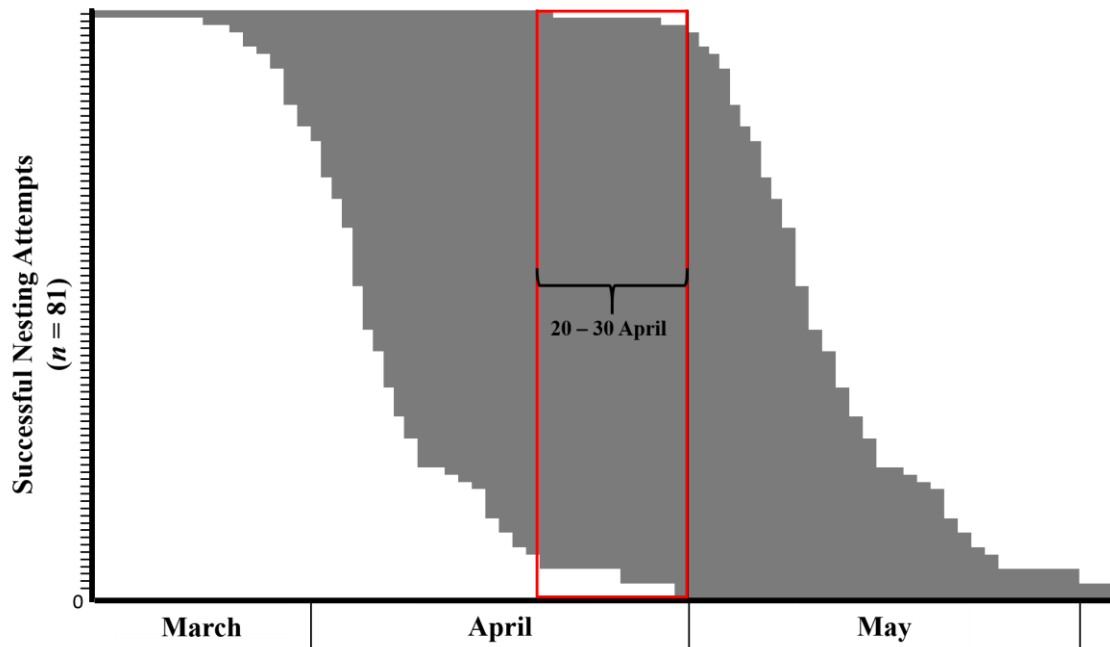


Figure 2.2. Incubation window (shown in red) where all successful nests (gray bars) contained eggs for monitored mute swan nests in Michigan’s Lower Peninsula 2016 – 2018.

Table 2.2. Accuracy of flotation methods for estimating hatch date of successful mute swan nests ($n = 82$) in Michigan 2016 – 2018 where hatch and incubation initiation dates could be determined.

Float Category ^a	Estimated Age ^a (days)	Actual Age (days)	Δ Age (days)
1	3	2.1	0.9
2	9	6.3	2.7
3	15	15.5	-0.5
4	21	24.4	-3.4
5	27	26.3	0.7
6	33	30.8	2.2

^aNest age was estimated using flotation methods and categories outlined by (Westerskov 1950) and Walter and Rusch (1997) that were adjusted for mute swan incubation interval of 36 days.

GPS-marking

Thirty-two breeding females were GPS-marked 2016 – 2018. Seven male mates of GPS-marked females were also fit with plastic neck collars. We documented 23 instances of mute swans nesting in consecutive years and 7 instances when females only nested in 1 year (76.7% nesting constancy). Incubation length (35.5 days; range 32 – 37) was estimated for 7 GPS-

marked females in 2017. Median distance between successive nests (i.e., breeding dispersal) was 123.1 m (range: 0.91 – 20,342.38 m; $n = 20$). Seven adult females that dispersed (i.e., moved ≥ 300 m between successive nests; Włodarczyk et al. 2013) had a median dispersal of 2.14 km (mean = 5.48 km). One instance was noted in which a GPS-marked female nested successfully with an unmarked male on a new territory even though the previous mate (neck collared) was alive and defending their historic territory.

Egg survival

Mean egg length (11.32 ± 0.45 cm), width (7.52 ± 0.22 cm), and volume (328.2 ± 26.6 cm³) was similar among years (Table 2.3). Mean hatching rate 2016 – 2018 was 0.66 ± 0.041 . Apparent egg survival was 0.804 ± 0.015 . The most parsimonious model for egg survival included a fixed effect for egg volume ($\hat{\beta} = 0.610$, $z = 3.23$, $p = 0.001$) and a random effect of nest (Table 2.4).

Probability of hatching increased with egg volume (Figure 2.3).

Table 2.3. Mean and standard deviation for egg length, width, and volume for eggs ($n = 748$) in mute swan nests in Michigan, USA, during 2016 – 2018.

	2016	2017	2018
Length (cm)	11.26 ± 0.4	11.35 ± 0.5	11.33 ± 0.5
Width (cm)	7.51 ± 0.2	7.52 ± 0.2	7.53 ± 0.2
Volume (cm ³)	325.9 ± 24.4	329.2 ± 27.8	329.1 ± 26.9

Table 2.4. Model selection for logistic regression on egg hatchability of mute swans in Michigan, USA, during 2017 and 2018.

Model	k^a	$AICc^a$	$\Delta AICc^a$	w_i^a
(1 Nest) + Egg Volume	1	370.687	0	0.991
(1 Nest)	0	380.244	9.558	0.008
(1 Nest) + Site	1	384.469	13.782	0.001

^a k = number of parameters in model; $AICc$ = Akaike's Information Criterion; $\Delta AICc$ = change in $AICc$ from lowest $AICc$ model; w_i = Akaike weight.

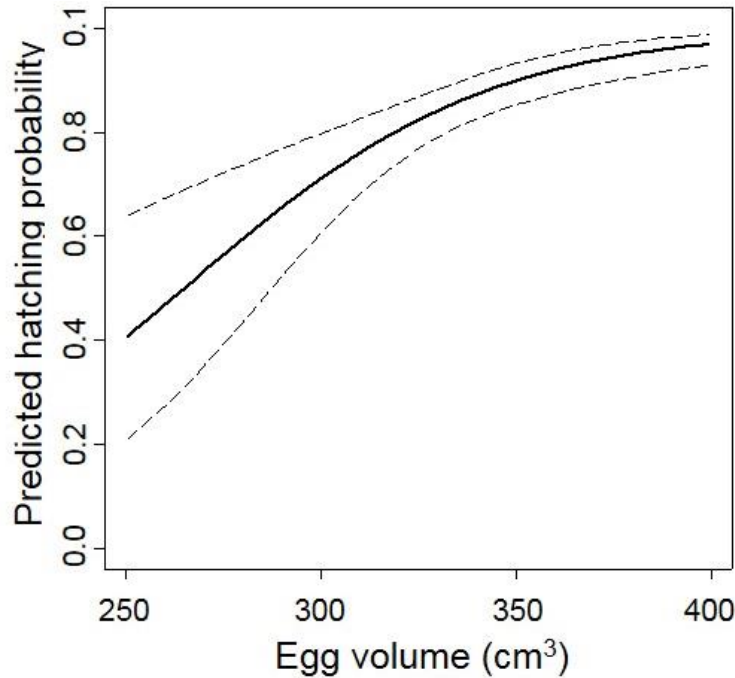


Figure 2.3. Model predicted hatching probability as a function of egg volume with 95% CI region across range of observed egg volumes (250.4 – 399.1 cm³) for successful mute swan nests 2016 -2018 in Michigan's Lower Peninsula.

Nest survival

Mean apparent nest survival ($n = 1$) was 0.817 ± 0.044 . Nest survival was modeled for 98 nests using a 72-day nesting interval (28 March – 7 June). The null model was the most parsimonious model (Table 2.5). We averaged estimated daily survival rate across all 4 models according to their Akaike weight (w_i). We used the model-averaged daily survival rate (0.9925, 95% CI [0.9878 – 0.9971]) to calculate a nest survival estimate for the 36-day incubation period ($\hat{S} = 0.761$) and for the total nesting period (47 days) that included an estimated laying period ($\hat{S}$

= 0.701). We used mean clutch size and an egg laying interval of 36 hours to estimate a mean laying period of 11 days for mute swans in Michigan. Failure of nests to hatch ($n = 16$) were caused by predation of eggs ($n = 3$), mortality of the incubating female ($n = 2$), small clutches of infertile eggs ($n = 2$), flooding and nest destruction caused by storm surge ($n = 2$), abandonment ($n = 2$), or unknown ($n = 5$).

Table 2.5. Model selection for mute swan nest survival 2016 – 2018 in Michigan’s Lower Peninsula.

Model	k^a	AICc ^a	$\Delta AICc^a$	w_i^a
Null	1	190.267	.	0.587
Year	2	191.490	1.224	0.319
Site + Year	6	195.002	4.736	0.055
Site	6	195.699	5.433	0.039

^a k = number of parameters in model, AICc = Akaike’s Information Criterion adjusted for small sample sizes, $\Delta AICc$ = difference between AICc of best fitting model and current model, w_i = Akaike’s weight.

Post-hatch parameters

Mean true initial brood size was 5.80 ± 0.34 cygnets per successful nest ($n = 55$) 2017 – 2018. Observed initial brood size was 4.9 ± 0.10 cygnets per successful nest (2016 – 2018). Median interval between observed hatch date and first nest visit where young could be observed was 4 days (range: 0 – 75). Gray morph cygnets made up 36.9% of all young observed during first brood re-sightings; however, percentage of cygnets in each color morph varied by site (0 – 80% gray morph). Apparent cygnet survival calculated with the true initial brood size was 0.27 ± 0.01 . Apparent cygnet survival using initial observed brood sizes was 0.33 ± 0.03 . Cygnet survival did not vary with regard to color morph (Table 2.6). Mean estimated survival for eggs to fledging was 0.198 when sites and years were pooled. Mean estimated survival probability for eggs to fledging calculated from mean fledged per pair among sites (1.42; Table 2.1) and mean clutch size was 0.203. Mean brood survival (0.58 ± 0.03) was calculated for monitored nests that hatched young. Mean brood size at fledging was identical across all years at 3.1 fledged

cygnets/pair. Overall pooled breeding productivity was 1.2 cygnets/pair. Brood size distribution for monitored nests at fledging was left-skewed (Figure 2.4). Mean estimated fledge date for mute swan nests using a 120-day brood-rearing period was 8 September.

Table 2.6. Apparent hatch to fledge survival estimates by year and color morph for mute swan cygnets 2016 – 2018 in Michigan’s Lower Peninsula calculated from observed brood size at initial sighting post-hatch (i.e., initial observed brood) and from true initial brood size (i.e., brood size calculated from all hatched eggs).

	2016			2017			2018		
	$\bar{x}$	SD	p^*	$\bar{x}$	SD	p^*	$\bar{x}$	SD	p^*
Initial Observed Brood	0.31	0.37		0.38	0.35		0.29	0.3	
Leucistic	0.35	0.69	0.84	0.35	0.37	0.52	0.30	0.32	0.99
Gray	0.38	0.35		0.43	0.38		0.29	0.34	
True Initial Brood	0.26	0.30		0.28	0.29		0.26	0.3	

* p -value for 2 sample t-test between year-specific survival of leucistic and gray morph cygnets

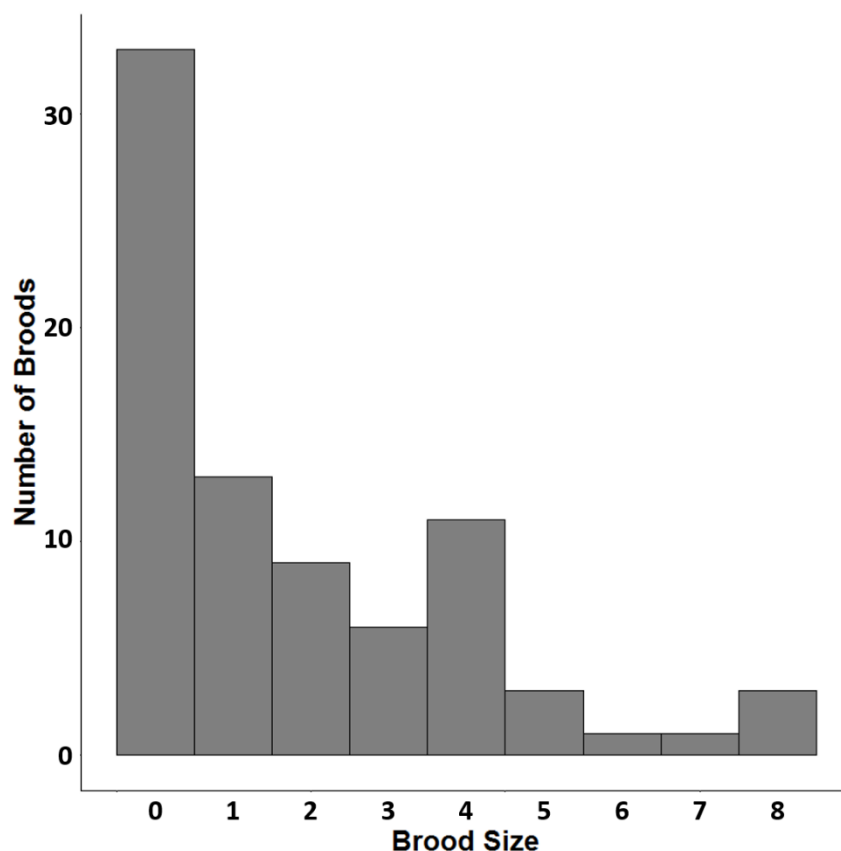


Figure 2.4. Left-skewed distribution of brood sizes at estimated fledging (1 September) for all monitored mute swan nests with eggs 2016 – 2018 in the Lower Peninsula of Michigan, USA.

DISCUSSION

Nesting ecology studies typically estimate many parameters throughout nesting and brood-rearing cycles by conducting repeated site visits and nest checks. This study used new research methods to investigate nesting ecology across mute swan range in Michigan's Lower Peninsula, with an experimental design that represented spatial variability in parameter estimates without personnel or equipment usually needed for comparable investigations. We monitored fate of individual eggs throughout the incubation period by uniquely marking eggs with colored markers. We documented fate for eggs and ascertained whether eggs hatched, failed, or were predated/lost during incubation (Reynolds et al. 1965).

iButton temperature loggers placed below eggs in nests determined hatch or failure dates for most nests; however, determination of nest status change was most easily measured for semi-terrestrial nests that were less prone to water saturation of nesting material which buffered fine-scale changes in nest temperature. Additionally, breeding females continually built and repaired nesting mounds during incubation which required adjustment of iButtons to ensure they remained just below eggs in the nest bowl. Interestingly, this observed behavior to continually rebuild nests resulted in accidental burial of viable eggs by females on several occasions. Proper use of iButtons in mute swan nests remains a practical way to estimate hatch and failure timing despite initial setbacks experienced based on nest positioning and female behavior.

Our estimates of nest survival are comparable to those reported in the published literature for mute swans in introduced range on the eastern coast of North America (Reese 1980, Conover and Kania 1999, Hindman et al. 2014); however, a few key differences relating to productivity and cygnet survival exist. Mute swans tend to have higher clutch sizes in introduced ranges (Ciaranca et al. 1997, Conover and Kania 1999), compared to their native range (Perrins and

Reynolds 1967) and this trend held in Michigan. Additionally, mean volume for mute swan eggs observed in this study were between values reported for their native range (Bacon and Mountford 1990, Czapulak 2002) and we noted that smaller eggs tended to remain unhatched in the nest more often (Figure 2.3) consistent with observations by Czapulak (2002). Czapulak (2002) found that larger eggs, due to their proportionately higher increase in yolk and lipid stores (Birkhead 1984), influenced cygnet survival to 100 days post-hatch, but did not explain variation in the first month of life when cygnets are more susceptible to influences of weather extremes or potential predators. We were unable to investigate this relationship in Michigan because we did not individually mark cygnets according to their respective egg.

Our post-hatch parameters deviated from ranges in the published literature. Mean initial observed brood size after hatch (4.9 cygnets/pair) was slightly higher than values noted for Connecticut (Conover and Kania 1999) and Maryland (Reese 1980), but was identical to values obtained from Long Point in Ontario, Canada (Knapton 1993). This likely results from similar nest survival estimates coupled with a slightly elevated clutch size and egg survival rates. True initial brood size, not reported in most investigations, was higher (5.8 cygnet/pair). Uniquely marking all eggs in nests with different colored markers allowed us to accurately account for potential disparity in number of eggs known to hatch and brood size at initial resighting. Importantly, the method we used removed bias in apparent egg survival related to eggs that were removed or lost from the nest prior to hatch (i.e., their uniquely-marked eggshells were not present during post-hatch nest checks).

Cygnets color morph ratio was easily determined for broods at first visit after hatch. Gray morph cygnets were characterized by gray downy plumage and gray feet and bills whereas white or leucistic morph cygnets had brownish-white plumage and flesh-colored feet and bills (Nelson

1976). Mean ratio of gray to white young (36.9%) varied geographically across Michigan's Lower Peninsula (0 – 80% gray) but was stable across years likely due to genetic similarity of breeding pairs among years. Prevalence of leucistic morph cygnets in Michigan's population differs from many native (Bacon 1980, Wieloch and Czapulak 1991) and introduced populations (Conover et al. 2000) which are dominated by gray morph individuals, with the exception of mute swans in nearby Ontario, Canada (Knapton 1993).

Conover et al. (2000) documented effects of gray and leucistic morph cygnets on population demographics. Pre-fledge survival was lower for leucistic morph cygnets and differences in parental behavior toward cygnets were noted between both color morphs (Conover et al. 2000). Additionally, Conover et al. (2000) found that leucistic males had lower survival rates for first 2 years of life, but were able to pair and mate earlier than gray morph males. We did not find statistical differences in cygnet survival between color morphs (Table 2.6); however, gray cygnets had higher apparent survival than leucistic morph cygnets in the first two years, but not in the final year (which also had the lowest overall cygnet survival). No juvenile-marked swan nested at 1 or 2 years of age. The first nesting attempts for GPS-marked cygnets occurred after the conclusion of the study at 3 years of age (R. Knapik, unpublished data). Estimated survival was lower for leucistic individuals from fledging to their first April although differences were not statistically significant (Chapter 4).

Lower cygnet survival and brood survival ($\hat{S} = 0.58$) in Michigan resulted in a lower egg to fledge survival estimate ($\hat{S} = 0.198$) when compared to Connecticut ($\hat{S} = 0.41$; Conover and Kania 1999), Maryland, ($\hat{S} = 0.48$; Reese 1975), and England ($\hat{S} = 0.48$; Reynolds et al. 1965). Subsequently, overall productivity in Michigan (1.2 cygnets/pair) was below the 2.7 cygnets per nesting pair reported by Conover and Kania (1999) and 2.2 cygnets/pair reported by Reese

(1980); however, it was identical to estimates already reported for Michigan mute swans (1.2 cygnets/pair; Wood and Gelston 1972). Conover and Kania (1999) concluded that their higher breeding productivity may result from an expanding mute swan population that was not near carrying capacity. Interestingly, despite lower cygnet survival and brood survival, mean brood size at fledging in our research (3.1 cygnets/pair) was near values reported for Connecticut (3.2 cygnets/pair; Conover and Kania 1999). These findings suggest that lower overall breeding productivity in Michigan results from increased brood mortality for some pairs rather than homogenously lower cygnet survival across all broods. Therefore, heterogeneity in territory quality or available brood-rearing habitat between pairs is likely influencing overall productivity through brood and cygnet survival rates.

MANAGEMENT IMPLICATIONS

Managers are increasingly interested in reducing abundance of introduced mute swan populations. As abundance increases, effects on wetlands and native wildlife are realized, and public tolerance for wildlife conflict decreases. Concomitantly, the public desires science-based natural resources management policies that are carried out by trained professionals (Reiter et al. 1999). Management plans for non-native invasive species, such as mute swans, require scientific information on their basic biology to inform future strategies. Region-specific information on survival or movement is typically unavailable due to novelty of the species in the area or because of the need for early detection and decision making (Mack et al. 2000, Edelaar and Tella 2012). Therefore, management or eradication plans typically use demographic and movement data from other introduced regions or from native range. This practice may lead to undesirable results if dynamics differ between native and introduced ranges due to varying climactic conditions, predator assemblages, or interspecific competition. This research focused on quantifying

management-relevant nesting ecology parameters for mute swans in introduced range in Michigan.

Oiling eggs or destruction of nests can be effective for reducing the number of mute swans that enter the non-breeding population at local scales, and is sometimes preferable to culling of breeding adults in high density areas since pairs remain on territories despite the now-infertile clutch (Hindman et al. 2014). Managers interested in reliably locating nests for oiling or for culling of adult pairs should utilize low-level aircraft surveys of target areas when most females are incubating eggs (20 – 30 April) due to the conspicuous nature of mute swan nests. Egg flotation methods (Westerskov 1950, Walter and Rusch 1997) adapted for the 36 day mute swan incubation period can be used to determine estimated hatch date for nests in a specific region, or management efforts could be scheduled prior to mean estimated hatch date (12 May).

Broad-scale use of egg oiling or other techniques aimed at reducing number of hatched young per nest may be of limited benefit at current levels of mute swan abundance in Michigan. Widespread egg oiling for large populations of mute swans is labor and cost intensive (Hindman et al. 2014). Additionally, realized benefit of egg oiling in Michigan will be low due to high natural cygnet and brood mortality rates. Our results indicate that egg oiling will be most effective for pairs with highest predicted cygnet survival. Highest cygnet survival rates for a population likely occur in areas where access to nesting and brood-rearing resources is high and competition from other nesting pairs is low. Such areas are likely to be small secluded wetlands or isolated shallow lakes with few breeding pairs in the core of their distribution; however, these could include larger wetland complexes and lakes along an invasion front where intraspecific competition is low.

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CHAPTER 3: DENSITY DEPENDENCE IN PRODUCTIVITY OF A NORTH AMERICAN MUTE SWAN POPULATION

INTRODUCTION

Lack (1954) noted that wildlife populations tend to fluctuate around a certain number rather than growing indefinitely at a sustained rate. This observation, density-dependent regulation of populations, has become a fundamental underpinning of many wildlife population models although its pervasiveness and generalizability has sparked debate in the scientific literature (Hanski et al. 1993, Berryman 2004, White 2007). Definitive demonstration of density dependence in wild populations has historically proven difficult (Lack 1966) due to the need for long-term datasets on population demographics (Hassell et al. 1989, Godfray and Hassell 1992) although density dependence is implicated for many species (Woiwod and Hanski 1992, Lima and Jaksic 1998, Nummi and Saari 2003, Gunnarsson et al. 2013).

Newton (1998) noted that density dependence likely manifests through principle demographic factors (e.g., birth, death, and emigration rates) and could be regulated by intraspecific resource competition. Lebeuf and Giroux (2014) and Sedinger et al. (1998) suggested that density dependence was important in determining outcomes of reproductive effort for territorial waterbirds and manifested through several mechanisms (Ferrer and Donazar 1996). Lack (1966) and Fretwell and Lucas (1969) proposed that overall productivity would decrease and variation between individuals would remain stable with increasing density. They hypothesized that increased agonistic interactions would accompany increased density and, therefore, would reduce mean territory quality for all individuals regardless of realized quality at lower densities. Kadmon (1993) suggested that negative density dependence in productivity could also be explained by heterogeneity in habitat quality for pairs. This would manifest in a

population in which productivity declines with increased density, but variation in breeding performance among individuals increases rather than be equal as proposed by Lack (1966). Variation in individual performance relating to habitat heterogeneity follows the hypothesis that the best habitats are filled first (Hildén 1965, Ferrer and Donazar 1996, Rodenhouse et al. 1997, Lovette and Fitzpatrick 2016). Ferrer and Donazar (1996) summarized and investigated these 2 hypotheses (i.e., habitat heterogeneity hypothesis, [hereafter, HHH]; and interference hypothesis, [hereafter, IH]) for a population of Spanish imperial eagles (*Aquila adalberti*) and concluded that HHH is the regulating mechanism for population growth rates. However, Sergio and Newton (2003) noted the importance and difficulty of distinguishing between quality territories and quality individuals when investigating support for or differentiation between HHH and IH. Understanding mechanisms triggering density-dependent relationships is important for managing harvested (Gunnarsson et al. 2013), reintroduced (Armstrong et al. 2005), special concern (Carrete et al. 2006), and invasive species (Nummi and Saari 2003).

Nummi and Saari (2003) conducted a longitudinal study (1976 – 1998) to analyze reproductive parameters for mute swans (*Cygnus olor*) in an introduced range of the Finnish archipelago. They hypothesized that breeding success would differ between territories of varying quality, with quality measured as length of time it has been occupied. Density of breeding pairs was inversely related to clutch size, brood size, and fledged young per pair. Nummi and Saari (2003) found several cygnets with crushed skulls in high density areas which is evidence for IH; however, they also found that sites occupied longest (i.e., were of highest quality) produced more young, and that coefficient of variation for brood size increased with increasing density. Their results, much like Ferrer and Donazar (1996), predominantly provide support for HHH which results in lower survival of young due to increased variation in territory quality of nesting pairs.

Their findings and accounts published elsewhere in the scientific literature (Lack 1954, Sedinger et al. 1998) signified that dynamics in the brood rearing phase for birds become increasingly important as densities increase (Ferrer et al. 2008).

We assessed influence of density dependence on productivity for mute swans in Michigan. A pair of mute swans was introduced into Michigan's Charlevoix County in 1919. Population growth was slow throughout the 1900s; however, their population grew to an estimated 17,520 individuals in 2013 (D. Luukkonen, unpublished data) making it the largest population of mute swans in North America. The Michigan Department of Natural Resources (DNR) formalized their management goals and objectives for mute swans in 2012 (Michigan Department of Natural Resources 2012). This policy established a long-term goal of no more than 2,000 mute swans in Michigan by 2030 as determined via their annual breeding waterfowl survey; however, this policy did not outline levels of control needed to accomplish that goal due to uncertainty in demographic parameters for this introduced population. Furthermore, there were no empirical data to examine the role of density as it relates to breeding productivity within North America despite it being demonstrated in other introduced populations (Nummi and Saari 2003). Ellis and Elphick (2007) mentioned that density dependence was likely occurring in mute swan populations that have been established for more than three decades; therefore, investigation of density dependence is warranted for well-established sub-populations in Michigan. We observed productivity under a range of breeding densities within the core mute swan range in Michigan and compared densities relative to amount of characteristic nesting cover to identify whether incorporation of density dependence in breeding productivity is appropriate for population modeling.

STUDY AREA

Site Selection

The core of breeding range for Michigan mute swans is found in the Lower Peninsula (Michigan Department of Natural Resources, unpublished data). We overlaid mean estimated spring density of mute swans in 2011 – 2015 with hydrography data (Center for Shared Solutions and Technology Partnerships 2015) in a geographic information system (GIS; ArcGIS 10.3.1, ESRI, Redlands, CA, USA) to identify waterbodies that may harbor breeding pairs of mute swans. We stratified the Lower Peninsula of Michigan using township boundaries as outlined through the United States' Public Land Survey System (PLSS; Center for Shared Solutions and Technology Partnerships 2015). We performed a query in GIS to identify all PLSS townships where mean estimated spring density was ≥ 1 mute swan per 259 ha (roughly 1 per square mile) during 2011 – 2015 and took the mean shoreline distance within those identified townships (40 km; a coarse proxy for nesting cover potential) to estimate where mute swan presence was likely in the Lower Peninsula during the following breeding season (i.e., 2016). We identified 15 preliminary study sites (6 x 6 km each) using these methods (Figure 3.1). We used fixed-wing aircraft (Cessna 185; Northwoods Aviation Inc, Cadillac, MI, USA) to survey preliminary study areas for mute swan presence and nesting habitat in December 2015 or April 2016. We chose 5 study sites in Bay (Tobico), Cass (Juno), Kent (Wabasis), Oakland (Pontiac), and St. Clair (St. Clair) Counties to investigate density dependence in breeding productivity 2016 – 2018 (Figure 3.1). One additional site (6 by 6 km) in Antrim County (Clam) was included in this investigation for 2017 – 2018 (Figure 3.1).

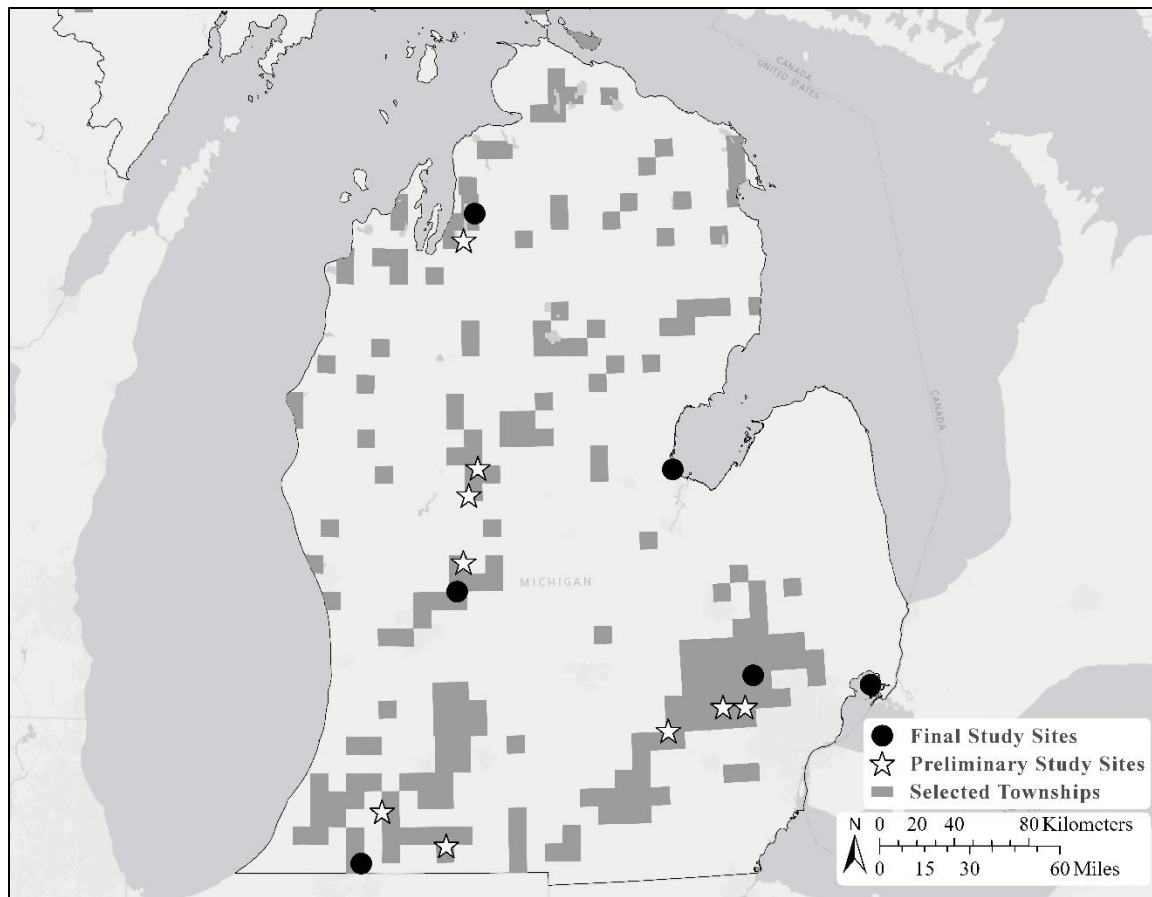


Figure 3.1. Preliminary and final study sites 2016 – 2018 were located throughout the Lower Peninsula of Michigan, USA, within selected public land survey system (PLSS) townships that had a high likelihood of breeding pair presence (i.e., ≥ 40 km of shoreline).

Site Descriptions

Land cover composition varies latitudinally in the Lower Peninsula of Michigan, USA, (Homer et al. 2015), and concomitantly varied across our 4 inland (Juno, Pontiac, Wabasis, Clam) and 2 coastal study sites (Tobico, St. Clair). Inland waterbodies contained a mix of natural and developed shoreline with moderate to heavily developed upland areas adjacent to areas of permanently-flooded open water (L1UBH; U. S. Fish and Wildlife Service 2015). Natural shoreline consisted of characteristic mute swan nesting cover (PEM; U. S. Fish and Wildlife Service 2015) such as broad-leaved cattail (*Typha latifolia*), bulrushes (*Schoenoplectus* spp.), narrow-leaved cattail (*Typha angustifolia*), and phragmites (*Phragmites australis*) or woody

vegetation (buttonbush [*Cephalanthus occidentalis*], willow [*Salix* spp.], ash, [*Fraxinus* spp.], maple [*Acer* spp.], cottonwood [*Populus deltoides*], and oak [*Quercus* spp.]). The 2 coastal sites included areas of persistent emergent vegetation that is semi-permanently flooded (PEM1F) and open water (PABG; U. S. Fish and Wildlife Service 2015) among areas of agriculture, human development, and forest cover (Homer et al. 2015). The St. Clair study site was primarily open water (L1UBH and L2UBH) with large areas of freshwater wetlands that consisted of emergent vegetation (PEM; e.g., broad-leaved cattail, bulrushes, narrow-leaved cattail, and phragmites). The St. Clair study site also had small developed islands (< 5 ha each) dispersed within the matrix of open water and emergent vegetation.

METHODS

Field methods

Nest density

We used boat and aerial surveys to detect actively nesting pairs within study sites and determine GPS coordinates of all observed nests. Annual aerial surveys of nesting mute swans were conducted (12 April – 1 May) for sites ($n = 5$, 2016; $n = 6$, 2017 – 2018). Two observers worked together to detect incubating females on the large (≥ 1 m) conspicuous nests (Conover and Kania 1999) against the backdrop of senesced emergent vegetation. Cooper (1979) and Kear (1972) estimated that incubation recesses for female swans were < 30 minutes daily; therefore, detection probability of active nests was likely near 1 during low-level aerial surveys. All detected nests were recorded on orthophotographs and were later transferred to a GIS. We recorded flights using wing strut-mounted video camera systems in 2016 – 2017 (MotoCam 360, Bothell, WA, USA) and 2018 (GoPro Hero 4 Silver, San Mateo, California, USA) to aid in

determining exact physical location of nesting pairs. We documented flight paths with 1 second GPS fix intervals using a cellphone application (Strava, Inc., San Francisco, CA USA).

Breeding productivity

Aerial and boat surveys were used to estimate breeding productivity per pair near estimated fledging (1 September) for all sites. Aerial surveys were flown in fixed-wing aircraft with flight paths and flight video recorded in the same manner as the spring nest detection surveys. We counted white (i.e., adult or leucistic-morph cygnets) and gray swans (i.e., gray-morph cygnets) and recorded approximate location of all pairs and broods on aerial photos which were later transferred to a GIS. We used boats within study sites to confirm brood size and color morph ratio (i.e., count leucistic-morph cygnets separately from adults). Number of fledged cygnets per site was compared to total number of nesting pairs to derive an estimate of productivity that includes failed nests and failed broods.

Characteristic nesting cover

We documented extent and location of characteristic nesting cover (i.e., cattails, bulrush, and phragmites; Ciaranca et al. 1997) available to mute swans (i.e., dense vegetation adjacent to water; Baldassarre 2014) for all study sites during the 2018 nesting season. We recorded where stands of characteristic cover bordered water on recent (2014 – 2016) orthophotographs and then conducted in-field surveys to verify detection of characteristic cover using orthophotographs. Location of characteristic nesting cover was transferred from orthophotographs to digital polyline features using a GIS (ArcGIS Pro 2.1.2, ESRI, Redlands, CA, USA).

Data analysis

Nest spacing

We determined median distance to closest conspecific nest for all detected nests within study site boundaries 2016 – 2018. We used a GIS to determine Euclidean distance between mute swan nests that resided on the same waterbody ($n = 143$ comparisons). Calculating nest spacing in this manner eliminated measurements of nest spacing between adjacent but distinct waterbodies which may be biologically irrelevant since mute swans are nearly fully aquatic (Sousa et al. 2008) and are likely not directly influenced by presence of pairs on adjacent waterbodies during the nesting period. Nest spacing measurements were summarized for each year with sites pooled because we wished to understand the typical conspecific nest spacing across sites.

Digitization of characteristic nesting cover

We used a GIS and recent (2014 – 2016) high-resolution (< 1 m per pixel) leaf-off (April) orthophotos to manually digitize transition between open water and other cover types (e.g., emergent herbaceous vegetation, forests, developed land). Digitizing transition between open water and adjacent cover types allowed us to use this border for predicted placement of characteristic nesting cover. We converted open water polygons to line features using a GIS. We then subset the open water line features into 2 categories (i.e., areas adjacent to characteristic nesting cover and areas adjacent to other cover types). We created a new line feature that contained all the segments where characteristic nesting cover was immediately adjacent to open water. We created equally-spaced points (10 m spacing) along areas of characteristic nesting cover to represent potential nest locations for the optimization process (Figure 3.2).

Saturation of nesting cover

We were interested in understanding maximum nesting pair density possible (i.e., saturation) for the 6 study sites given arrangement of characteristic nesting cover and observed spacing of conspecific nests. Our estimates of saturation assume that mute swans optimally space nests in characteristic cover to obtain the highest possible number of nests. Mute swans are likely not optimally spacing nests in this manner (see results); however, this method provides a liberal estimate of nesting pair saturation to which actual density can be compared. Actual pair densities that are near or exceed estimated saturation densities (i.e., saturation ratios of ≥ 0.7) and instances of swans establishing nesting territories outside of characteristic nesting cover will indicate that site nesting density is likely at saturation especially since mute swan nesting pairs are likely spaced sub optimally within characteristic cover. We used a manual spatial optimization approach through GIS to estimate saturation of characteristic nesting cover. Our methods were conceptually similar to the anti-covering location problem (ACLP; Moon and Chaudhry 1984, Murray and Church 1997) approach employed by Downs et al. (2008) to estimate nesting carrying capacity for territorial sandhill cranes. Our manual optimization methods likely approximate estimates that could be derived through mathematical optimization in this system due to the discrete patches of characteristic nesting cover (Figure 3.2); however, the exact placement of nests within the cover, which we are uninterested in, may slightly differ between a manual and mathematical optimization.

Comparison of observed breeding productivity among sites

The functional relationship between breeding productivity (i.e., the number of fledglings per nesting pair) and nesting pair density is important in determining density dependence. We conducted a linear regression in program R (R Development Core Team 2018) to examine

relationship of productivity to observed pair density and to the ratio of observed pairs to estimate saturation. We ranked our competing models using Akaike's Information Criterion corrected for small sample sizes (AICc; Anderson and Burnham 2002). This allowed us to see if adjusting the observed number of nesting pairs on each site by availability of characteristic nesting cover (i.e., calculating an ecological density) furthered our understanding of the relationship between nesting pair density and productivity.

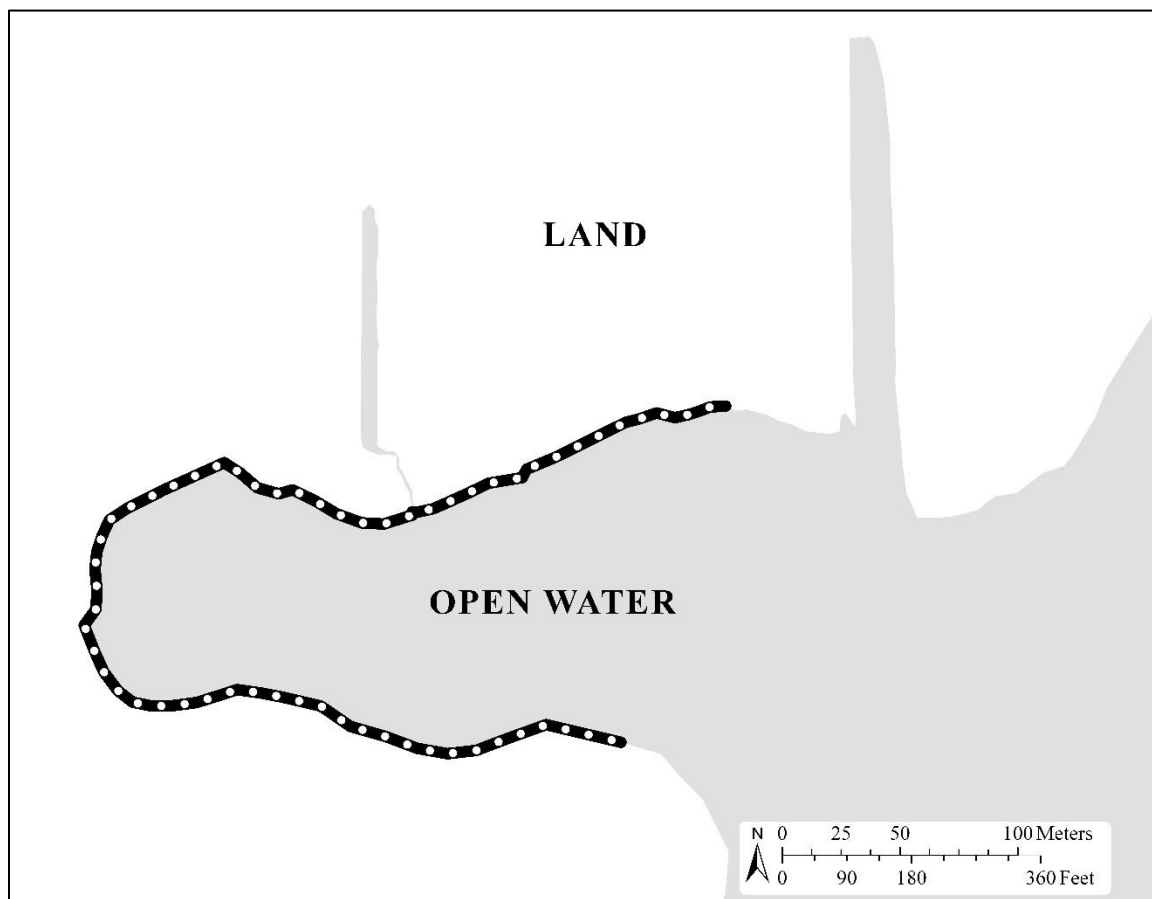


Figure 3.2. Example determination of potential nesting locations (white circles) within characteristic nesting cover for mute swans (black line) at the transition of open water and adjacent cover types for focal waterbodies in the Lower Peninsula of Michigan, USA.

RESULTS

We detected 228 pairs of mute swans with nests within study site boundaries 2016 – 2018 (Table 3.1) using aerial and boat surveys. Median distance between closest conspecific nest was

418.1 m ($\bar{x}$ = 495.1, SD = 388.7; range: 22.6 – 2959.2). Mean number of nests and number of fledged young per pair 2016 – 2018 varied among the 6 equal-sized study areas (3.5 – 26 nests per site and 0.6 – 2.3 fledglings per pair; Table 3.1).

Table 3.1. Reproductive parameters for 6 equal-sized study areas (36 km² each) ordered by increasing latitude in the Lower Peninsula of Michigan, USA, 2016 – 2018.

	2016		2017		2018		Pooled Mean		Estimated Saturation	
	Pairs	Fledge per Pair	Pairs	Fledge per Pair	Pairs	Fledge per Pair	Pairs	Fledge per Pair	Pairs	Sat. Ratio
Juno	21	1.6	20	1.3	10*	1.5	17.0	0.5	17.0	1.2
St. Clair	25	0.9	19	1.2	6*	2.4	16.7	0.5	67	0.3
Pontiac	31	1.0	25	0.9	22	0.4	26.0	0.7	32.0	0.8
Wabasis	9	2.6	9	2.1	7	1.0	8.3	0.2	40	0.2
Tobico	7	2.7	5*	1.8	5	2.6	5.7	0.2	31	0.2
Clam	.	.	5	0.6	2	1.0	3.5	0.1	6	0.7
All Sites	93	1.4	84	1.2	52	1.1	76.3	0.4	193	.

*Total does not include nests that were influenced by investigators or nests of pairs culled during incubation in official removal efforts, Fl. = Fledge, Sat. = Saturation

Mean number of fledged young per pair tended to increase with decreasing pair density (Adjusted R^2 = 0.1798; Figure 3.3a); however, the site with the lowest number of nesting pairs also fledged the fewest young (Table 3.1). Converting observed pair densities to saturation ratios (i.e., ratio of actual nesting pairs to estimated saturation) provided a slightly better fit to the data (Adjusted R^2 = 0.1989) although variation among sites was still evident (Figure 3.3b). The most parsimonious model in the linear regression of breeding productivity (Table 3.2) included a fixed effect for ratio of observed nesting pairs to estimated saturation ($\hat{\beta}$ = -0.9792, p = 0.04). The next competing model was within 2 AICc units of the top model and contained a fixed effect for number of nesting pairs ($\hat{\beta}$ = -0.0392, p = 0.05; Table 3.2). Correlation between observed number of nesting pairs and estimated saturation ratio was 0.6273; therefore, we did not include these covariates together in an additive model.

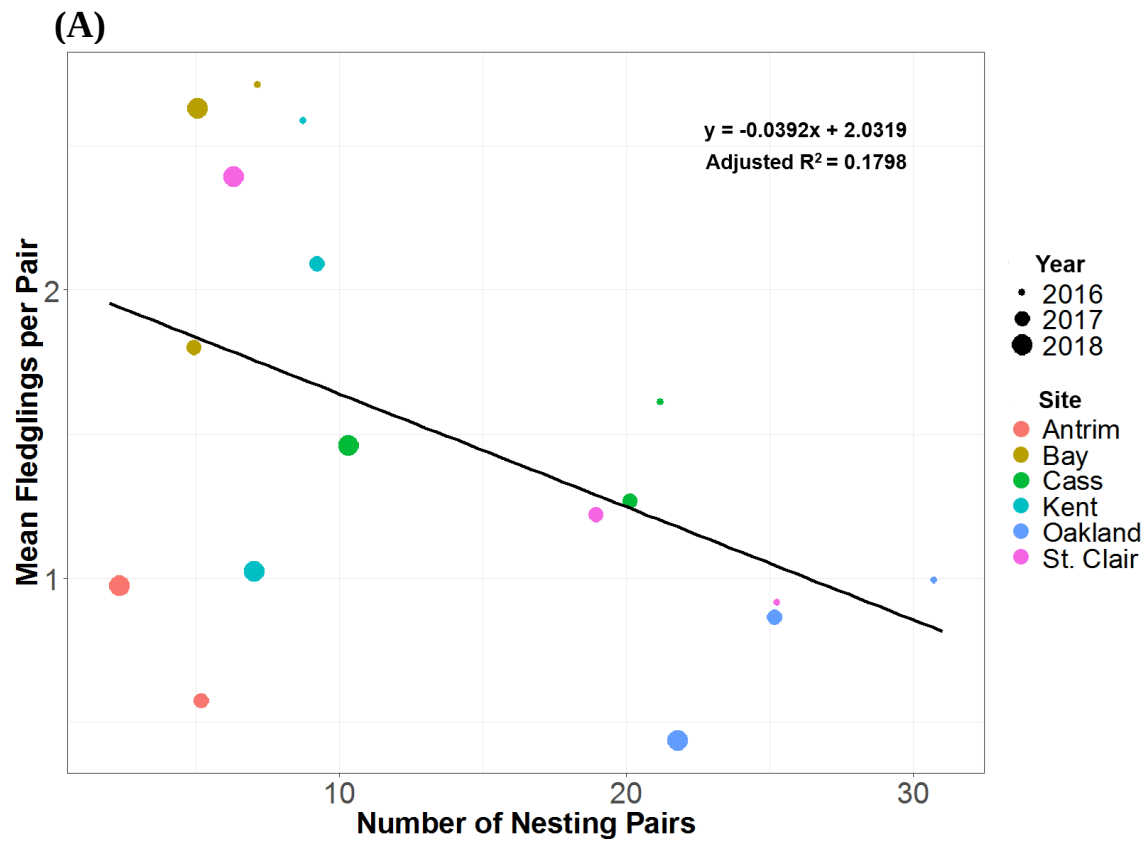


Figure 3.3. Comparison of breeding productivity to number of pairs per site **(A)** and breeding productivity to estimated nesting pair saturation ratio **(B)** 2016 – 2018 for 6 equal-sized study sites in the Lower Peninsula of Michigan, USA.

Figure 3.3 (cont'd)

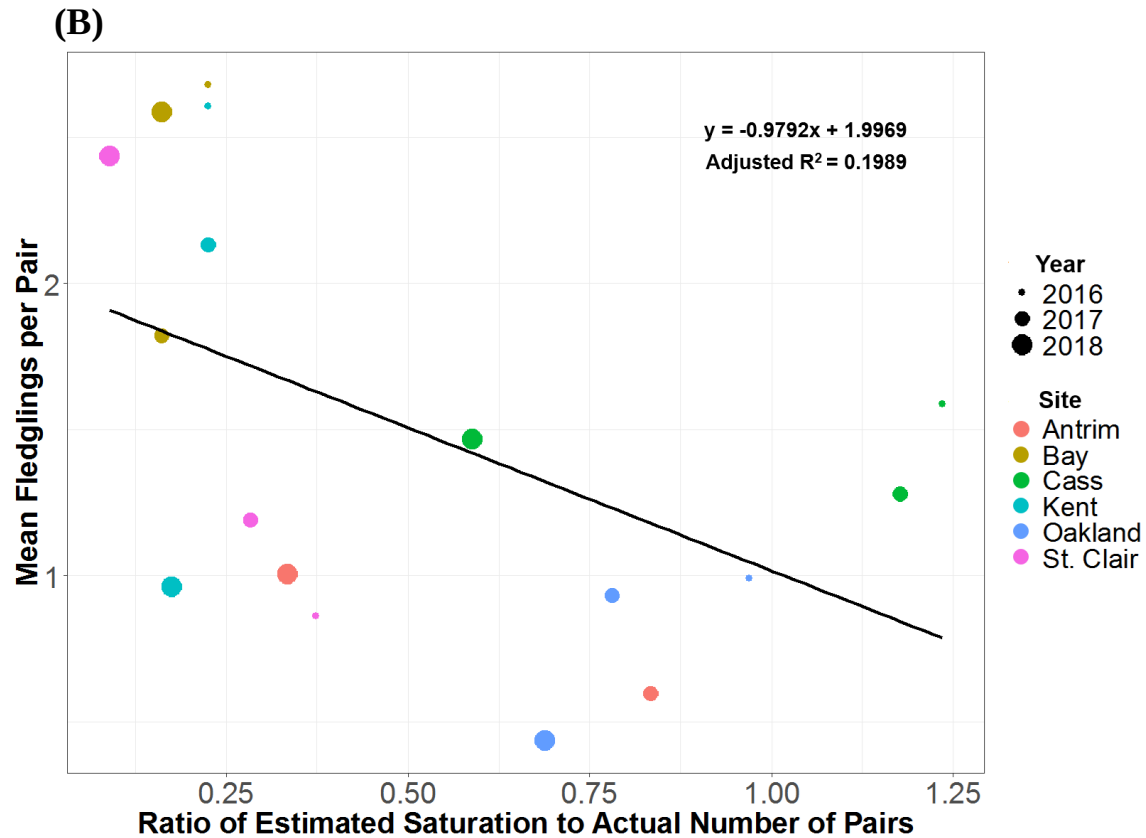


Table 3.2. Model selection for linear regression on breeding productivity of mute swans in Michigan, USA, during 2016 – 2018.

Model	k^a	AICc ^a	Δ AICc ^a	w_i^a
Saturation Ratio	1	38.085	0	0.372
Number of Pairs	1	38.486	0.401	0.304
Null Model	1	40.952	2.867	0.089

^a k = number of parameters in model, AICc = Akaike's Information Criterion adjusted for small sample sizes, Δ AICc = difference between AICc of best fitting and current model
 w_i = Akaike's weight

Nesting pairs were not spaced optimally in characteristic nesting cover (Figures 3.4 and 3.5). Sites nearest saturation of nesting pair density tended to have pairs nesting in non-characteristic nesting cover (Figure 3.4), whereas pairs almost exclusively nested in characteristic cover on less saturated sites (Figure 3.5). Uncorrected estimates of pair density (i.e., pairs per km²) provided a suitable estimation of pair saturation (i.e., saturation ratios) for 4

of the 6 sites (Juno, Pontiac, Wabasis, and Tobico); however, interpretation of pair saturation changed on 2 sites (Clam and St. Clair) when adjusting observed pair density by expected saturation of pairs (Table 3.1). The St. Clair site had a low saturation ratio (Table 3.1) due to the large amount of characteristic cover present despite having a high number of nesting pairs. The Clam site had few nesting pairs, but also had a paucity of well-spaced characteristic nesting cover resulting in a site that was near saturation even though the observed number of pairs was low (Table 3.1).

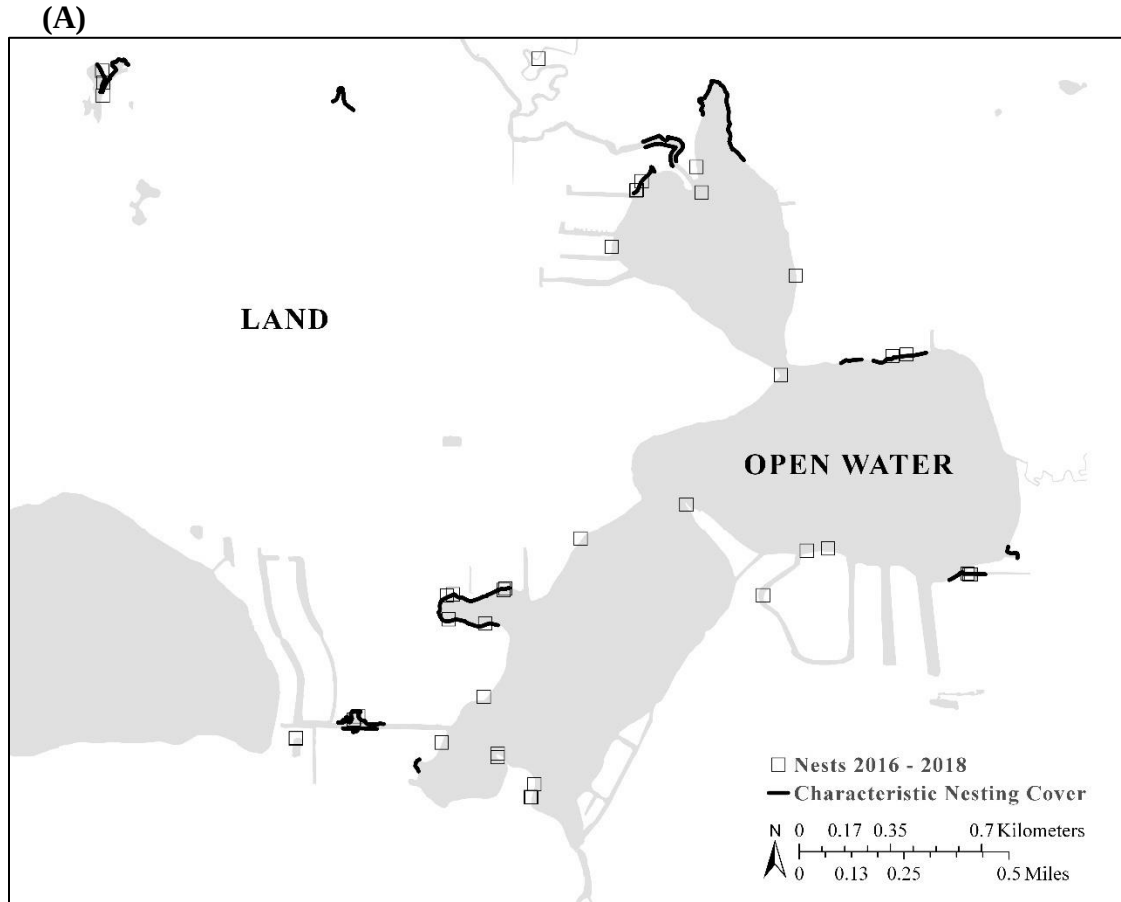
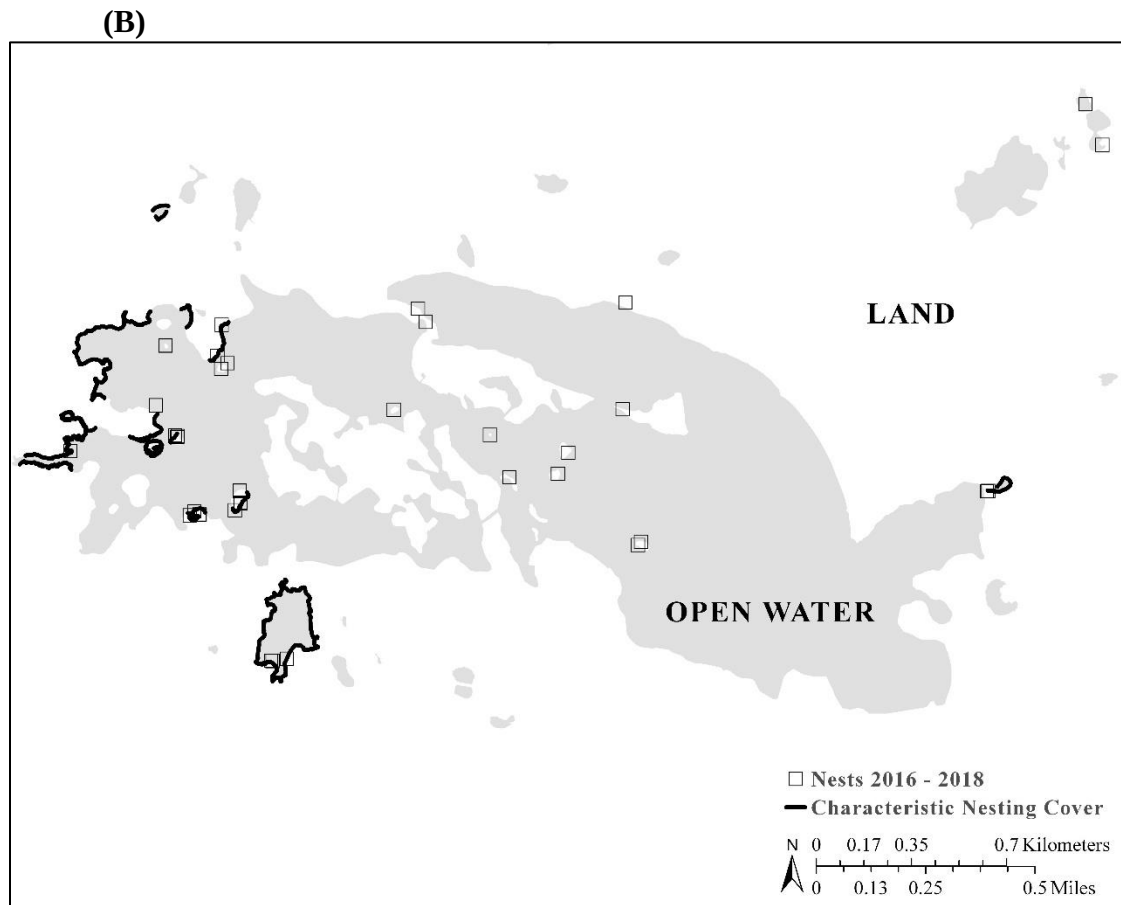


Figure 3.4. Comparison of nest locations 2016 – 2018 within characteristic and non-characteristic nesting cover for select waterbodies within the Juno site in Cass County, MI, USA **(A)** and Pontiac site in Oakland County, MI, USA **(B)** which had nesting pairs establishing territories outside of characteristic nesting cover and low observed productivity.

Figure 3.4 (cont'd)



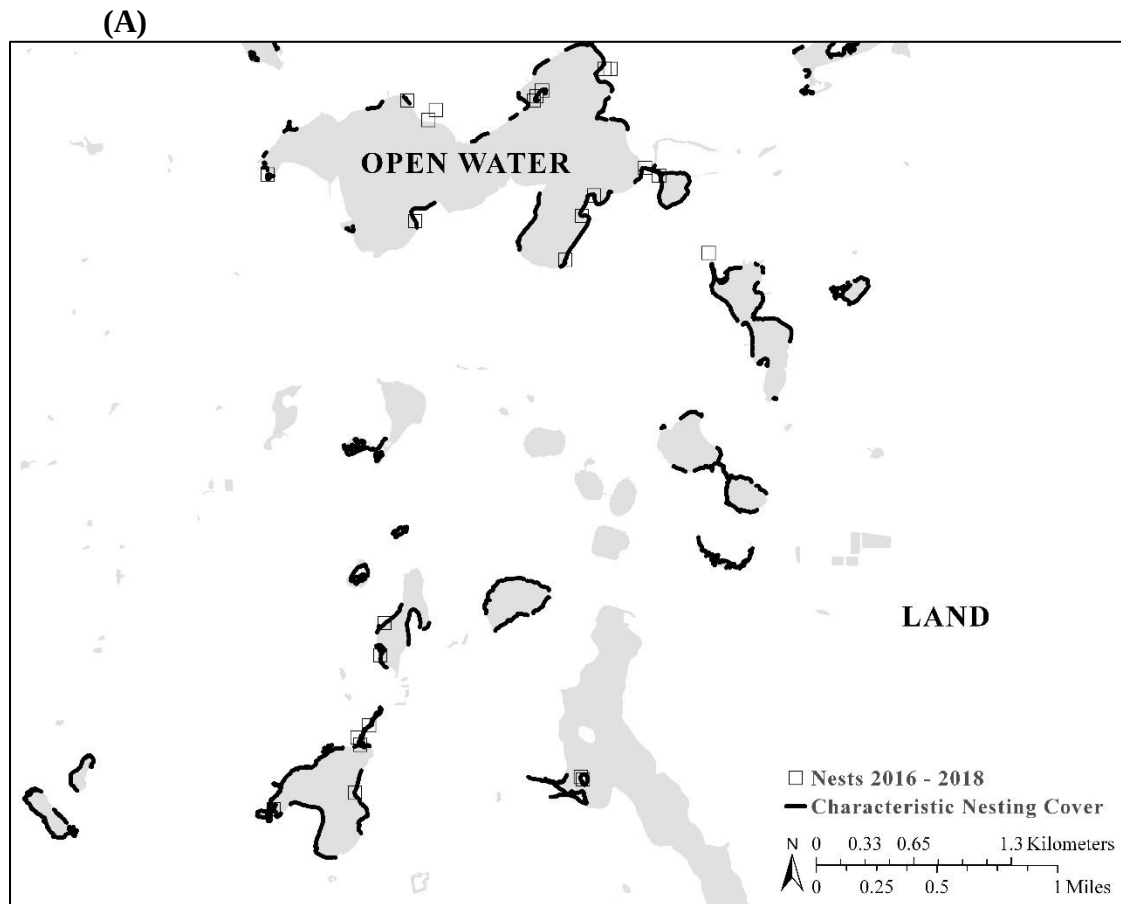
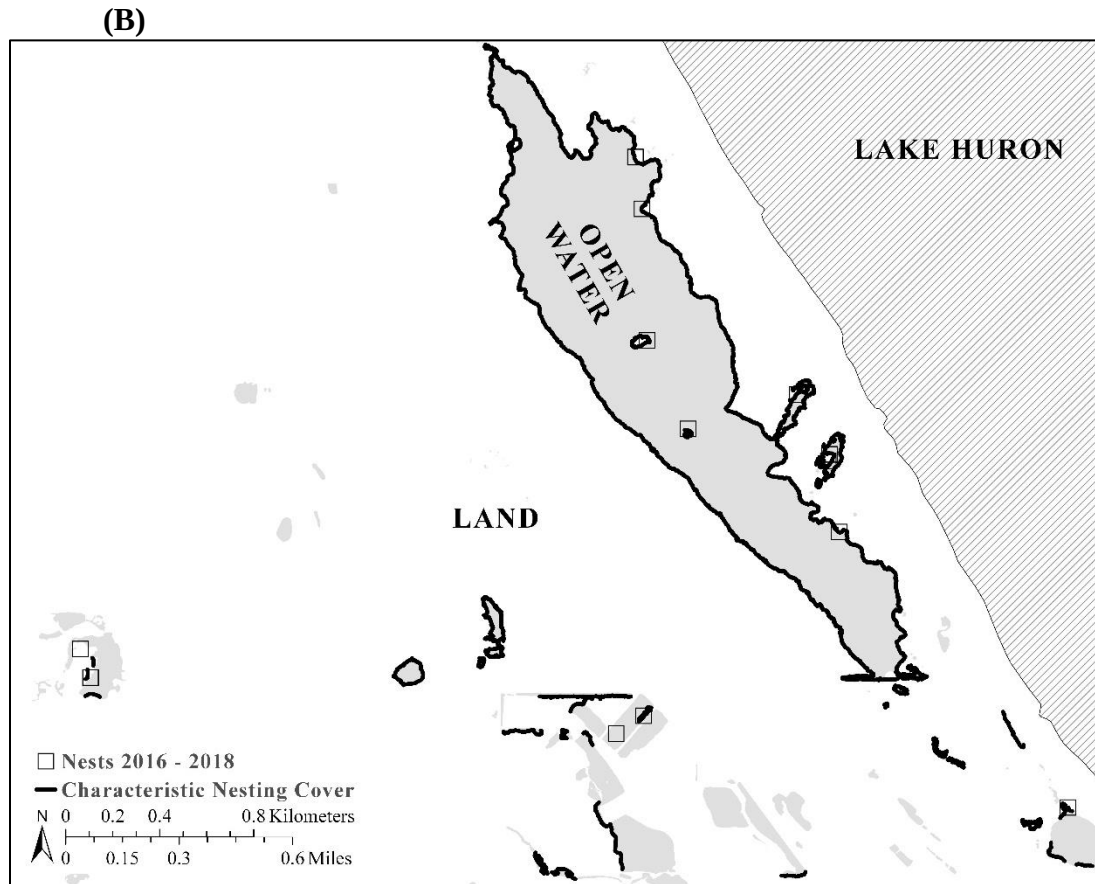


Figure 3.5. Comparison of nest locations 2016 – 2018 within characteristic and non-characteristic nesting cover for select waterbodies within the Wabasis site in Kent County, MI, USA **(A)** and Tobico site in Bay County, MI, USA **(B)** which had most nesting pairs use territories in characteristic nesting cover and higher observed productivity.

Figure 3.5 (cont'd)



DISCUSSION

Effects of density dependence in territorial avian species typically first manifest in aspects of breeding productivity like hatching success (Lebeuf and Giroux 2014), growth of young (Sedinger et al. 1998), or nearly all breeding parameters (Nummi et al. 2015).

Longitudinal studies of breeding parameters under naturally fluctuating species abundances are typically used to demonstrate presence or absence of density dependence (Godfray and Hassell 1992); however, the mechanisms causing this pattern are not always identified. Two hypotheses have been proposed to explain the mechanism by which density of territorial species effects breeding performance. Kadmon (1993) and Rodenhouse et al. (1997) argued that heterogeneity in habitat suitability (i.e., HHH) influences reproductive performance for populations resulting in

a lower mean productivity and increased variance in productivity at higher densities. A second hypothesis (i.e., IH) asserts that agonistic interactions between conspecifics at higher densities lowers overall productivity for all pairs resulting in similar variance under high and low densities (Lack 1966, Sutherland 1996). Our approach allowed us to look for the presence of and mechanism by which density dependence is acting on nesting mute swans within Michigan's Lower Peninsula.

We found evidence for density dependence in breeding productivity for mute swans in Michigan. Mean productivity per pair declined as number of breeding pairs per site increased (Figure 3.3a). Our range in observed nesting density across ($0.1 \text{ nesting pairs/km}^2 - 0.7 \text{ nesting pairs/km}^2$) was similar to values estimated by Nummi and Saari (2003) in early ($\leq 0.1 \text{ nesting pairs/km}^2$) and late ($0.6 \text{ nesting pairs/km}^2$) stages of invasion for part of a Finnish archipelago. Nummi and Saari (2003) noted that density of nesting pairs during late stages of invasion was the highest recorded density in Europe for a non-colonial population. We observed similar extreme nesting densities and low productivity on 2 inland sites and 1 coastal site (Table 3.1) in Michigan's Lower Peninsula; however, the site with the fewest pairs also produced the fewest young. We found that this site (Clam) was near saturation of characteristic nesting cover despite the low number of nesting pairs (Table 3.1); therefore, it was similar to sites with higher nesting pair densities. Interestingly, a site (St. Clair) with many nesting pairs that fledged few young was not close to estimated saturation of nesting cover using this methodology (Table 3.1). These results for St. Clair could be due to its uniqueness among the study sites (i.e., an open water site located in the largest contained freshwater delta in North America) which could potentially have other extrinsic factors limiting cygnet survival not encountered on inland sites nor captured in this analysis (e.g., storm surges, cooler water temperatures). Additionally, our estimated

saturation level using these methods may be unrealistic in that other factors may become limiting before nesting habitats become saturated. Density of nesting pairs under our estimated saturation for St. Clair (Table 3.1) would be 1.86 pairs per km² which is 3 times higher than any reported mute swan pair density outside of colonial populations (Nummi and Saari 2003). Therefore, we considered St. Clair to be a high-density site since its observed density of nesting pairs (Table 3.1) is near the maximum density reported in the literature (Nummi and Saari 2003). Further, nesting pair density was reduced on the St. Clair site under permit by the U.S. Department of Agriculture Wildlife Services during the final year of investigation to reduce human wildlife conflict. Nesting pairs that remained fledged more cygnets per pair and utilized larger areas during brood rearing than in previous years (R. Knapik, unpublished data). This suggests that density impacts were realized at observed nesting pair density in previous years even though it was below the estimated saturation. Our optimization methods to estimate saturation of characteristic nesting cover aligned well with observed density and productivity for the other sites (5 of 6 total sites; Table 3.1).

Our spatial comparison of nesting pair density to characteristic nesting cover provided insights into the mechanism by which density is influencing breeding productivity. Our results support the HHH (Andrewartha and Birch 1954, Kadmon 1993, Rodenhouse et al. 1997). Pairs almost exclusively nested in characteristic cover on sites with few nesting pairs and unfilled characteristic nesting cover remained (e.g., Wabasis, Tobico, and Clam; Figure 3.5) whereas pairs filled characteristic nesting cover and nested, presumably, in suboptimal areas on sites at or near estimated saturation (e.g., Juno, St. Clair, and Pontiac; Table 3.1, Figure 3.4). Additionally, mean brood survival was lower (0.58 ± 0.03 ; Chapter 2) in Michigan when compared to other introduced populations (Conover and Kania 1999) despite a normal mean brood size at fledging

for pairs that fledged young (3.1 cygnets/pair; Chapter 2). This means that pairs which successfully fledged young did so with brood sizes comparable to other areas of their introduced range (Conover and Kania 1999) despite an overall lower mean breeding productivity across sites (1.42 cygnets/pair; Table 3.1) compared to low-density areas of their introduced range (Reese 1975, Conover and Kania 1999, Nummi and Saari 2003). Our distribution of brood sizes at fledging (Chapter 2) is expected for territorial long-lived bird species exhibiting density dependence due to heterogeneity in nesting habitat (Ferrer et al. 2008). These findings lend further credit to the HHH which expects increased variance in mean brood size produced per pair (Andrewartha and Birch 1954, Rodenhouse et al. 1997) rather than a uniform reduction in number of fledged young across all pairs (Lack 1966). We cannot claim that agonistic interactions (i.e., IH) had no effect on productivity because both HHH and IH can simultaneously occur (Ferrer and Donazar 1996, Krüger et al. 2012); however, our observed patterns provide the most support for HHH rather than IH in Michigan mute swans.

We could not control for all factors potentially influencing productivity on sites. Furthermore, we could not separate effects of individual and territory quality in this short-term study because not all nesting individuals within sites were uniquely marked (Chapter 2). We noted 10 instances on sites with highest observed nesting pair densities where territories and exact nesting mounds in characteristic nesting cover were immediately taken over by new pairs following dissociation of a nesting pair (i.e., through death of a mate or pair; Chapter 2). Therefore, we could not assume that unmarked individuals observed on territories were constant between years. The surviving member of pairs joined non-breeding flocks and did not nest throughout the remainder of the study (R. Knapik, unpublished data) signaling high competition for territories in characteristic cover. Additionally, presence and abundance of non-breeding

flocks could have also influenced productivity; however, non-breeding flocks were successfully excluded from areas with actively nesting pairs especially after hatching of cygnets (R. Knapik, personal observation). Birkhead et al. (1983) demonstrated that inexperienced pairs had slightly lower breeding productivity than experienced pairs; however, inexperienced pairs still produced young. Therefore, while individual quality may be partly confounded with territory quality for mute swans in this study, variation in individual quality is not likely to be the mechanism driving our observed support for the HHH.

Our evidence for habitat-mediated density dependence in breeding productivity of an introduced North American mute swan population is similar to findings reported by Nummi and Saari (2003) for an introduced population in a Finnish archipelago. Further, we demonstrated that strength of density dependence in breeding productivity varies spatially within Michigan, USA, based on local dynamics of nesting pairs and coverage of characteristic nesting habitat. We argue that density-mediated breeding productivity should be considered when developing demographic models for North American mute swan populations especially when using regionally-estimated demographic parameters.

MANAGEMENT IMPLICATIONS

The Michigan DNR has chosen to pursue a wildlife damage management approach to invasive mute swans in the Great Lakes region rather than a targeted eradication program (Michigan Department of Natural Resources 2012). A wildlife damage management program will likely be a more successful form of mute swan management in the short term since immigration is likely still occurring from neighboring provinces and states, and not all reproductive swans can be targeted for management (Bomford and O'Brien 1995) due to Michigan's current permitting process for removals. While management of invasive species should be initiated when abundance is low (Usher 1989, Edelaar and Tella 2012), wildlife

damage management programs for established invasive species can be successful if they incorporate local demography and proclivities of the species (Bomford and O'Brien 1995). Such programs must also be cognizant of potential density-dependence in demographic rates (Newton 1998, Nummi and Saari 2003).

We derived region specific demographic rates for mute swans through this research (Chapter 2 and 4) which will parameterize matrix population models (Chapter 5) aimed at guiding in-field management. Further, this analysis not only provides evidence that density dependence should be incorporated into breeding productivity of matrix population models (Table 3.1), but it provides practical in-field guidelines for efficient methods to perform culling of swans or destroying of nests.

Targeted removal of breeding pairs should be first prioritized for areas which are likely to be most productive. These are lakes and wetlands where the number of breeding pairs is low but characteristic nesting cover (i.e., cattails, phragmites, or reeds next to shallow open water) is abundant. Our results indicate that these pairs are recruiting the most immature swans into the population; however, we also recognize that targeting low density areas increases costs needed to remove each swan in the short term, but the long-term costs of management should be lower since fewer total swans would need to be removed (Chapter 5; Ellis and Elphick 2007) . Post-removal surveillance of these areas should occur to ensure that pairs do not return because newly colonizing swans will likely have high breeding productivity while nesting pair density is low.

Removal of swans in summer or winter concentration areas remains a viable management strategy; however, these efforts should also be focused in areas that have low nesting densities but large amounts of characteristic nesting cover representing high potential productivity areas. Although mute swans are capable of large movements, they tend to move to the closest open

water areas during summer molting and winter which is particularly true for established pairs (Chapter 4). Therefore, immature or non-breeding swans in summer flocks will likely try to settle in the region where they are flocking. Winter flocks of mute swans can contain established breeding pairs, their current and former cygnets, and non-breeding swans (Chapter 4); therefore, these efforts should also be first focused in regions where overall swan density is low. This is because local (Chapter 4) established breeding pairs may be culled during winter removal efforts which then effects local breeding density and dynamics the following spring. Anything short of a complete removal of breeding pairs within or adjacent to an area of saturated suitable nesting cover could allow remaining pairs to be more productive due to lower nesting density (Table 3.1; Nummi and Saari 2003).

Our evidence for habitat-mediated density dependence in breeding productivity also has implications for lethal management options targeted during incubation stage, such as egg oiling. Oiling mute swan eggs during incubation is a highly effective method for preventing hatch (Hindman et al. 2014); however, it is not effective at reducing the overall population in the short term (Ellis and Elphick 2007, Hindman et al. 2014). Nevertheless, it is a method that can have localized impact, reduce summer population of cygnets (Hindman et al. 2014), and is sometimes the only management option desired by landowners and lake associations. Our results show that egg oiling will be most effective when the probability of cygnet survival is high (i.e., when breeding pair densities are low); therefore, egg oiling procedures should first be focused on lakes and wetlands with few pairs or with pairs that have proven ability to produce and fledge cygnets. Egg oiling in areas where intraspecific competition is high and where pairs are nesting in non-characteristic nesting cover (Figure 3.4) will be inefficient since most pairs would not have fledged young anyway. We demonstrated that management aimed at achieving long-term

population goals (Michigan Department of Natural Resources 2012) should be cognizant that density dependence in breeding productivity is occurring in Michigan. In-field and demographic modeling should account for this relationship as populations are reduced.

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LITERATURE CITED

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CHAPTER 4: LIFE-STAGE SPECIFIC SURVIVAL AND MOVEMENTS OF MUTE SWANS IN MICHIGAN, USA

INTRODUCTION

Mute swans (*Cygnus olor*) are large waterbirds native to portions of central Europe (e.g., Poland, Sweden, Denmark), the Baltic States, and regions in western Russia and central Asia (Allin et al. 1987, Wieloch 1991), but recently introduced into many areas by humans as early as 1186 (Reeber 2015). Mute swans were translocated to areas beyond their native range as an ornamental and in some instances as a source of readily available protein (Perrins and Ogilvie 1981, Baldassarre 2014). The long history of mute swans and humans throughout Europe, Asia, and North America makes it difficult to definitively outline their native range; however, mute swans present in North America are the direct result of human-assisted movements beginning in the late 1800s (Alison and Burton 2008, Elphick 2009). The close association of mute swans with humans, their semi-domestication (Austin 1961, Ogilvie 1967), and selective breeding for leucistic-morph individuals (Bacon 1980) has potentially altered aspects of their biology from their naturally occurring state.

Mute swans are non-migratory across their range in western Europe and North America; however, some populations in central Europe (i.e., Poland) exhibit migratory behaviors between breeding and wintering grounds (Wieloch and Remisiewicz 2001). Individuals in sedentary populations depend on anthropogenic food resources year-round (Włodarczyk et al. 2013) and infrequently move more than 50 km from location of marking (Collins 2002), with movements typically following water courses or coastlines (Ogilvie 1967). Non-migratory populations of mute swans in temperate climates will move to nearby areas of shallow ice-free water during winter (Mathiasson 1993), including urban areas (Campbell 1960). Migratory and sedentary

populations in their native range have historically been monitored via swan counts, coded leg bands, and neck collars (Ogilvie 1967, Wieloch 1991, Kirby et al. 1994, Włodarczyk et al. 2013). Over 80% of individuals in some regions have been marked with combinations of metal or plastic-coded leg bands and plastic neck collars (Coleman et al. 2001, Watola et al. 2003), resulting in very large sample sizes and studies that last a decade or more. These long-term studies (Coleman et al. 2001, Collins 2002) contributed to our understanding of mute swan across their range; however, derived demographic parameters and observed movement patterns may not be universally applicable across native and introduced ranges due to varying climactic, genetic, and anthropogenic histories. Researchers acknowledge that relying on resightings to infer mortality or movements has potential to introduce movement-biased variation because individuals that emigrate from study regions may be lost to follow-up (Coleman et al. 2001, Collins 2002, Watola et al. 2003). Additionally, few survival studies use quantitative analyses that estimate detection probability of individually-marked swans (Watola et al. 2003). Parameterizing demographic models with data not representative of the population under study will lead to unrealistic abundance estimates and, in the case of actively-managed invasive populations, potentially inappropriate management prescriptions that may not allow for achievement of population objectives.

We studied survival and movement patterns for mute swans in the Lower Peninsula of Michigan. Our intention was to describe intrastate variation in survival and movements while deriving region-specific demographic parameters that could be incorporated into a population model. We also aimed to understand seasonal movement patterns of sub-adult and adult swans and hoped to identify summer molting areas and wintering concentrations that could be targeted for management.

STUDY AREA

We investigated survival and movements for mute swans originating from six study areas across 5 of 8 physiographic regions found in the Lower Peninsula of Michigan, USA (Schaetzl et al. 2013). Terrestrial land cover and wetland density varied latitudinally across four inland and two coastal study sites (Homer et al. 2015). Inland waterbodies had areas of natural and developed shoreline adjacent to moderately or heavily developed upland areas. Most open water areas on these sites were permanently-flooded (L1UBH based on the National Wetland Inventory Classification System; U. S. Fish and Wildlife Service 2015). Two coastal sites were characterized by semi-permanently flooded persistent emergent vegetation (PEM1F) and open water (PABG; U. S. Fish and Wildlife Service 2015) adjacent to areas of agriculture, human development, and forest cover (Homer et al. 2015). A detailed description of study sites and their selection process can be found in Chapter 3.

METHODS

A pilot marking project was undertaken by staff of the Michigan Department of Natural Resources (DNR) and U.S. Department of Agriculture (USDA) Animal Plant Health Inspection Service (APHIS) Wildlife Services (WS) in 2014 to gather preliminary movement data (Appendix A.). Plastic neck collars were affixed to non-breeding mute swans within summer molting flocks ($n = 26$), although a few actively nesting swans were also marked ($n = 5$). Observed inter- and intrastate movements during the pilot study (98 citizen reports of 23 individuals 2014 – 2018; Appendix A.) confirmed the need for tracking individual swans with remotely accessible GPS technology rather than traditional very high frequency (VHF) telemetry or coded plastic neck collars.

GPS-marking

We targeted actively breeding (i.e., incubating or brooding) female mute swans ($n = 32$) within study sites for capture 2016 – 2018 using boats equipped with longtail (S.W.O.M.P. 26.5, Backwater, Inc., Freeport, MN, USA) or surface-drive mud motors (GTR35, Gator-Tail Outboards, Loreauville, LA, USA). We captured adult females using an extendable aluminum catch pole ($n = 25$; Coleman and Minton 1979) or a shoulder-fired netgun ($n = 7$; CODA Enterprises Inc. Mesa, AZ, USA). We fit breeding female mute swans with alphanumeric plastic neck collars (56 mm internal diameter X 90.5 mm tall; Spinner Plastics, Inc., Springfield, Illinois, USA) that included a GPS-GSM (Global System for Mobile Communication) transmitter (CTT-1070 BT3; Cellular Tracking Technologies, Inc., Rio Grande, New Jersey, USA) and weighed 117 - 121.5 g total ($< 1.4\%$ of body weight). We also placed plastic neck collars on select male mute swans paired with GPS-collared females ($n = 7$). We captured pre-fledge mute swans ($n = 40$) from broods hatched within study sites in 2016 and 2017 using an extendable aluminum catch pole ($n = 39$; Coleman and Minton 1979) or shoulder-fired netgun ($n = 1$). Pre-fledge mute swans were captured from separate broods except on two occasions in 2016 where siblings were accidentally GPS-marked. We placed neck collar-mounted GPS-GSM transmitters (117 - 121.5 g total) on pre-fledge swans ($< 1.4\%$ of body weight). GPS-GSM transmitters were set to record a GPS fix every 15 minutes 24 hours per day during spring and summer but were reduced to a GPS fix every 15 minutes during daylight only for winter due to reduced solar charging capacity. The 2-way communication of the GPS transmitter units allowed us to occasionally set a more restrictive temporary duty cycle (1 fix/hour) for select units to let solar-charged batteries recover. Some units, primarily those deployed on juvenile-marked swans, were set to use an accelerometer-triggered duty cycle (i.e., FlightMode) that began collecting a

GPS fix every 10 seconds when flight was detected (Appendix B). For the purpose of movement and survival analyses, we considered swans juveniles from approximate fledge date (1 September) to their 1st spring (31 March). Juvenile swans transitioned to being considered juvenile-marked non-breeding swans (i.e., non-breeding swans originally marked as juveniles) beginning with their 1st spring (1 April) when they were approximately 11 months old. All swans other than juveniles were characterized as breeders if they initiated a nest with eggs in the current year or non-breeders otherwise. No juvenile-marked swans nested within the duration of this study (Chapter 2).

We weighed (40 kg digital, PESOLA Präzisionswaagen AG, Schindellegi, Switzerland), cloacally sexed, and banded (28.5 mm diameter (9C); National Band and Tag Co., Newport, KY, USA) all captured swans. We also measured tarsus, wing, and skull length using a dial Vernier caliper (300 mm, Flexbar Machine Corporation, Islandia, NY USA) or stopped wing ruler (Brown et al. 2003). Eleven mute swans were recaptured 2016 – 2018 to replace malfunctioning GPS-GSM transmitters. Recovery of carcasses was attempted for all mute swans where mortality was indicated based on GPS coordinates. Recovered carcasses were transferred to the Michigan DNR for necropsy. All capture and handling of live mute swans was led by staff of the U.S. Department of Agriculture Wildlife Services section of the Animal Plant Health Inspection Service (USDA APHIS WS). As such, the Michigan State University (MSU) Institutional Animal Care and Use Committee (IACUC) granted an animal-use exemption for MSU personnel during this project. This work was also partially supported by salary support for Scott R. Winterstein from the USDA National Institute of Food and Agriculture (Project No. MICL02588).

Displacement from capture location

We documented annual movement patterns for adult- and juvenile-marked mute swans with interest in the timing and distance of displacement from capture location (i.e., nesting territory for adult-marked females and natal area for juvenile-marked swans). We compiled GPS locations for all swans from first initial capture in this study (19 April 2016) until the end of the study (31 August 2018). We removed GPS locations with horizontal dilution of precision (HDOP) > 4 m, fixes that were not three-dimensional, and where elapsed time until GPS fix (a measure of signal strength) was > 118 seconds based off manufacturer recommendations (A. McGann, Cellular Tracking Technologies, personal communication). We used the “geosphere” (Hijmans 2016) and “dplyr” (Wickham et al. 2018) packages in Program R (R Development Core Team 2018) to calculate distance between each GPS location and capture location for individual mute swans using a ‘Vincenty’ ellipsoid representation of the earth (Vincenty 1975). We calculated a mean weekly displacement distance from capture location for each individual. We also wanted to understand how far swans moved from their nesting territory or natal area during winter; therefore, we also calculated maximum distance from capture location during winter (i.e., December – March) for adult- and juvenile-marked swans with working transmitters that survived the entire winter period.

We structured movement analyses differently for juvenile-marked swans and those marked as adult females. Movement patterns likely change between years for juvenile-marked swans as they mature, find mates, and establish territories; therefore, we pooled swans marked at estimated fledging in 2016 and 2017 and analyzed weekly displacement from capture location (i.e., natal territory). Adult breeding females typically have a seasonal pattern to displacement since they have already paired and established nesting territories. We pooled adult females

captured in different years (i.e., 2016, 2017, or 2018) into one dataset that represented their mean weekly displacement from capture location (i.e., nesting territory) for the annual period. Adults that were GPS-marked for multiple years (i.e., had displacement distances for a given week in multiple years) were included in this analysis, but had their displacement averaged by week across multiple years. Summarizing movements using weekly intervals only for individuals that had GPS data for each week lessened potential bias that could result from GPS transmitters that malfunctioned.

Life-stage specific survival analyses

We used the known fates approach in Program MARK (ver. 8.1; White and Burnham 1999) to model life-stage specific survival estimates derived from GPS-collared swans. Survival was estimated separately for each life-stage of interest (e.g., juvenile, breeding, and non-breeding swans) using 7-day intervals which are typically adequate for providing unbiased estimation of survival parameters (Murray 2006). Murray (2006) suggested that wildlife telemetry studies modeling survival should have a baseline of at least 30 mortalities with 10 additional observed mortalities per variable of interest, while also noting that species with low mortality rates often need larger sample sizes. Our moderate sample size for each life stage and relatively low mortality rates limited our ability to fit complex models with many variables of interest; therefore, we were conservative in our *a priori* model development and only considered including variables that directly related to study-oriented questions. We were still able to generate estimates of life-stage specific survival despite relatively small sample sizes for each life-stage.

Juvenile survival modeling

We summarized fates for 40 juvenile mute swans using a 30-week period from estimated fledging (1 September) through 31 March of the following year (i.e., their 1st spring). Juveniles marked in 2016 ($n = 22$) and 2017 ($n = 18$) were pooled for this analysis. We included effects for month and color morph (i.e., leucistic or gray) in *a priori* models since we were interested in the influence of color morph frequency (see Chapter 2) and temporal variability on juvenile survival probability. We ranked competing models using Akaike's Information Criterion corrected for small sample sizes (AICc; Anderson and Burnham 2002). We averaged the derived survival estimate across all *a priori* candidate models according to their Akaike weights.

Survival modeling for breeding and non-breeding swans

We were primarily interested in generating annual survival estimates for breeding and non-breeding swans through this analysis; therefore, we did not test effects of competing *a priori* models. We included non-breeding and breeding swans ≥ 1 year of age into an annual (i.e., 52 week) survival analysis and examined derived annual survival estimates for breeding and non-breeding swans. We were unable to generate separate estimates for immature non-breeding (i.e., ≥ 1 years old, but < 2 years old) and adult non-breeding (i.e., ≥ 2 years old) swans as was accomplished by Watola et al. (2003); however, the similarity of estimates obtained by Watola et al. (2003) for these two stages (immature = 0.73 ± 0.02 , nonbreeder = 0.71 ± 0.02) provides biological justification for combining these life stages of non-breeding swans in our analyses.

RESULTS

Seventy-two mute swans (53 females, 18 males, 1 unknown) were marked with neck collar-mounted GPS-GSM transmitters 2016 – 2018 on the Juno ($n = 14$), St. Clair ($n = 18$), Pontiac ($n = 16$), Wabasis ($n = 15$), Tobico ($n = 3$), and Clam ($n = 6$) study sites. Seven adult

male mute swans were marked with plastic neck collars on the Juno ($n = 3$), Pontiac ($n = 1$), Wabasis ($n = 2$), and Tobico ($n = 1$) study sites. We obtained 1,853,771 locations through GPS-GSM transmitters deployed on juvenile and adult mute swans resulting in 1,553,253 GPS fixes with acceptable error and fix quality (i.e., HDOP ≤ 4 m, 3-dimensional location, and time to GPS fix ≤ 118 seconds). Average HDOP for all acceptable locations was 1.97 m (range: 0.7 – 4 m). Captured males were heavier and morphologically larger than females when comparing between sexes for both age classes although females of both age classes tended to have larger wings than males (Table 4.1). However, some adult males were captured during their annual flight feather molt which biased wing length low and increased standard deviation of wing length (Table 4.1). Cloacal sexing can be difficult for subadult mute swans (Brown et al. 2003); however, similarity of sex-specific tarsus length between juvenile- and adult-marked swans indicates that captured fledglings likely had the correct sex assigned since the tarsus length is nearly maximized at fledging and remains constant in adults (Mathiasson 1981).

Table 4.1. Physiographic measurements for juvenile- and adult-marked mute swans 2016 – 2018 in the Lower Peninsula of Michigan, USA.

	Juvenile-marked*				Adult-marked			
	Males (n = 18)		Females (n = 21)		Males (n = 7)		Females (n = 32)	
	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Weight (kg)	9.39	1.14	8.54	0.97	12.32	0.59	8.83	0.91
Tarsus (cm)	11.87	0.40	11.27	0.42	11.84	0.43	11.30	0.91
Wing (cm)	45.24	9.54	47.00	6.18	54.53	12.50	57.34	2.09
Skull (cm)	17.66	0.63	17.25	0.56	18.46	0.43	17.33	0.31

*This table does not include 1 unknown sex juvenile-marked swan.

Displacement from capture location

Largest mean weekly displacement from capture occurred during winter for adult-marked female mute swans (Figure 4.1). Largest mean weekly displacement from capture location for juvenile-marked mute swans was observed during their first summer; however, the two other times of peak weekly displacement occurred during their 1st and 2nd winters (Figure 4.2). Mean

weekly displacement was typically higher for juvenile-marked females when compared to juvenile-marked males; however, juvenile-marked males had larger displacement values for the last 15 weeks of the study (i.e., their second summer after fledging; Figure 4.2). Mean maximum winter displacement for juvenile-marked mute swans (49.4 km) was 37.1 km in 2016-17 and 72.5 km in 2017-18. Juvenile-marked females tended to move farther (72.0 km) from natal areas during winter than males (28.7 km), but difference was not statistically significant ($t_{21} = 1.58$, $P = 0.21$). Mean maximum winter displacement for adult-marked females (11.3 km) was 11.9 km in 2016-17 and 10.6 km in 2017-18. Adult-marked females typically left nesting territory by week 51 (i.e., mid-December) and returned to nesting territories in week 8 (i.e., late February; Figure 4.1). Juvenile-marked swans moved further from place of capture (i.e., natal/nesting territory) than adult-marked female mute swans (Figure 4.3). It is unknown if movements of juvenile- or adult-marked swans occurred in flocks or by themselves. Regional maps of mute swan movements can be found in Appendix C.

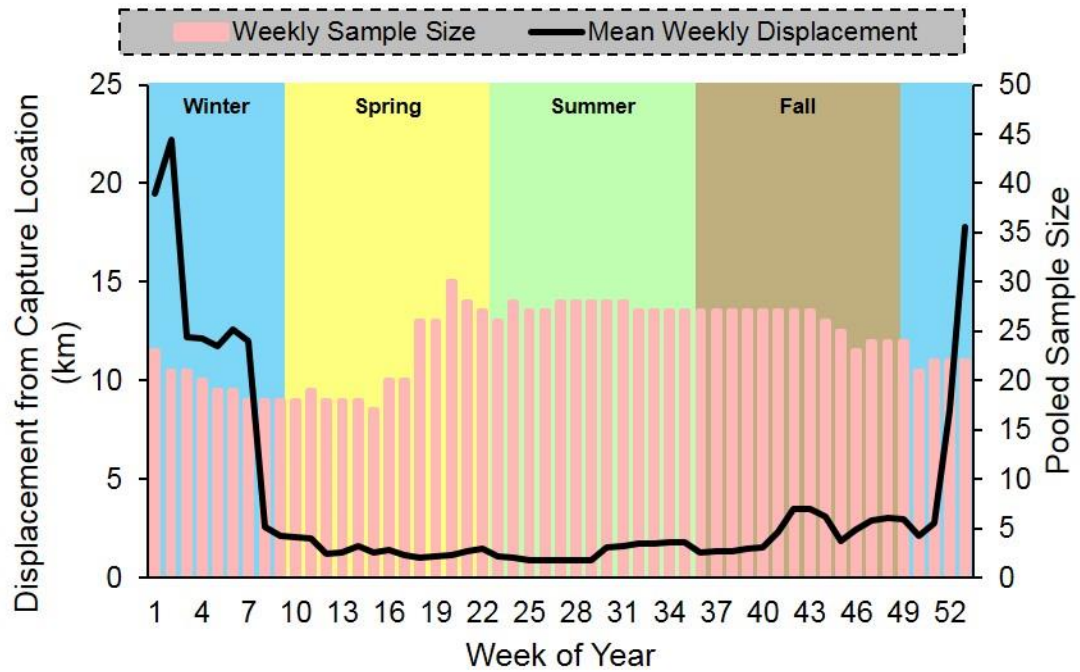


Figure 4.1. Mean weekly displacement from capture location (i.e., nesting territory) for adult-marked female mute swans captured within 6 study sites in the Lower Peninsula of Michigan, USA, 2016 – 2018 pooled across years with sample size for weekly displacement averages indicated on the secondary y-axis.

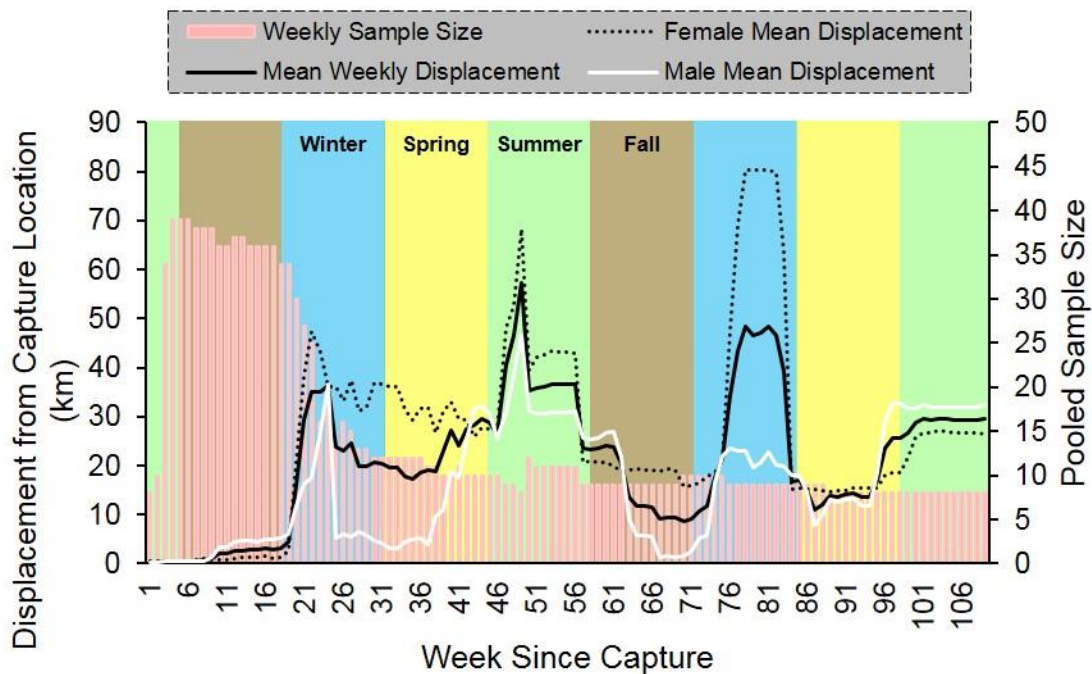


Figure 4.2. Mean weekly displacement since capture (range: 1 – 109 weeks) for juvenile-marked mute swans captured at 6 study sites in the Lower Peninsula of Michigan, USA, 2016 – 2018 with sample size for weekly displacement averages indicated on the secondary y-axis.

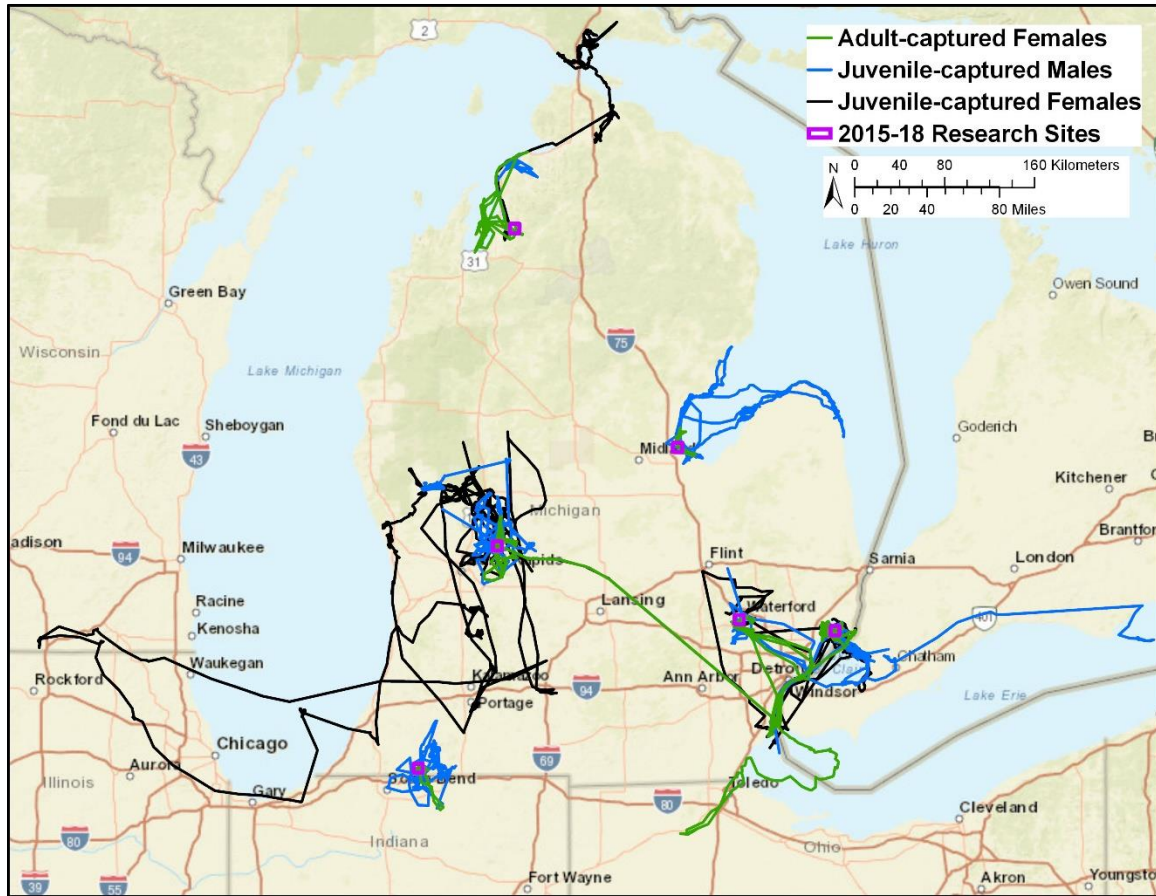


Figure 4.3. Total GPS-derived movements for adult- and juvenile-marked mute swans from 6 capture locations (purple rectangles) April 2016 – August 2018 in the Lower Peninsula of Michigan, USA

Life-stage specific survival analyses

Juvenile survival modeling

Juvenile survival was estimated from 40 individuals captured in 2016 ($n = 22$) and 2017 ($n = 18$). An average of 26 GPS-marked juveniles were at risk for each weekly survival interval. Thirteen individuals had encounter histories partially censored due to transmitter failure. Observed transmitter failures were independent of mortality (10 of 13 censored juveniles were reported alive after transmitter failure). Fourteen mortality events were documented for swans in the juvenile life stage. Only 3 causes of mortality were able to be diagnosed by necropsy (T. Cooley, Michigan Department of Natural Resources, personal communication) for juvenile

swans due to location of mortality (i.e., near open water pockets on ice-covered waterbodies) and the ability of carcasses to sink or wash away with melting of ice. The three mortality diagnoses for GPS-collared juveniles were pulmonary congestion/pulmonary edema, verminous hemorrhagic ulcerative enteritis caused by infestation of *Sphaeridiotrema globulus*, and canid predation facilitated by malnutrition. We documented mortality by verminous hemorrhagic ulcerative enteritis ($n = 10$), acute lead poisoning (ingestion of lead fishing weights; $n = 1$), trauma/predation ($n = 1$), and pulmonary congestion/pulmonary edema ($n = 1$) for other unmarked juvenile mute swans in areas used by juvenile-marked swans; however, it is important to note that proportional cause of mortality in recovered carcasses of unmarked swans may not equal proportional cause of mortality realized by juvenile swans (i.e., unmarked swans killed through predation are unlikely to be found and necropsied).

The most parsimonious model for juvenile survival included additive effects for month and color morph (Table 4.2). This model was ranked within a $\Delta AICc$ of 2 from the next competing model which only included the month effect. The model-averaged 30-week maximum likelihood survival estimate was $\hat{S} = 0.526$, 95% CI = 0.342 – 0.703. Leucistic-morph individuals typically had lower estimated survival ($\hat{S} = 0.400$, 95% CI = 0.202 – 0.637) than gray morph juveniles ($\hat{S} = 0.685$, 95% CI = 0.397 – 0.878), but the confidence interval of the coefficient contained 0 ($\hat{\beta}_{\text{leucistic}} = -0.908$, 95% CI = -2.086 – 0.269). Weeks with lowest estimated survival occurred in December and January.

Table 4.2. Model selection results for *a priori* candidate model set to explain temporal and morphometric variation in survival for juvenile-marked mute swans 1 September – 31 March 2016 and 2017 in the Lower Peninsula of Michigan, USA.

Model	k^a	AICc ^a	ΔAICc^a	w_i^a
Month + Color Morph	8	125.447	0	0.561
Month	7	125.940	0.493	0.439
Color Morph	2	150.127	24.680	0
Constant (null)	1	150.753	25.306	0

^ak = number of parameters in model, AICc = Akaike's Information Criterion adjusted for small sample sizes, ΔAICc = difference between AICc of best fitting and current model, w_i = Akaike's weight.

Non-juvenile survival modeling

Juvenile-marked swans that survived to their first spring (i.e., 1 April) with working GPS-transmitters ($n = 12$) and adult-marked ($n = 29$) swans were pooled across years for estimation of breeding and non-breeding survival rates. Forty-one unique individuals were included in the pooled analysis. Individuals that survived between years ($n = 16$) were entered as new individuals in the 2nd year's risk set. Fourteen individuals had encounter histories partially censored due to transmitter failure ($n = 12$) or incidental culling by USDA APHIS Wildlife Services ($n = 1$) and the Michigan DNR ($n = 1$). Two of the swans with failed transmitters had units replaced within the year they failed and were entered into the analysis as new individuals from point of recapture. As noted above with the juvenile survival analysis, transmitter failure was independent of mortality (11 of 12 individuals with malfunctioning transmitters were resighted alive after failure of GPS units). Nine mortality events were documented in 2016-17 ($n = 1$) and 2017-18 ($n = 8$). Cause of mortality was determined by in-field evidence or laboratory necropsy (T. Cooley, Michigan Department of Natural Resources, personal communication) for 5 of 9 mortality events (Predation = 3, Hepatitis = 1, West Nile Virus = 1, Unknown = 4). Verminous hemorrhagic ulcerative enteritis, lead poisoning, avian predation (likely by bald eagle [*Haliaeetus leucocephalus*] or great horned owl [*Bubo virginianus*]), mammalian predation (likely by red fox [*Vulpes vulpes*] or coyote [*Canis latrans*]), collisions with trees and

powerlines, starvation, and drowning were implicated in mortalities of non GPS-marked mute swans encountered while performing field work in areas with GPS-marked individuals. An average of 42 breeders or non-breeders were at risk for each weekly survival interval. Breeding swans typically had higher annual survival rates ($\hat{S} = 0.850$, 95% CI = 0.686 – 0.936) than non-breeding swans ($\hat{S} = 0.698$, 95% CI = 0.419 – 0.881), but the confidence interval of the coefficient overlapped 0 ($\hat{\beta}_{\text{breeder}} = 0.793$, 95% CI = -0.525 – 2.111). Five of 9 mortalities occurred in January or February, two occurred in May, and one was recorded in each of June and July.

DISCUSSION

We confirmed that mute swans found in Michigan are non-migratory but can move as necessary to shallow open water areas during periods of ice cover. Most adult-marked female swans remained relatively close to nesting territories during winter when compared to juveniles (Figure 4.1 and 4.2). Some adult-marked females in southeast and northern Michigan exhibited movements to open water areas associated with the Great Lakes (i.e., Detroit River or Grand Traverse Bay; Figure 4.3), but not all adult-marked females in southeast or northern Michigan moved large distances. Adult-marked females from all sites that remained near nesting territories typically relocated to shallow streams or rivers that were connected to the waterbody of their territory or were near (< 11.3 km) their nesting waterbody. Generally, these shallow areas of flowing water contained a wintering flock of mute swans, Canada geese (*Branta canadensis*), and several species of dabbling and diving ducks in addition to GPS-collared mute swans, but not all areas used by GPS-marked swans during winter were visited by researchers.

Winter movements or displacement from nesting territory has not been rigorously investigated for many non-migratory populations of mute swans. Although our data analysis was

not directly comparable to that of Collins and Whelan (1994), our mean maximum displacement from nesting territory for adult female mute swans is reasonable given the movement rates observed for banded mute swans in their Irish population (32% of all marked swans regardless of age moved ≤ 16 km). Additionally, peak movements for their population occurred during October – March (Collins and Whelan 1994), which is comparable to peak observed movement for adult-marked swans in Michigan.

Juvenile-marked swans moved farther from their natal area than adult-marked females moved from their nesting territory (Figure 4.1 and 4.2). Mean displacement from natal area for juvenile-marked swans observed in this study peaked in their 1st summer after fledging and during winter (Figure 4.2). Displacement of juvenile-marked swans from natal areas during winter was likely related to the same factor (i.e., ice coverage of natal territory) causing adult-marked females to move from nesting territories; however, juvenile-marked swans moved farther from their natal areas during both winters than adult-marked females moved from their nesting territories during winter. The peak in juvenile-marked swan movements from natal territories during their 1st summer likely resulted from non-breeding swans being excluded from typical nesting areas while searching for locations to complete their annual flight feather molt with less disturbance from breeding pairs and humans (Holm 2002). Molt migration of non-breeding individuals has been observed for some mute swan populations (Mathiasson 1993). We did not detect widespread migration to a few select molting sites although juvenile-marked non-breeding mute swans tended to complete their molt on medium (170 ha) to large (800 ha) inland lakes, coastal lakes of the Great Lakes (e.g., White Lake, Muskegon Lake, Mona Lake, Pentwater Lake), or secluded shallow water areas of the Great Lakes themselves (e.g., Saint Martin's Bay

of Lake Huron, nearshore areas around the Beaver Islands, nearshore areas of Lake Huron between Grindstone City, MI, and Port Hope, MI).

We were unable to observe true natal dispersal through this research since age at first nesting is likely near 5 or 6 years of age for established populations (Collins 1991, Coleman et al. 2001, Włodarczyk et al. 2013); however, we were able to document movement of juvenile-marked swans for the first 28 months of life. Female juvenile-marked swans moved farther from their natal area than subadult males in nearly all weeks of the analysis except for the final 15 weeks of this study. Mute swans exhibit male-biased natal dispersal (Coleman et al. 2001, Włodarczyk et al. 2013) that is typical for waterfowl (Anderson et al. 1992). However, we found that juvenile-marked females tended to move farther from their location of capture in early life than did juvenile-marked males (Figure 4.2; also see Collins 2002). Collins (2002) found that non-breeding females tended to have a 46.9 km mean maximum displacement from capture location, whereas non-breeding males had a 39.8 km mean maximum displacement from capture. We found that juvenile-marked females tended to move farther from their point of capture during winter than juvenile-marked males (72.0 km and 28.7 km, respectively), although differences between sexes were not statistically significant. It is possible that mean maximum distances moved during winter observed in this study are not the maximum winter displacement that will occur for juvenile-marked non-breeding swans before they breed since they will likely not establish nesting territories for at least another year, but most pre-nesting movement for swans does occur in their second year of life (Collins and Whelan 1994).

Most mortality of juvenile, non-breeding, and breeding adult swans occurred during the winter months when they were furthest from their natal or nesting territory, although two adult-marked females were killed on their nests. The principle documented cause of mortality for all

swans found dead during this research was verminous hemorrhagic ulcerative enteritis caused by infection of *Sphaeridiotrema globulus*, although mortality from lead poisoning, predation, and collision with fixed obstacles (i.e., power lines or trees), hepatitis, and drowning were also observed in marked and unmarked swans. Verminous hemorrhagic ulcerative enteritis was the likely cause for most mortalities where carcasses could not be retrieved for diagnosis (based on locations of mortality). Most mortality for juvenile- and adult-marked swans occurred during winter. This contrasts with populations in their native range where most documented mortality occurs during movement peaks in spring and autumn (Perrins and Reynolds 1967) by collisions with power lines or other fixed objects (Ogilvie 1967, Mathiasson 1993, Coleman et al. 2001, Collins 2002). This could partly be explained by prevalence of *Sphaeridiotrema globulus* and lack of anthropogenic food resources specifically offered to mute swans in Michigan compared to areas of their native range where such supplemental feeding can be common (Scott and Birkhead 1983, Sears 1989).

Estimated survival for juvenile swans was slightly lower in Michigan ($\hat{S} = 0.526$) than in other populations ($\hat{S} = 0.68$, Watola et al. 2003; $\hat{S} = 0.66$, Perrins and Reynolds 1967), with a caveat that exposure periods for which survival was estimated are not equivalent (30 weeks in this study; 12 weeks, Watola et al. 2003; ~35 weeks, Perrins and Reynolds 1967). Survival for juvenile swans in Michigan seemed to be biologically related to color morph ($\hat{S}_{leucistic} = 0.400$, $\hat{S}_{gray} = 0.685$), but the relationship was not statistically significant. Lower observed survival for leucistic morph individuals during 30-weeks post-fledging could result from lower parental care and increased exposure to environmental hazards (e.g., predation, intraspecific agonistic interactions, or feeding locations where infection by *Sphaeridiotrema globulus* can occur) compared with gray-morph juveniles. Conover et al. (2000) found that parents would dissociate

with leucistic juveniles during their first winter or force them from the natal territory, but allowed gray-morph cygnets to remain with them during this period. Conover et al. (2000) also found that leucistic juvenile males had lower survival than did gray-morph males for their 1st two years of life. Overall lower juvenile survival rates observed in this study could be partly explained by the higher percentage of leucistic morph individuals in Michigan (Chapter 2) coupled with seemingly lower survival for leucistic individuals.

Estimated survival rates for breeding ($\hat{S} = 0.850$) and non-breeding ($\hat{S} = 0.698$) individuals were not statistically different, but were each within reported ranges for those life-stages (Watola et al. 2003). Our decision to pool juvenile-marked non-breeding swans (i.e., first year) and adult-marked non-breeding mute swans was likely justified given the similar (and overlapping) estimates for these two life-stages (Watola et al. 2003). It should be noted that we estimated breeding adult survival using only adult females rather than a sample of males and females. Annual mortality for adults is typically low and normally not estimated separately for females and males (Watola et al. 2003) due to linked behavior of mated pairs throughout the year. Collins (2002) found no difference in cause-specific mortality between males and females. Additionally, major causes of mortality noted in this research (e.g., verminous hemorrhagic ulcerative enteritis, lead poisoning) are not sex-specific mortality factors. Therefore, we believe that our estimated survival rate for breeding adults is representative of both breeding males and breeding females.

MANAGEMENT IMPLICATIONS

Juvenile- and adult-marked mute swans are capable of long-distance movements; however, we observed different movement patterns between these two life-stages. The largest displacement from nesting territory for adult-marked mute swans occurred during winter;

however, subadult mute swans moved furthest from their natal territory during their 1st summer even though they also moved large distances during their 1st two winter periods. Juvenile-marked swans moved farther throughout the year than did adult-marked females. Adult-marked female mute swans typically stayed close to their nesting territory during winter but did make local movements to shallow ice-free areas which were typically within 11.3 km of their territory. Some, but not all, adult-marked female mute swans nesting in southeastern and northern Michigan joined wintering flocks on waterbodies associated with the Great Lakes (i.e., Grand Traverse Bay or the Detroit River). This suggests that wintering flocks found in those areas primarily consist of non-breeding individuals with fewer breeding pairs that nest nearby. Observed survival rates for juvenile, non-breeding, and breeding mute swans suggest that culling efforts targeted at breeding mute swans (i.e., highest survival rate) will be most effective at reducing the overall population although removal of non-breeding individuals should also be considered due to their relatively high survival and ability to replace breeding mute swans when territories are vacated.

Recommendations for location and timing of culling vary between subadult and adult mute swans due to differences in observed movement patterns. Efforts to remove adult breeding pairs must either target pairs during the incubation or brood-rearing period or focus on small wintering flocks near their nesting territories. Territorial behavior of mute swans typically results in many small lakes, ponds, or wetlands that have few nesting pairs. Therefore, targeting breeding pairs during the nesting season requires more effort than during winter when pairs are concentrated in wintering flocks. Unfortunately, inland wintering locations typically have poor access (i.e., are privately-owned or cannot be accessed by boat due to ice-coverage on connected lakes) or are located in urban environments; however, these locations must be targeted if removal

of breeding adults is desired since the majority of breeding females (thereby breeding pairs) in Michigan do not go to waters of the Great Lakes during winter (Figure 4.3). Removal of non-breeding mute swans can occur at summer molting sites or at wintering areas. Our observed movements for non-breeding mute swans suggests that summer culling programs will be most effective after swans have settled into molting areas, but before early fall (15 July – 31 August; Figure 4.2). Breeding adult mute swans could also be easily removed during this same period (i.e., immediately before young fledge) if molting flocks are in proximity to breeding pairs. Removal of non-breeding swans at wintering locations can also be highly effective and removal efforts at these locations may also incidentally cull breeding adults as well. Winter removal efforts for non-breeding and breeding swans will be most effective after inland ice coverage prompts movement to wintering locations (late December), but before adult females attempt to return to nesting territories (late February).

APPENDICES

APPENDIX A: MOVEMENTS OBSERVED THROUGH PILOT NECK COLLARING OF MUTE SWANS CONDUCTED BY MICHIGAN DNR AND USDA APHIS WILDLIFE SERVICES 2014 – 2018

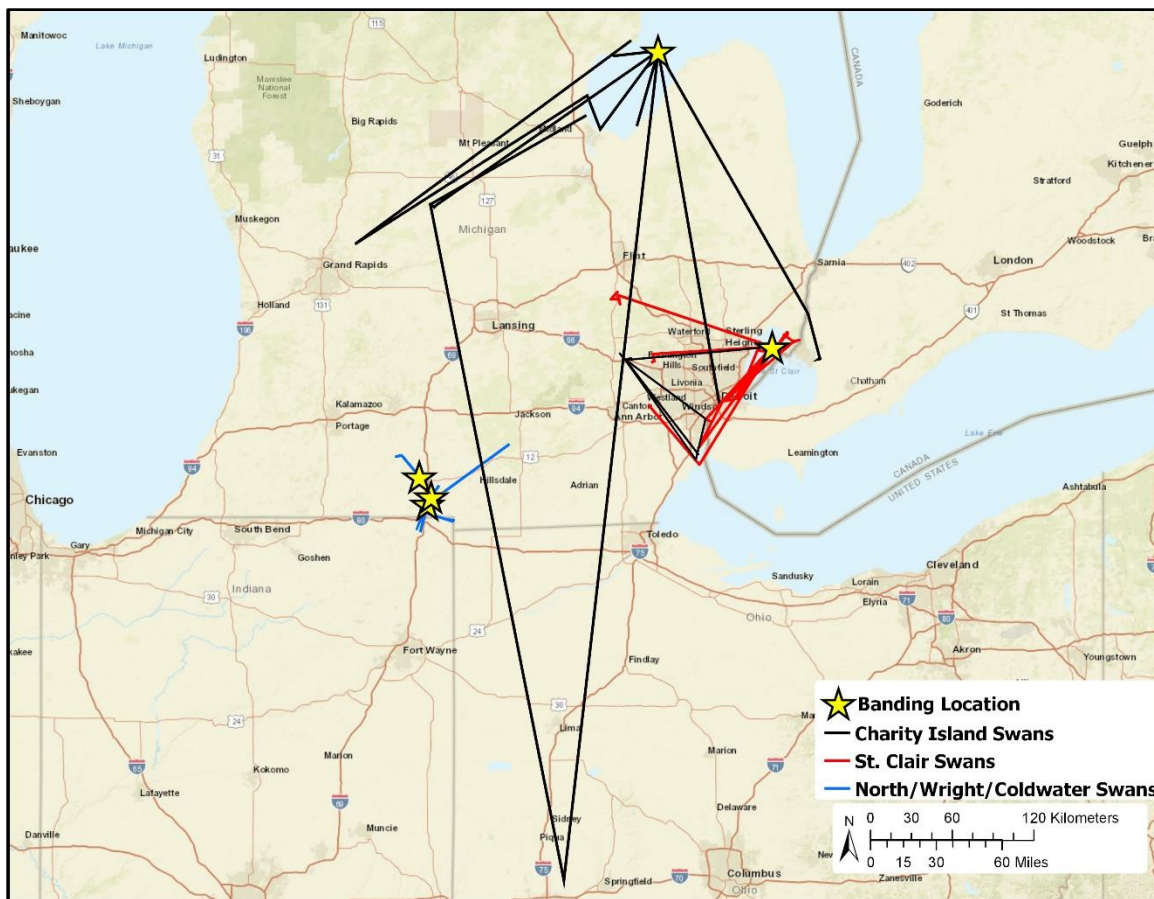


Figure A.1. Overall movements coded by region of capture for plastic neck collared mute swans during a pilot research effort of the Michigan Department of Natural Resources and the Wildlife Services Department of the U.S. Department of Agriculture Animal Plant Health Inspection Service in the Lower Peninsula of Michigan, USA, 2014 – 2018.

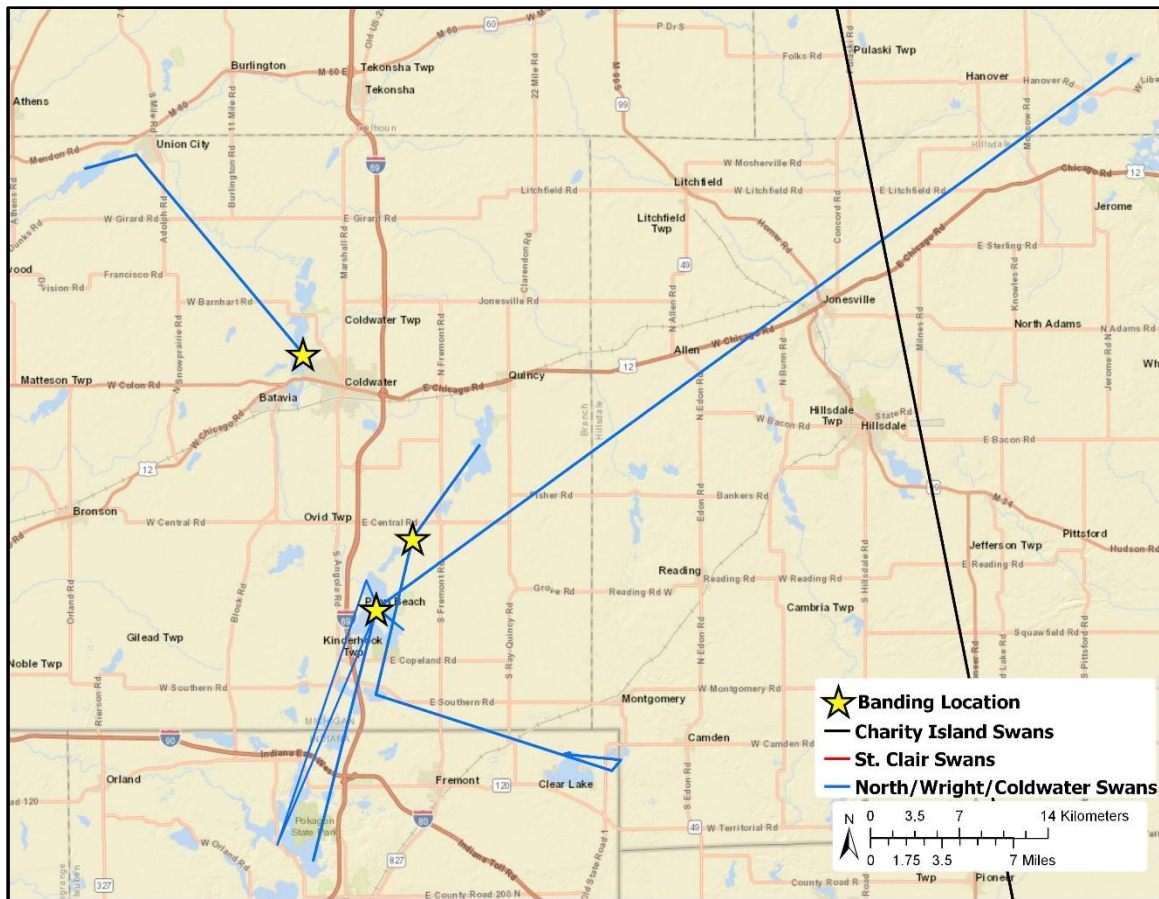


Figure A.2. Overall movement for plastic neck collared mute swans captured in southcentral Michigan during a pilot research effort of the Michigan Department of Natural Resources and the Wildlife Services Department of the U.S. Department of Agriculture Animal Plant Health Inspection Service in the Lower Peninsula of Michigan, USA, 2014 – 2018.

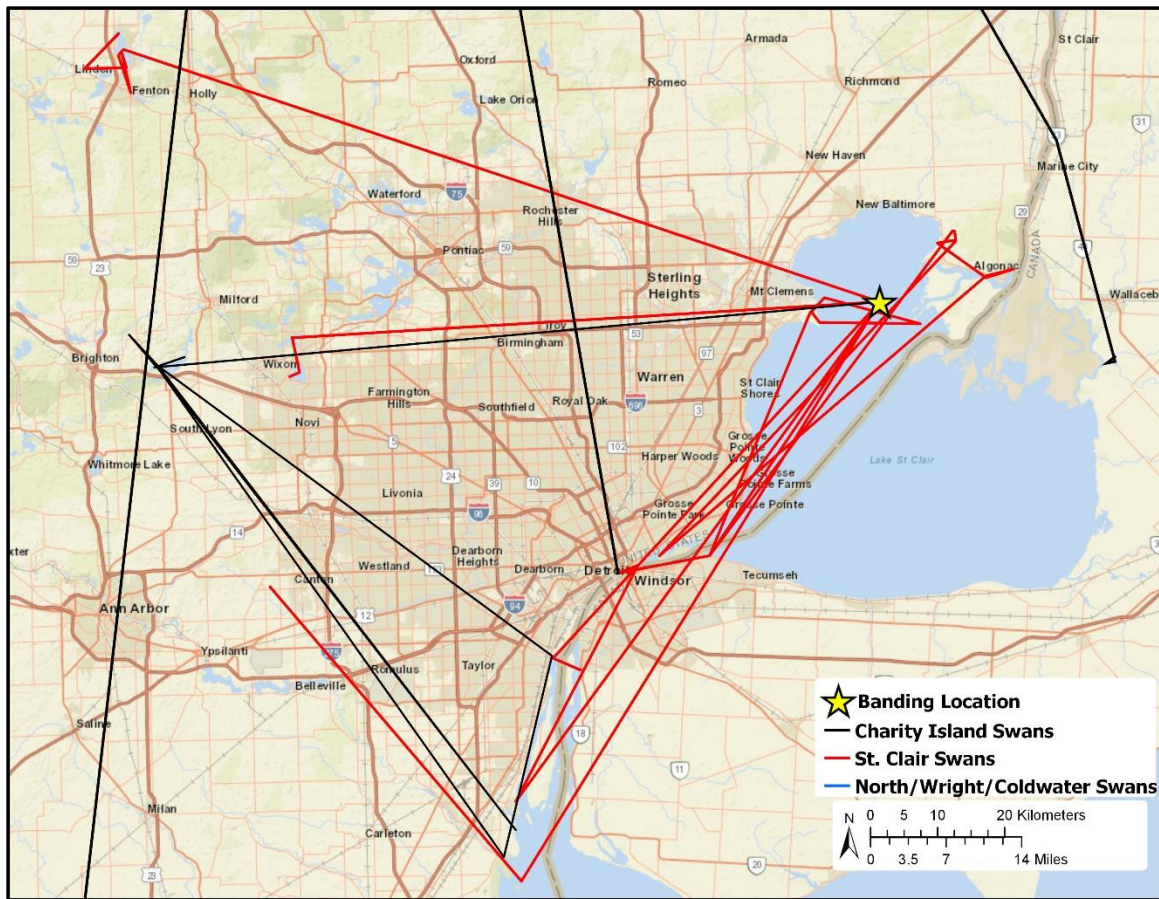


Figure A.3. Overall movement in southeast Michigan for plastic neck collared mute swans during a pilot research effort of the Michigan Department of Natural Resources and the Wildlife Services Department of the U.S. Department of Agriculture Animal Plant Health Inspection Service in the Lower Peninsula of Michigan, USA, 2014 – 2018.

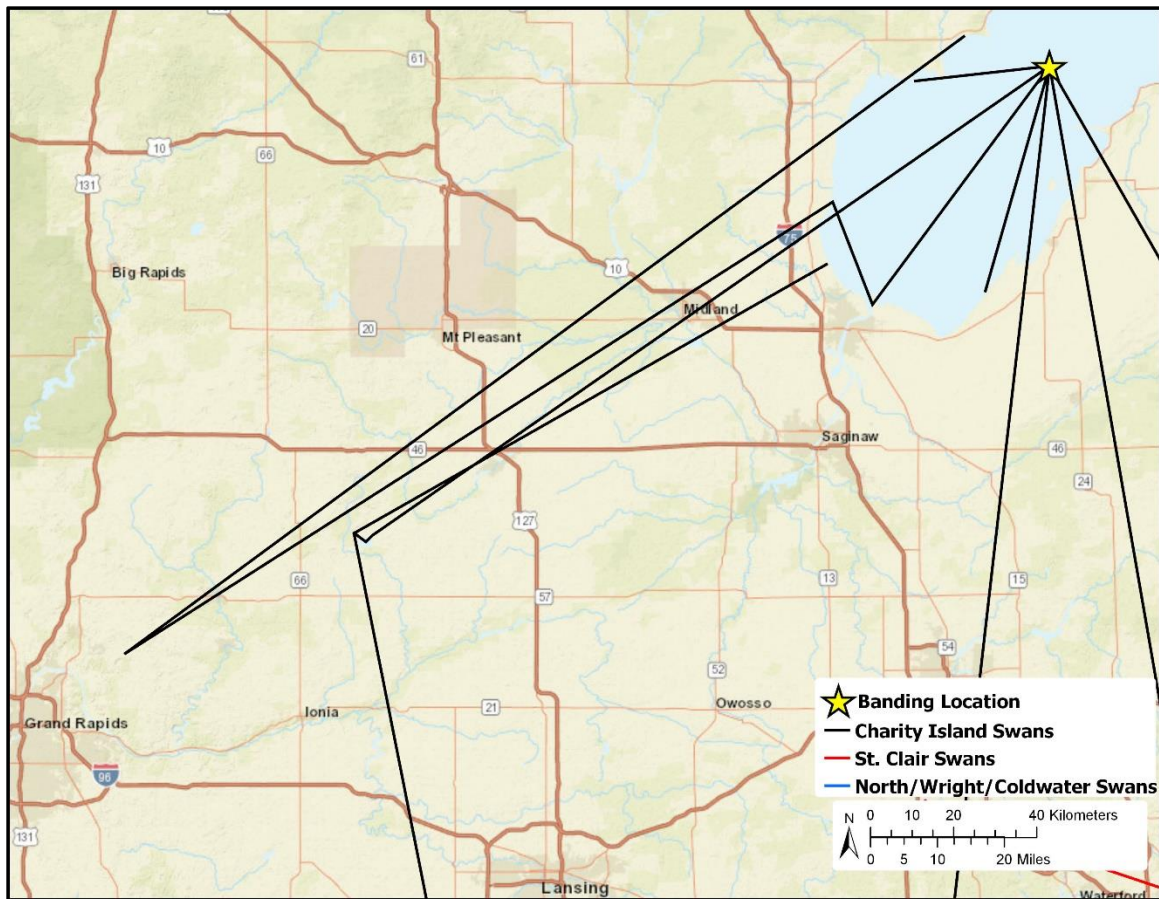


Figure A.4. Overall movement in central Michigan for plastic neck collared mute swans during a pilot research effort of the Michigan Department of Natural Resources and the Wildlife Services Department of the U.S. Department of Agriculture Animal Plant Health Inspection Service in the Lower Peninsula of Michigan, USA, 2014 – 2018.

APPENDIX B: FLIGHT CHARACTERISTICS ON MUTE SWANS DETERMINED THROUGH GPS-GSM TRANSMITTERS

Table B.1. Summarized flight speeds and altitudes estimated through flexible duty cycles (i.e., FlightMode) available on neck collar-mounted GPS-GSM transmitters ($n = 13,897$) on mute swans marked within the Lower Peninsula of Michigan, USA, in 2016 – 2018.

	Juvenile-marked				Adult-marked	
	Males ($n = 5209$)		Females ($n = 5533$)		Females ($n = 1936$)	
	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Ground Speed						
MPH	35.11	7.48	35.89	6.68	35.01	6.22
Knots	30.51	6.50	31.19	5.81	30.42	5.40
Altitude						
AGL(m)	11.98	25.34	29.70	33.81	19.60	24.95
MSL (m)	217.65	54.75	255.17	64.69	260.13	40.11

APPENDIX C: DETAILED MOVEMENT OBSERVED THROUGH GPS-GSM TRANSMITTERS ON MUTE SWANS

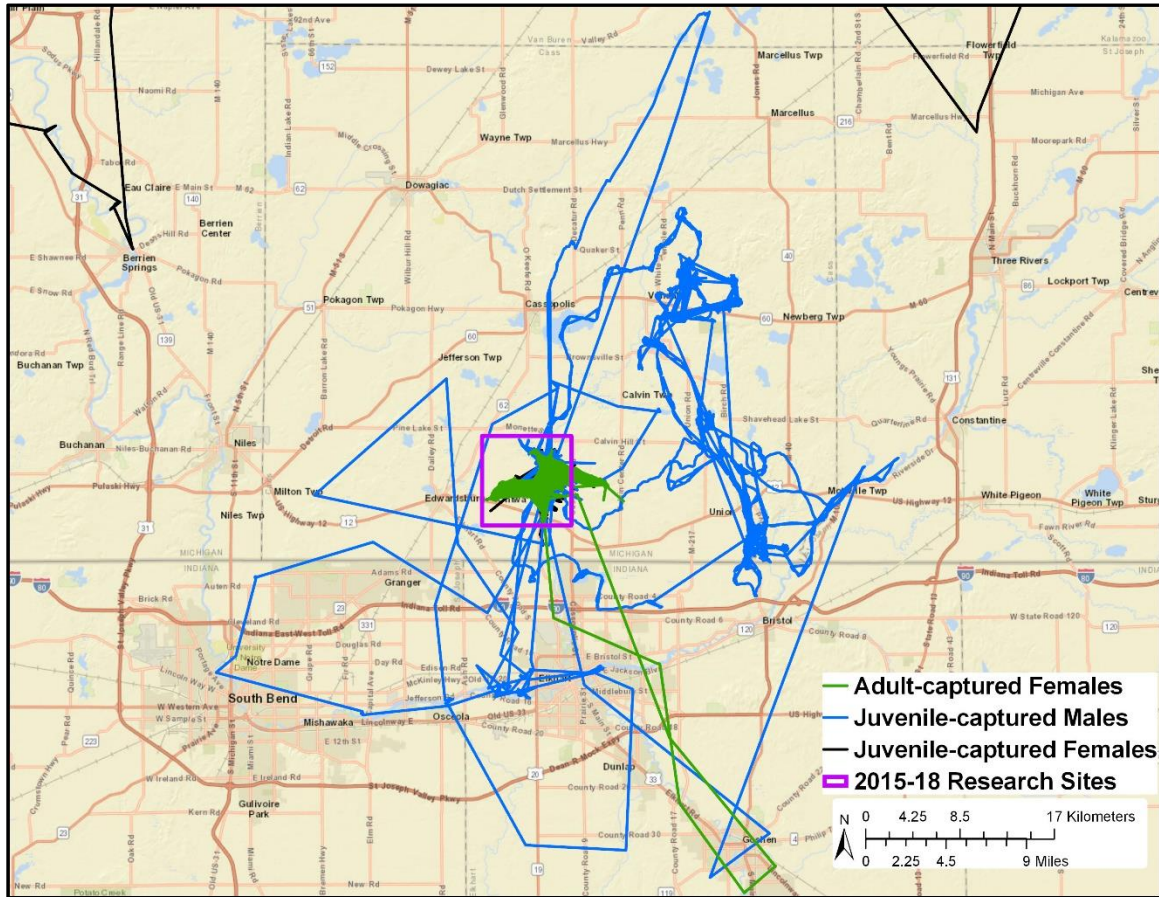


Figure C.1. Detailed movement of mute swans in southwestern Michigan, USA, as determined by GPS-GSM transmitters.

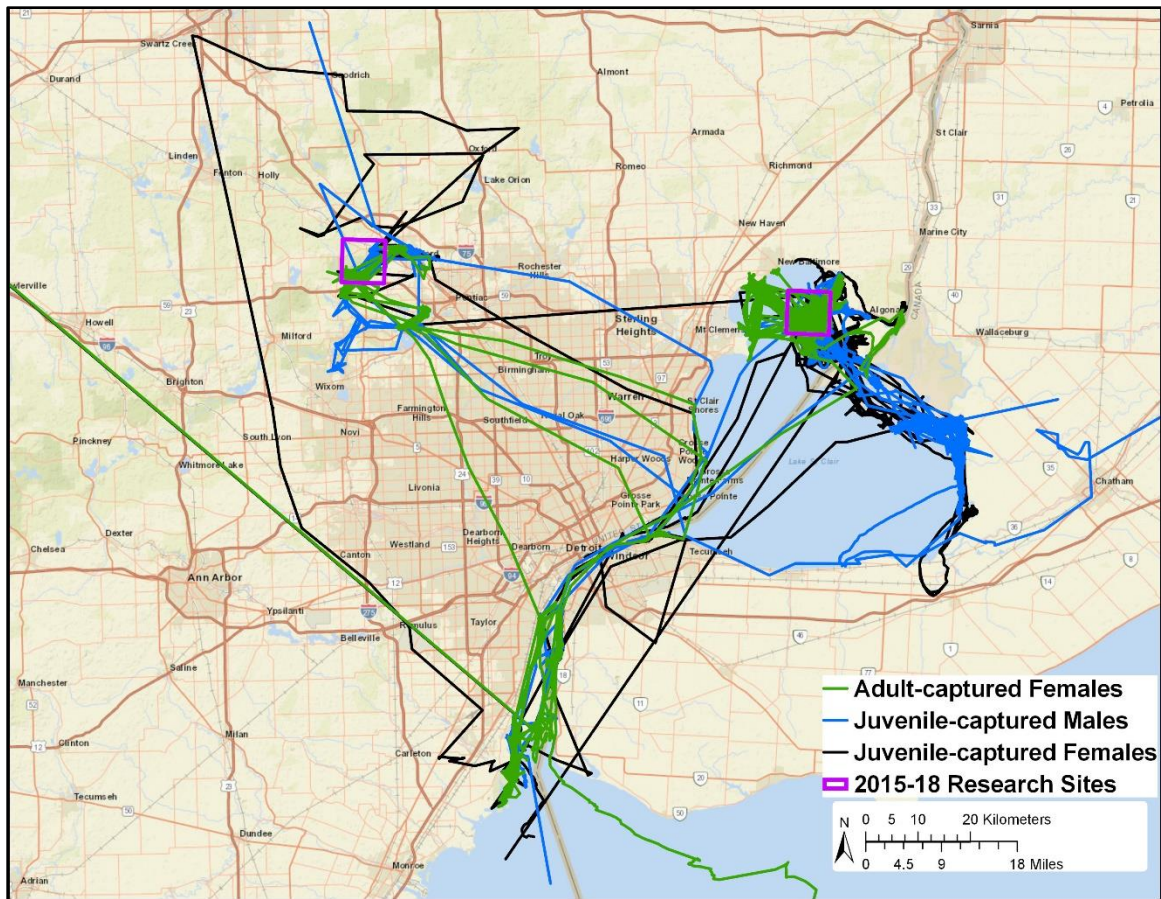


Figure C.2. Detailed movement of mute swans in southeast Michigan, USA, as determined by GPS-GSM transmitters.

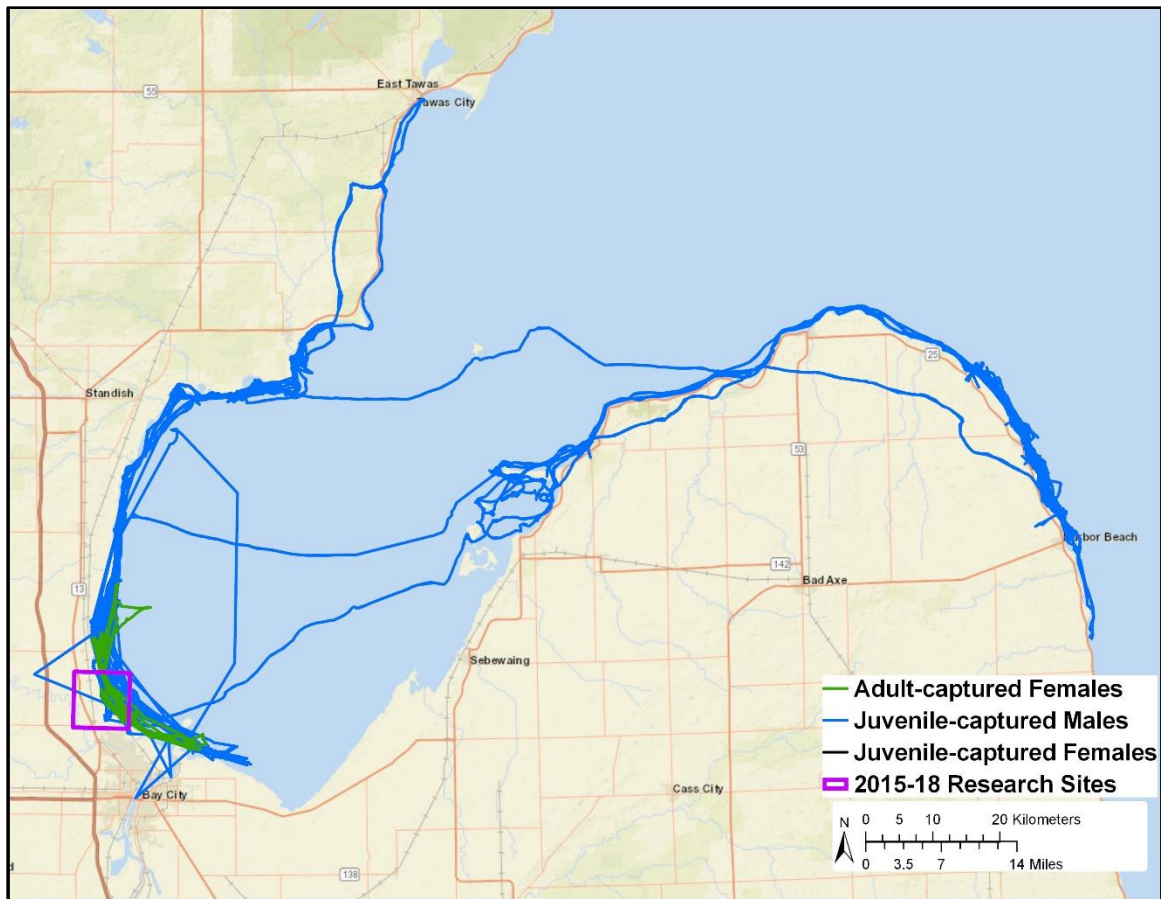


Figure C.3. Detailed movement of mute swans in east central Michigan, USA, as determined by GPS-GSM transmitters.

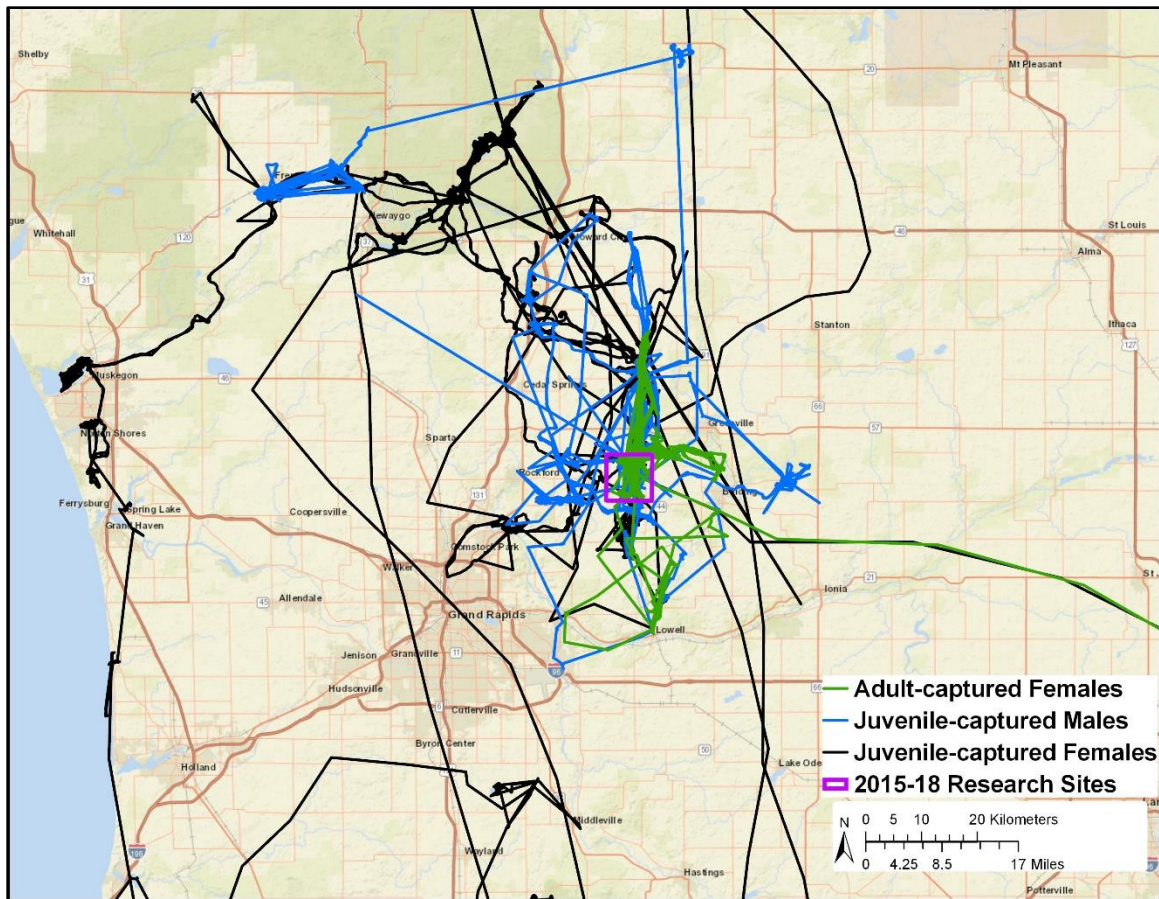


Figure C.4. Detailed movement of mute swans in west central Michigan, USA, as determined by GPS-GSM transmitters.

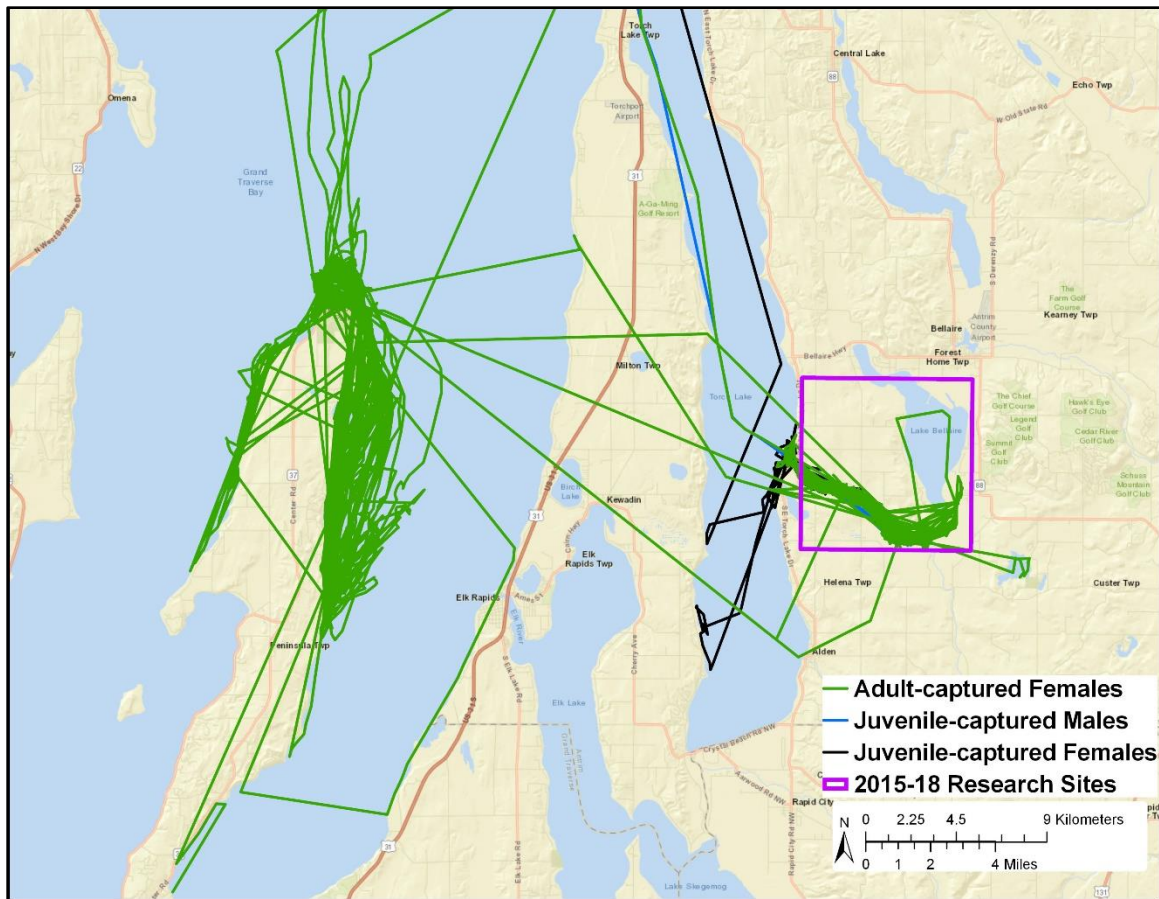


Figure C.5. Detailed movement of mute swans in the northwest Lower Peninsula of Michigan, USA, as determined by GPS-GSM transmitters.

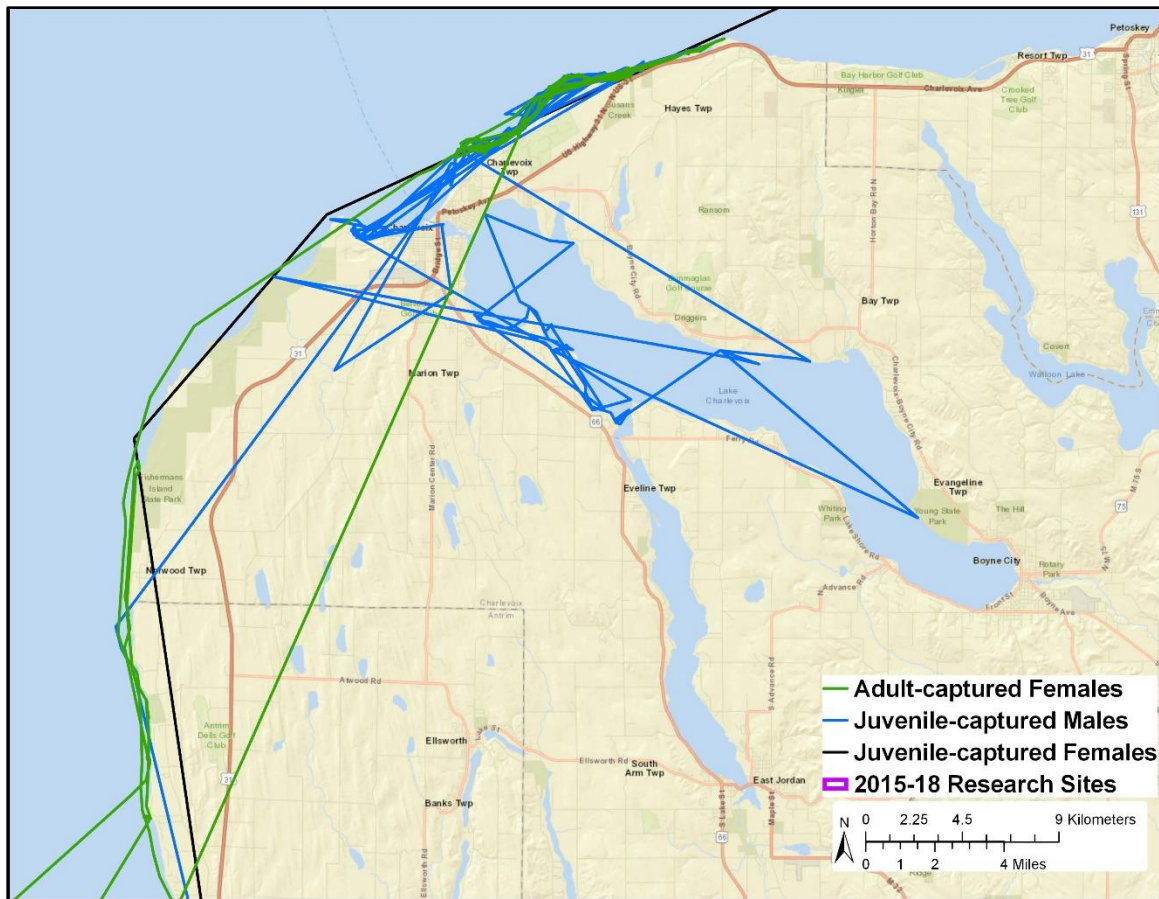


Figure C.6. Detailed movement of mute swans in the northern Lower Peninsula of Michigan, USA, as determined by GPS-GSM transmitters.

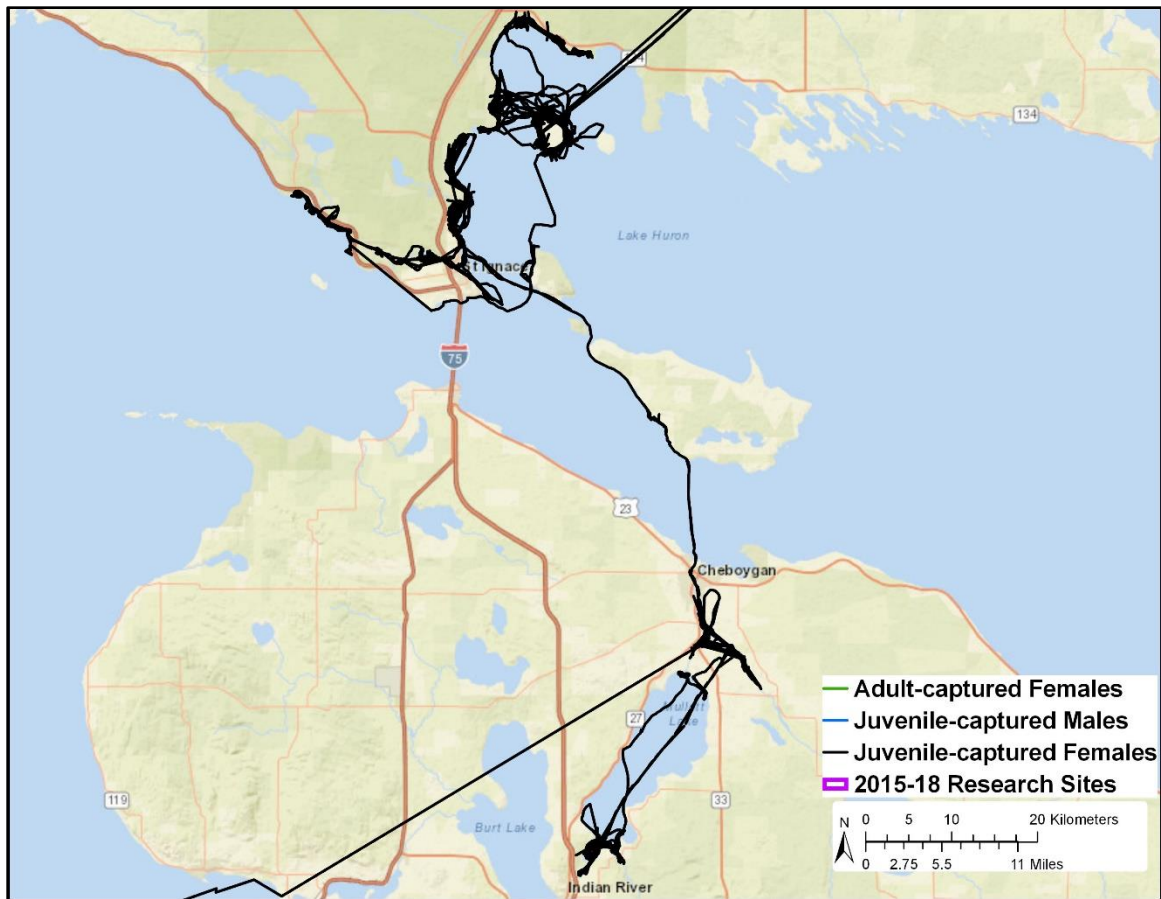


Figure C.7. Detailed movement of mute swans in the northern Lower Peninsula and southeastern Upper Peninsula of Michigan, USA, as determined by GPS-GSM transmitters.

LITERATURE CITED

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CHAPTER 5: A DENSITY-DEPENDENT MATRIX POPULATION MODEL TO INFORM MUTE SWAN MANAGEMENT IN MICHIGAN, USA

INTRODUCTION

Demographic modeling through life tables, matrix population models, and other techniques have been used for nearly a century to model factors influencing abundance change in human and wildlife populations. Early efforts estimated mortality rates by following individuals or cohorts through time using life tables (Cox 1972). Matrix population models (MPMs) have been used extensively by ecologists since the 1970s (Leslie 1945, Caswell 2001); however, extensions of MPMs (integral projection models; IPMs) have been developed to better handle continuous ecological data (Easterling et al. 2000, Besbeas et al. 2002). IPMs offer analytical flexibility for groups like plants that are observed across continuous scales (i.e., growth measurements) rather than discrete stages (Miller et al. 2009). However, matrix population models remain useful for species that are organized into and can be measured at naturally occurring life stages such as mute swans (*Cygnus olor*).

Mute swans were introduced to North America by humans in the late 1800s and first brought to Michigan's Charlevoix County in 1919 (Wood and Gelston 1972). Abundance in Michigan remained low throughout the 20th century despite additional introductions (Wood and Gelston 1972), but quickly grew in the late 1990s and early 2000s to a peak estimated abundance of 17,520 in 2013 (Michigan Department of Natural Resources, unpublished data). The Michigan Department of Natural Resources (MDNR) formalized their mute swan management plan in 2012 which aimed to have fewer than 2,000 mute swans statewide by 2030 (Michigan Department of Natural Resources 2012). Mute swan control conducted by the MDNR and the U.S. Department of Agriculture Wildlife Services removed < 650 swans annually prior to 2010,

but efforts were expanded after 2011 partially due to increased funding through the Great Lakes Restoration Initiative (Arsnoe and Duffiney 2018). Expanded control reduced mute swan abundance in Michigan (MDNR, unpublished data); however, annual abundance stabilized despite continuing removal efforts (Arsnoe and Duffiney 2018). Uncertainty of regional demographic parameters translated to uncertainty in how to most effectively and efficiently reach the long-term goal established by the Michigan DNR.

Demographic models exist for introduced populations of mute swans in North America (Allin et al. 1987, Hindman and Harvey IV 2004, Ellis and Elphick 2007); however, these models were parameterized exclusively or in part with demographic parameters estimated from native range of mute swans. Long-established populations in native range likely have different demographic rates than newly established populations in introduced range. Watola et al. (2003) also found that native sub-populations in relative proximity had varying demographics. Variation in demographic rates may arise due to semi-domestication which has altered genetic composition (Munro et al. 1968), or introduced populations could be responding to different predator communities and environmental factors not found in the native range. Demographic models for introduced populations should incorporate regionally estimated demographic parameters where possible otherwise life stage-specific management strategies derived from poorly parameterized models may be unrealistic or inappropriate.

Our goal was development of a stage-based MPM representing dynamics of Michigan's mute swan population that could be used to inform future management. We used the model structure developed by Ellis and Elphick (2007) to predict mute swan abundance using native- and Michigan-estimated demographic parameters within a deterministic framework. We then refined the Michigan-specific demographic model by incorporating density dependence in

breeding productivity based on observed variation in site-level productivity between varying nesting densities (Chapter 3). We used the density-dependent matrix population model to estimate number and proportion of each life stage that must be removed annually from 2018 – 2029 to reach the long-term goal set forth by the Michigan DNR (Michigan Department of Natural Resources 2012). We also simulated level of alternative management strategies (i.e., egg oiling or nest destruction) needed to obtain the same level of control by 2030.

STUDY AREA

We modeled population demographics for mute swans in the core of their Michigan distribution which occurs in the Lower Peninsula and eastern Upper Peninsula (Michigan DNR, unpublished data). Demographic data used in parameterization of the Michigan-specific matrix population model was estimated for mute swans found in Michigan's Lower Peninsula (Chapters 2, 3, and 4).

Land cover varies latitudinally across Michigan from a combination of developed farmland and hardwoods (i.e., oak [*Quercus* spp.], beech [*Fagus grandifolia*], and maple [*Acer* spp.]) in the southern portions of Michigan's Lower Peninsula to more homogeneously-distributed mixed forests (i.e., pines [*Pinus* spp.], spruces [*Picea* spp.], firs [*Abies* spp.], maples, oaks, and aspen [*Populus* spp.]) in the northern Lower Peninsula and eastern Upper Peninsula (Pugh et al. 2017). Michigan has several distinct geographic regions with coastlines on four of the five Great Lakes (Schaetzl et al. 2013). These coastlines contain many inlet waterbodies, river deltas, and coastal wetlands (Sommers 1984). There are more than 46,000 lakes >2.02 ha in Michigan (Institute for Fisheries Research 2013), with 18,000 individual lakes in Michigan's Lower Peninsula that are ≥ 0.4 ha in size (Breck 2004). Detailed descriptions of the study sites used to estimate demographic parameters can be found in Chapters 1 and 3 of this dissertation.

METHODS

We replicated the life-stage structure used by Ellis and Elphick (2007) using the “popbio” package (Stubben and Milligan 2007) in Program R (R Development Core Team 2018). The “popbio” package incorporates much of the MATLAB (MathWorks, Natick, MA, USA) code and foundational concepts found in Caswell (2001) within the Program R computing framework (Stubben and Milligan 2007). The transition matrices used within MPMs in this research contained the 6 x 6 structure found in the transition matrix of Ellis and Elphick (2007). This structure has varying survival and transition probabilities for six life stages: juvenile (0-1 immature swans; fledging to 1st April), immature first-year non-breeding swans (1-2-year-old immature), inexperienced non-breeding swans (are not currently breeding and never have nested), experienced non-breeding swans (are not currently breeding but have previously nested), inexperienced breeding swans (are currently breeding, but never have previously nested), and experienced breeding swans (are currently breeding swans that have nested previously; Ellis and Elphick [2007]). A graphical representation of model structure can be found in Figure 1 of Ellis and Elphick (2007). We wanted to utilize the structure found in Ellis and Elphick (2007) because 1) it captures the life cycle of mute swans and 2) we wanted to perform a life table response experiment (LTRE) to understand how differences in parameters from native and introduced ranges contribute to changes in estimated population growth rate (λ). We used the transition matrices described above and an initial population vector that corresponded to Michigan’s estimated mute swan population in 1948 (Gelston and Wood 1982) to conduct projection analyses for 150 years (1949 – 2098) for each of the models described below, and compared model-predicted abundances to observed abundance as estimated through the MDNR’s annual breeding waterfowl survey.

Comparison of native- and Michigan-parameterization

Formulation of the native-parameterized model

We parameterized the transition matrix of the native model using the survival and transition values found in Table 1 of Ellis and Elphick (2007) which are replicated in Table 5.1. This essentially simulated the MPM format used by Ellis and Elphick (2007) but used initial population values for Michigan in a deterministic framework. We used estimated population size of mute swans in Michigan in 1948 (i.e., 47 swans; Gelston and Wood 1982) to create the initial population vector (N) within the model $N_{t+1} = AN_t$, where A is the population projection matrix. We rounded up the estimated population size in 1948 to 48 individuals so that we could divide the total population by two (since matrix models only model the female population component), and assign integer values to stages within the initial population vector. Ellis and Elphick (2007) began modeling with all individuals placed into the experienced breeder stage; however, we placed 8 individuals into the 0-1 immature stage which represents juvenile swans from fledging to their 1st April. We placed the remaining 16 individuals into the experienced breeder category. This distribution of life stages likely approximates the distribution of life stages in the northern Michigan population when nesting cover was abundant, and density of swans was low. It is important to note that variation in input values of the initial conditions vector will influence time of transience, but initial conditions will not affect ultimate model behavior (Caswell 2001).

Table 5.1. Input probabilities for transition matrices of the Michigan-parameterized stage-based deterministic matrix population model and native-parameterized model with input values adapted from Ellis and Elphick (2007).

Parameter	Michigan Model	Native Model
	Value	Value
Juvenile survival ($\pm$ SE) (fledging to April of 1st Year)	0.526 ± 0.096	0.68 ± 0.04
Immature survival ($\pm$ SE) (1st April to second April)	0.698 ± 0.125	0.73 ± 0.02
Nonbreeder survival ($\pm$ SE)	0.698 ± 0.125	0.71 ± 0.02
Breeder survival ($\pm$ SE)	0.850 ± 0.062	0.90 ± 0.02
Annual mean clutch size ($\pm$ SE)	7.0 ± 0.15	5.9 ± 2.2
Ratio of average clutch size of inexperienced to experienced breeders	.	0.81
Survival from eggs to fledging; inexperienced breeder nests	0.198	0.40
Survival from eggs to fledging; experienced breeder nests	0.198	0.30
Probability of first breeding	0.45*	0.45
Probability of continuing breeding	0.767	0.90

*We used Birkhead and Perrins (1986) estimate for the probability of first breeding in both the Michigan- and native parameterized models.

Formulation of the Michigan-parameterized model

We used the same model structure and initial population vector as the native-parameterized model when creating a Michigan-parameterized matrix population model. All parameter values in the transition matrix for the Michigan-parameterized model were estimated in Michigan with exception of the probability of first breeding (Table 5.1). Most mute swans typically do not pair and establish breeding territories until at least 3 or 4 years of age (Reese 1980, McCleery et al. 2002). We did not observe first nesting attempts for juvenile-marked swans marked through this research; therefore, we relied on the probability of first nesting reported for other populations in the literature (0.45; Birkhead and Perrins 1986) also used by Ellis and Elphick (2007). Estimation of demographic parameters described in previous chapters and whose values are included herein involved the capture and handling of live mute swans led

by staff of the U.S. Department of Agriculture Wildlife Services section of the Animal Plant Health Inspection Service (USDA APHIS WS). Michigan State University (MSU) Institutional Animal Care and Use Committee (IACUC) granted an animal-use exemption for MSU personnel throughout this project. This work was also partially supported by salary support for Scott R. Winterstein from the USDA National Institute of Food and Agriculture (Project No. MICL02588).

We removed Ellis and Elphick's (2007) clutch size penalty (0.81) for inexperienced breeders in Michigan-specific models since differentiation of experienced and inexperienced pairs could not be determined in this study. Mean clutch size for pairs with known breeding experience was equal to the overall estimated clutch size (7.0 eggs/clutch), whereas mean clutch size for pairs with unknown experience (likely a mix of experienced and inexperienced pairs) was 7.2 eggs/clutch. Therefore, removal of the clutch size penalty was justified in this modeling. We also used identical survival rates for immature non-breeding (1-2-year-old immature) and adult non-breeding swans since those two life stages were pooled in survival analyses due to sample size constraints (Chapter 4). Ellis and Elphick (2007) used survival estimates for these two stages derived from Watola et al. (2003). Survival estimates for 1-2-year-old immature non-breeders (0.73) and adult non-breeders (0.71; Watola et al. 2003) were similar and near our estimated survival for these two life stages pooled (0.698); therefore, we used the same survival estimate for both life stages in our Michigan-parameterized models.

Life table response experiment between native- and MI-parameterization

Life table response experiments are useful for comparing matrix population models of identical structure but different input parameters (Caswell 1989). Results of LTREs show proportional change in population growth rate attributed to each input parameter of the transition

matrix (Caswell 2001). We compared relative contributions of demographic parameters to change in λ between native- and Michigan-parameterized models. To conduct the LTRE, we averaged transition matrices for the native- and Michigan-parameterized models and then derived sensitivity for each parameter for the mean transition matrix. We then multiplied sensitivities for each parameter in the mean transition matrix by change in input values between the transition matrices of the native- and Michigan-parameterized models to determine the influence that the difference in input values had on the overall observed change in λ between the two models.

Development of a Density-Dependent Matrix Population Model for Michigan

We were able to estimate life stage-specific demographic parameters for mute swans within Michigan (Chapters 2 and 4); however, we noted that site-level breeding productivity was influenced by number of nesting pairs and saturation of characteristic nesting habitat (Chapter 3), also demonstrated in another introduced population (Nummi and Saari 2003). Our six study sites spanned the geographic distribution of mute swans within Michigan's Lower Peninsula (see Figure 3.1 in Chapter 3). Sites also varied in nesting density, abundance of nesting cover, and breeding productivity (Chapter 3). Our estimated egg to fledge survival rates (0.198), which we have demonstrated is influenced by nesting pair density (Chapter 3), is one of the lowest egg to fledge survival rates reported in the literature and nearly approached the extreme low productivity observed by Nummi and Saari (2003) in the late stages of invasion in a Finnish archipelago.

Our site selection criteria sought study sites with multiple nesting pairs within a localized area. This criterion helps ensure that adequate sample sizes of nesting pairs could be obtained for intensive nesting ecology investigation while representing variability present geographically in

Michigan's Lower Peninsula. Selection criteria required that at least 5 nesting pairs were located within a 36 km² area at the start of the nesting ecology study in 2016. Observed density dependence in breeding productivity resulted in our selection criteria being suboptimal for estimating mean productivity across all mute swans in Michigan since areas with few (i.e., 1 or 2) nesting pairs were not represented in our sample of sites. Density-dependent breeding productivity represents the respective nesting pair densities of these sites; however, distribution of nesting pair density across our sites may not represent the distribution of nesting pair densities across Michigan (i.e., there are likely many areas with few nesting pairs but abundant nesting cover since observed population growth is not indicating that the population is at carrying capacity; MDNR, unpublished data). Further, our estimation of breeding productivity, which is known to be density-dependent (Chapter 3, Nummi and Saari 2003), is not likely applicable across all levels of mute swan abundance from the first stages of invasion to present day; therefore, it was appropriate to incorporate density dependence in productivity at varying levels of mute swan abundance.

We incorporated density dependence in productivity within the Michigan-parameterized MPM using a penalty term that changed breeding productivity according to abundance in previous year. The penalty term proportionally lowered breeding productivity as mute swan abundance increased in relation to a hypothesized carrying capacity (K). This penalty term for density specific breeding productivity (F_t) took the form $(F_t) = F(\frac{K-N_{t-1}}{K})$ where F is the initial breeding productivity rate (i.e., mean clutch size multiplied by an estimated egg to fledge survival rate) under low nesting pair densities, K is the hypothesized carrying capacity, and N_{t-1} is the total population of females in the previous time step (Jensen 1995). The penalty equation describes a linear relation between productivity and pair density we observed among local study

areas (Chapter 3); however, K in this equation refers to statewide mute swan abundance. The penalty term resulted in equal productivity for experienced and inexperienced breeders since we did not detect differences in breeding productivity related to prior breeding experience (see above).

Egg to fledge survival rates have been reported in the literature for native and introduced populations. We used an initial egg to fledge survival rate that minimized influence of density dependence; therefore, we reported egg to fledge survival rates for newly established introduced populations that represented vital rates for populations below carrying capacity. Nummi and Saari (2003) reported an egg to fledge survival rate of 0.44 during the early stages of invasion in a Finnish archipelago whereas values for introduced populations in North America were slightly different (Willey 1968, 0.49; Reese 1975, 0.46; Reese 1980, 0.40; Conover and Kania 1999, 0.41). We chose an initial egg to fledge survival rate of 0.46 reported by Reese (1975) for a population that had nested in the wild for ~10 years. A 0.46 egg to fledge survival rate coupled with our observed mean clutch size in Michigan (7.0 eggs per pair; Chapter 2) resulted in an estimated 3.2 fledged young per pair (1.6 fledged females per breeding female assuming a 1:1 sex ratio at birth; Willey 1968) during the early stages of invasion. Therefore, the penalty term started with a breeding productivity value (F) of 1.6 and was reduced in proportion to population abundance according to the penalty term described above. Other parameters in the transition matrix for the density-dependent matrix population model were identical to those listed for the Michigan-parameterized model in Table 5.1.

Use of the penalty term required a preset value of estimated carrying capacity for mute swans in Michigan. The empirical growth rate observed for Michigan's mute swan population from 1949 – 2010 was 9.3%; however, population growth appeared to slow from 1991 to 2010

(4.5% annual growth) indicating that density may have begun to influence vital rates (D Luukkonen, unpublished data). This period of observed slower growth corresponded to an estimated abundance of 4,069 swans in 1991 to 15,532 swans in 2010 (D. Luukkonen, unpublished data). While the carrying capacity of mute swans in Michigan is unknown, it seems reasonable that up to 31,250 nesting pairs (i.e., under the 125,000 K simulation) could establish territories on the more than 46,000 inland lakes (Institute for Fisheries Research 2013) or within wetlands associated with waters of the Great Lakes. This would assume that about half of the total estimated population (i.e., 62,500 individuals) would be found in mixed flocks of immature non-breeding or adult non-breeding swans which has been noted for established populations in their native range (Baker et al. 2006). We evaluated sensitivity of the density-dependent matrix population model using three different hypothetical values for carrying capacity (K) of mute swans in Michigan set within the penalty term (75,000 individuals, 100,000 individuals, and 125,000 individuals).

Estimation of removal rates needed to achieve long-term population goal

We used the Michigan-parameterized density-dependent MPM for a hypothesized carrying capacity of 100,000 individuals to estimate reduction in demographic parameters needed to achieve the long-term goal of no more than 2,000 mute swans by 2030 (Michigan Department of Natural Resources 2012). We began simulations with the 2018 estimated abundance (12,048 individuals) per the annual breeding waterfowl survey. We used an initial population vector for 2018 that consisted of 6,024 total females distributed across life stages according to the 100,000 K density-dependent model (1949 – 2098 simulation): 2085 juveniles (0-1-year-old immatures), 1055 immature non-breeders (1-2-year-old immatures), 501

inexperienced breeders, 613 inexperienced non-breeders, 1358 experienced breeders, and 412 experienced non-breeders).

We conducted simulations that proportionally reduced survival for all age classes (i.e., juveniles, immature non-breeders, non-breeders, and breeding swans) in 10% increments and observed estimated abundance in the year 2030. We reduced survival rates by 1% increments once estimated abundance was near acceptable levels in 2030 to determine the minimum percent reduction in survival needed to achieve the long-term goal. We chose to evenly reduce the survival of all age classes by the same percentage because determining life stages prior to removal during culling efforts is difficult especially during winter when all life stages may be present in the same flock. It is important to note that estimation of the reduction in survival through these methods assumes that annual removals of each life stage exhibit complete additive mortality.

We also estimated reduction in survival and removal needed to achieve the long-term goal by only targeting a specific life stage (i.e., juvenile, nonbreeder, or breeder). This allowed us to estimate the relative “value” of removing individuals in a specific stage with regard to reaching the 2030 goal. We accomplished this by systematically adjusting survival, as in previous simulations, but we only adjusted survival rates for one life stage in each simulation and held survival for the other stages at their values listed in Table 5.1. We were able to use these simulations to estimate the number (and proportion) of each life stage that must be removed annually to achieve the long-term goal if the remaining life stages were unavailable for removal. These simulations assumed that no artificial manipulation of clutch sizes or egg to fledge survival (i.e., nest destruction or egg oiling) occurred during the modeling period.

We also used the Michigan-parameterized density-dependent MPM to determine level of egg and nest destruction needed to achieve the same level of mute swan abundance by the year 2030. Similar to the simulations above that incrementally reduced adult survival, we incrementally reduced egg to fledge survival rates by 10% for each modeling iteration and then incrementally reduced egg to fledge survival by 1% once near threshold of acceptable abundance in 2030 to identify the minimum reduction needed to achieve the long-term goal (Michigan Department of Natural Resources 2012). These simulations allowed us to calculate the number of eggs and nests that must be destroyed annually to reach long-term objectives.

RESULTS

Comparison of native- and Michigan-parameterization

The native-parameterized matrix population model using an initial population vector from Michigan in 1948 overestimated abundance in Michigan during the 1991 – 2018 period when population estimates were available from the MDNR’s annual fixed-wing aerial abundance survey (Figure 5.1). The estimated intrinsic rate of population growth for the native-parameterized model was 1.142. The Michigan-parameterized density-independent matrix population model underestimated future abundance in Michigan (Figure 5.1) and resulted in a negative intrinsic growth rate ($\lambda = 0.979$). Generation time was similar between the native- (8.79 years) and Michigan-parameterized model (8.11 years). Survival of experienced breeders was most elastic in both models followed by survival of juvenile swans (0-1-year-old immature swans) and 1-2-year-old immature non-breeders (Figure 5.2). The life table response experiment demonstrated that much of the observed change in lambda between the native- and Michigan-parameterized density-independent MPMs (-0.163) resulted from reduction in the probability

that an experienced breeder survives and continues to breed (-0.075) although the reduction in reproduction of experienced breeders was also important (-0.059).

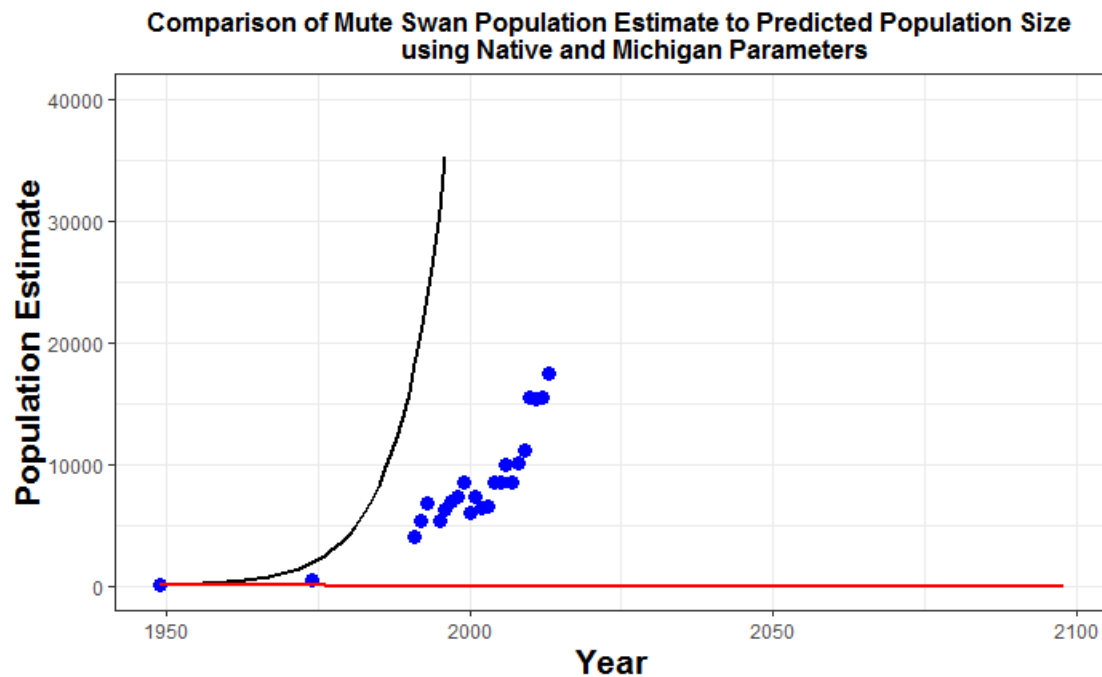


Figure 5.1. Comparison of observed mute swan abundance (blue points) to predicted mute swan abundance in Michigan, USA, for a 150-year simulation (1949 – 2098) between the native- (black line) and Michigan-parameterized (red line) deterministic matrix population model.

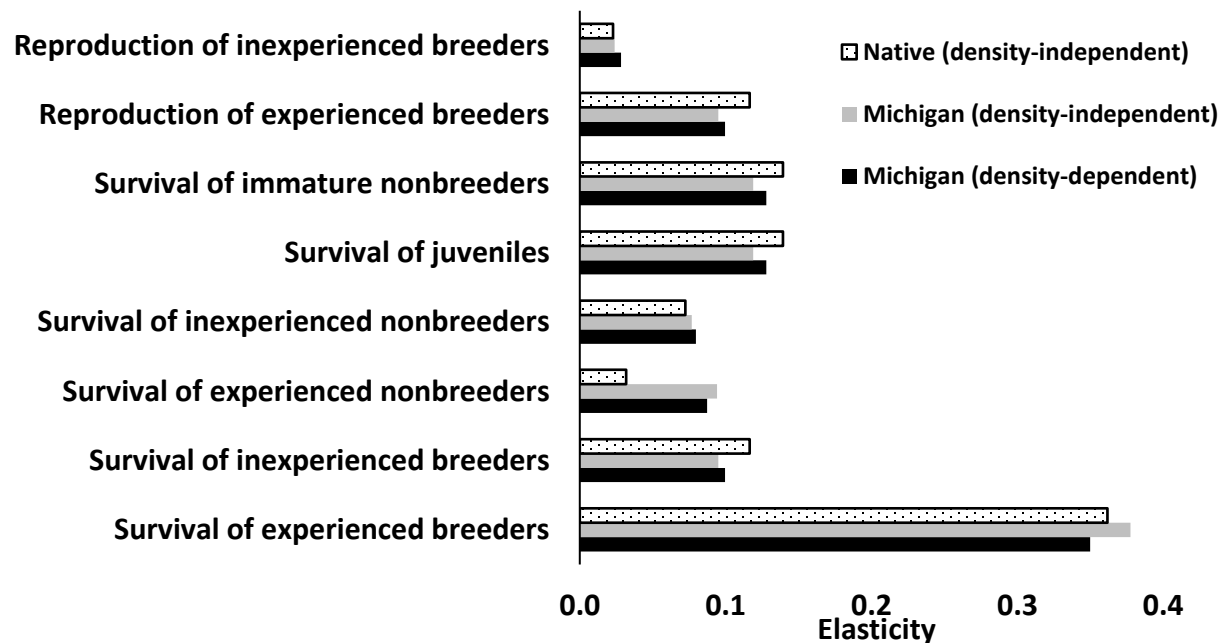


Figure 5.2. Comparison of parameter elasticity between deterministic density-independent native- and Michigan-parameterized matrix population models and the deterministic density-dependent Michigan-parameterized model.

Density-dependent matrix population model for Michigan

The Michigan-parameterized density-dependent MPM fit the observed mute swan population estimates better than the native-parameterized density-independent model (Figure 5.3). Predicted population size near observed population abundance estimates in 2018 (12,047 swans; MDNR, unpublished data) were similar between all three levels of K used within the penalty term (Figure 5.3) demonstrating that the model was not overly sensitive to the K chosen when abundance is not near K . Mute swan populations could have been expected to grow to 31,249 individuals, 39,608 individuals, or 47,131 individuals by 2030 under the three density-dependent simulations using varying levels of K in the penalty term, respectively, if expanded control efforts were not initiated in 2011. If control efforts were to stop in 2018, abundance of mute swans in Michigan could expect to grow to 26,034 individuals by 2030. Incorporation of density-dependence into the model caused the intrinsic rate of population growth and distribution

of life stages to vary throughout the simulations until the population was near a realized carrying capacity. During the simulation periods, abundance did not reach the carrying capacity set in the penalty term due to input values in more elastic parameters in the model (e.g., experienced breeder and juvenile [0-1-year-old immature] survival).

The relative elasticity ranking for parameters was similar in all density-dependent models although specific values varied among MPMs (Figure 5.2). Experienced breeder survival, juvenile survival (0-1-year-old immature), and immature nonbreeder (1-2-year-old immature) survival were the most elastic parameters (Figure 5.2). The penalty term in the 100,000 K density-dependent model varied from 3.2 fledged cygnets/pair at low pair abundance to 1.6 fledged individuals per pair when abundance was near estimated carrying capacity. Areas where pair productivity is below the value of a stable population (1.6 fledglings per pair; i.e., egg to fledge survival is 0.229 or lower) were not contributing to overall population growth at current estimated levels of life-stage specific survival.

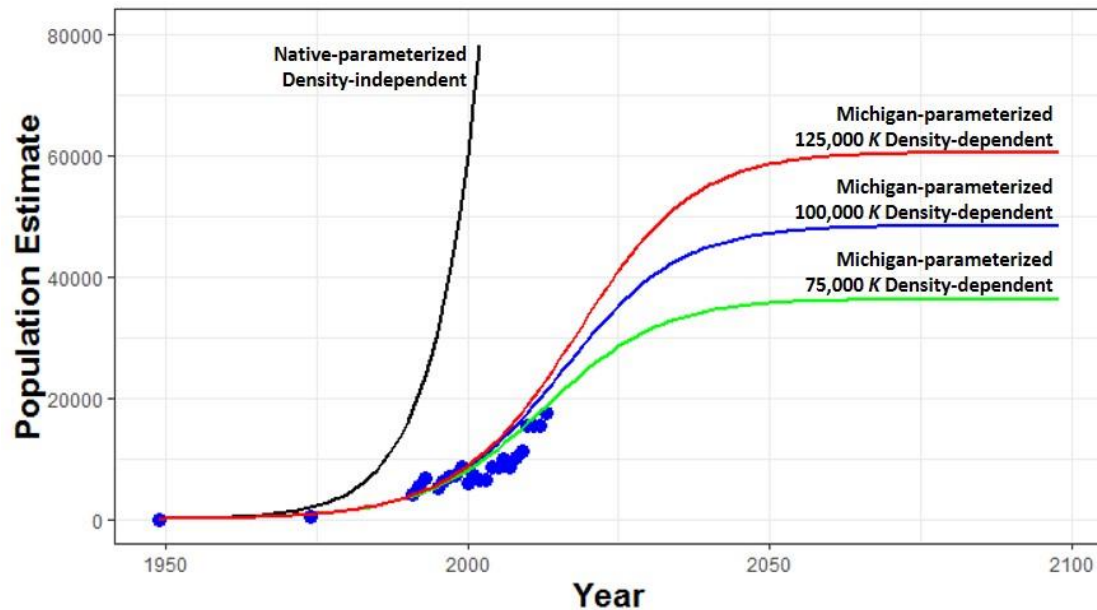


Figure 5.3. Comparison of native-parameterized density-independent matrix population model and a Michigan-parameterized density-dependent matrix population model under 3 simulated levels of carrying capacity for mute swans in Michigan, USA.

Estimation of removal rates needed to achieve long-term population goals

Proportional reduction in survival across all swan life stages

A 26% reduction in survival for all life stages was needed for mute swans in Michigan to reach the long-term goal of a population estimate of fewer than 2,000 mute swans based on the 2030 breeding survey conducted by the MDNR (Figure 5.4). A 26% reduction in survival for all life stages would require removal of 12,760 swans from 2018 –2029 which requires a mean annual removal rate of 17.2% of the estimated annual population (Table 5.2). Annual removals would need to be distributed across the three condensed life stages represented in the model to achieve the long-term goal (Table 5.2). Thirty-three percent of annual removals should be juvenile swans (i.e., post-fledging swans not yet 1 year old), 35% should non-breeding swans, and 32% should be breeding swans (Table 5.2).

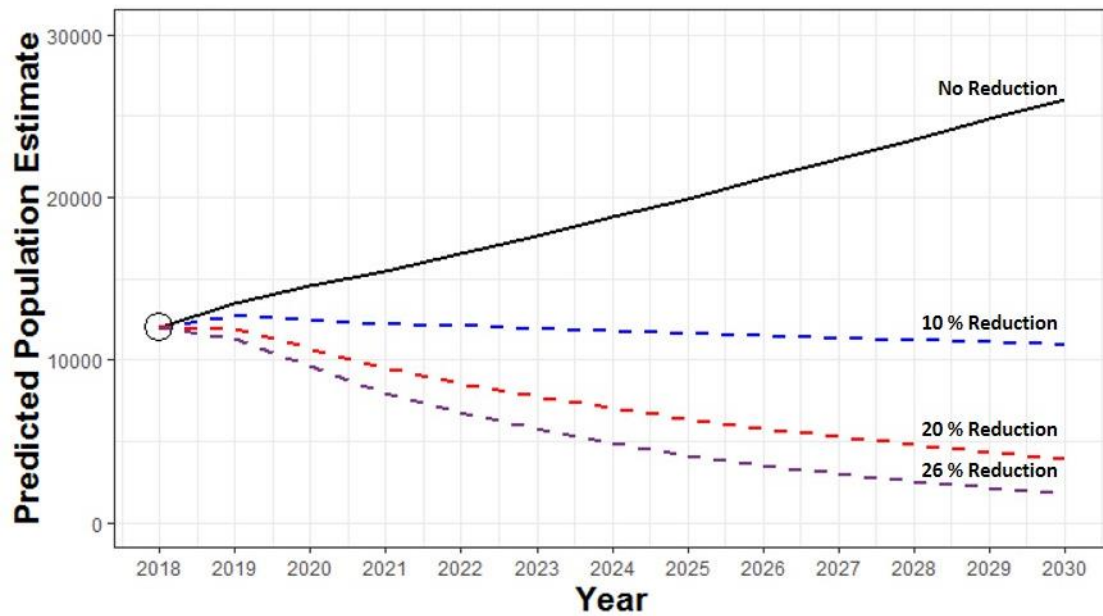


Figure 5.4. Comparison of density-dependent modeled reduction in survival needed across all mute swan life stages to achieve the long-term goal of fewer than 2,000 mute swans in Michigan, USA, by the year 2030.

Table 5.2. Annual removal needed by life stage to achieve long-term goal of fewer than 2,000 mute swans in Michigan, USA, by the year 2030 using the 100,000 *K* density-dependent matrix population model with an assumed 26% reduction in survival for all life stages over baseline rates.

Year	Annual Removal by Life Stage			Total
	Juveniles	Non-breeders	Breeders	
2018	570	755	822	2147
2019	716	583	640	1939
2020	562	593	497	1652
2021	445	504	426	1374
2022	388	412	362	1163
2023	334	351	303	989
2024	283	301	256	840
2025	241	255	217	713
2026	206	217	184	607
2027	176	185	156	518
2028	150	158	133	441
2029	128	135	113	377
Total	4199	4451	4110	12760

A maintenance level of 11% reduction in survival across all swan life stages is needed once the long-term goal is met in 2030 to keep annual abundance fewer than 2,000 mute swans.

This requires about 7.3% of the population to be removed annually which would be a mean annual removal of at least 146 swans with a similar distribution of removal across the three condensed life stages.

Comparison of life-stage specific removals needed to achieve long-term goal

Juvenile (0-1 immature) survival would need to be reduced by 96% to achieve the long-term goal in 2030 if all other life stage survival rates remained at values listed in Table 5.1. This would require an annual removal of 50.5% of the juvenile cohort which totals to a removal of 20,445 juvenile swans 2018 – 2029. Survival for non-breeding swans (i.e., 1-2-year-old immature non-breeders, experienced non-breeders, and inexperienced non-breeders) needs to be reduced by 65% annually to reach the long-term goal which would require 45.4% of the non-breeding swans in Michigan to be removed annually totaling 12,188 swans 2018 – 2029. About 60% of breeding swans would need to be removed annually (i.e., 70% reduction in survival) to achieve the same long-term goal. This would require a total of 10,036 breeding swans removed 2018 – 2029 assuming no removals occurred for other life-stages. Less than half of the total swans would need to be removed if culling efforts were targeted solely on breeding swans when compared to solely on juvenile swans.

Egg and nest destruction needed to reach long-term goal

Baseline levels of breeding productivity would need to be reduced by 88% annually to achieve the long-term population goal in 2030. This requires at least 94.5% of all mute swan nests in the state of Michigan to be destroyed annually 2018 – 2029 to reach the long-term goal which would require removal of at least 15,748 nests and approximately 110,237 eggs (Table 5.3). Low natural egg to fledge survival under optimal nesting conditions (0.46) and the inability

to know which remaining eggs can be expected to fledge will result in destroying approximately 63,000 eggs (61.6% of total) that would not have produced a fledged cygnet if left untouched.

Table 5.3. Number of eggs and nests that must be destroyed annually to achieve long-term goal of fewer than 2,000 mute swans in Michigan, USA, by the year 2030 using the 100,000 *K* density-dependent matrix population model with an assumed 88% reduction egg to fledge survival over baseline rates.

Year	Total Present		Total to Remove	
	Nests	Eggs	Nests	Eggs
2018	1859	13013	1756	12295
2019	1957	13696	1849	12940
2020	2054	14379	1941	13585
2021	1845	12917	1743	12204
2022	1617	11318	1528	10693
2023	1411	9879	1333	9334
2024	1230	8612	1162	8137
2025	1072	7506	1013	7092
2026	935	6543	883	6182
2027	815	5706	770	5391
2028	711	4977	672	4702
2029	620	4342	586	4102
2030	541	3789	511	3580
Total	16668	116677	15748	110237

DISCUSSION

Our Michigan-specific density dependent MPM, like many analyses that examine dynamics of long-lived species (Watola et al. 2003, Ellis and Elphick 2007, Alisauskas et al. 2011), suggests that adult survival (combined elasticity of 0.773) is the most influential parameter when compared to juvenile survival or breeding productivity (Figure 5.2). We found that the breeder subsegment of the adult population was most influential (0.477), although the non-breeding segment was also important (0.296). Results of the Life Table Response Experiment show that the change in lambda observed between the two density-independent models was caused by our lower observed survival rate and probability of continuing to breed for breeding adults. We successfully incorporated density-dependence into breeding productivity of

our matrix population model although strength of density dependence in productivity was low to moderate at our observed population abundance (Figure 5.3). However, incorporation of density dependence was helpful in estimating future trajectories of abundance if management of mute swans became infeasible due to political will or public desire.

Our simulation modeling using a density-dependent matrix population model shows that efforts that reduce productivity of breeding swans is relatively inefficient compared to removal of adults for reducing the overall mute swan population in Michigan. However, destroying nests or eggs through removal of nest vegetation or oiling of eggs remains a useful technique for locally reducing the number of cygnets during the summer months, alleviating aggressive behavior of brooding pairs, and retaining public support for comprehensive management programs (Watola et al. 2003, Allin and Husband 2004). Our modeling also shows that most eggs destroyed through egg oiling or nest removal efforts would not have produced a fledged cygnet if management actions were not taken further demonstrating its inefficiency as a population management strategy.

Our simulations of management alternatives that target differential culling of juvenile and adult swans provides flexible management options to agencies tasked with mute swan management. All life stages of mute swans are available for removal throughout Michigan; however, not all individuals in a life stage share an equal probability of being removed. Some breeding adults remain on private waterbodies or in heavily developed areas year-round (Chapter 4) protecting them from most removal efforts. Additionally, flocks of non-breeders may summer in remote shallow water areas of the Great Lakes and escape removal due to lack of detection or the inability for crews to reach the area. Our simulations also show that not all life stages of mute swans equally contribute to population demographics (i.e., culling a juvenile swan does not

provide the same population-level impact as removing an actively breeding swan). Simulations show that management agencies would need to cull approximately twice as many juvenile swans as breeding swans to reach the long-term goal if culling efforts focused only on the juvenile life stage instead of the breeding life stage.

MANAGEMENT IMPLICATIONS

Our density-dependent model provides managers with a tool for evaluating alternatives for mute swan population control. Simulations through our matrix population model suggest that management should focus on culling juvenile and adult swans rather than focusing on reducing breeding output. Additionally, culling efforts should target all life stages that are available for removal (i.e., juvenile, adult non-breeding, and adult breeding) rather than only focusing on one life stage. Removing swans from all life stages results in a management program that is robust to circumstances where the solely targeted life stage is unavailable for removal (i.e., breeding swans remaining on territories year-round due to less ice coverage under climate change).

Stratifying annual removals among life stages also allows for temporal targeting of specific stages. Molting flocks of non-breeding swans congregate in mid- to late-summer on large inland lakes and open water areas of the Great Lakes. These flocks are nearly entirely consisted of immature non-breeding and adult non-breeding swans. They could be targeted for removals to ensure that the culling quota for non-breeding swans is met or exceeded annually. A similar, although less efficient, strategy exists for ensuring that the annual quota of breeding swans is reached or exceeded. Culling efforts can target breeding pairs in early spring (i.e., April) through early summer (i.e., June) when they are either actively incubating eggs or brooding cygnets. Breeding swans that failed nesting or lost hatched cygnets early in the brood rearing period are still likely to be near their nesting location (R. Knapik, personal obs.).

Distinguishing between adult life stages during winter culling efforts can be impossible although juvenile swans (i.e., swans < 1 year old) can be reliably distinguished from adults. Temporally targeting specific life stages throughout the year can help ensure that removal quotas for each life stage are met.

Annual removal goals for each life-stage under a proportional reduction in survival (26%; Table 5.2) should be considered conservative minimum goals since slight annual variation in input parameters (e.g., stochasticity in adult survival, juvenile survival, or reproduction) can lead to changes in the absolute number of swans that must be removed to be certain of a decline (Ellis and Elphick 2007). Further, it should be noted that predicted annual removals to achieve the long-term goal assume that removal goals are met annually. Additional swans will need to be removed in subsequent years following the failure to achieve annual removal goals (Table 5.2). Alternatively, a strategy of removing more swans early in population control compared to a policy of an annually-constant removal rate would reduce the overall number of swans needed to be removed to achieve population goals by 2030. We have presented demographic outcomes of several realistic management strategies that target various life stages (i.e., reducing reproduction, proportional culling of all life stages, or targeting specific life stages); however, the management strategy that works best for a given agency is one that can be reliably accomplished annually given constraints of funding, staff time, and public cooperation. Our density-dependent matrix population model can be used to model additional management strategies that may work best for management agencies.

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CHAPTER 6: MANAGEMENT IMPLICATIONS

Human-assisted movements of mute swans to North America resulted in feral populations along the U.S. East Coast, in the Great Lakes region, and in isolated pockets throughout the western U.S. (Allin et al. 1987, Sullivan et al. 2009). Populations can grow quickly once established and persist for long periods due to relatively high survival for adult life stages (Chapter 4, Watola et al. 2003). Management agencies are often tasked with creating policies without understanding of regional dynamics and movements of mute swans since early detection and decision making is typically needed to combat invasive species (Mack et al. 2000, Edelaar and Tella 2012). Using poorly parameterized demographic models to project outcomes of future management can produce undesirable results if control levels are insufficient to reduce overall abundance. Additionally, management programs may not be initiated if there is a perceived inability to control the invasive species given resources available for management. Agencies also face public scrutiny over management plans due to the charismatic nature of some invasive species such as mute swans and their close association with humans (Allin et al. 1987); however, many individuals, at least in Michigan, are concerned with specific management techniques and not necessarily opposed to all control methods (Jager et al. 2016). The public wants to ensure that science-based management policies are selective, effective, considered nonlethal options, and carried out by trained biologists (Reiter et al. 1999).

Review of mute swan management in Michigan

The Michigan Department of Natural Resources (DNR) formally outlined their management policy for mute swans in 2012 along with stating short- and long-term goals which were to reduce population growth initially and to have fewer than 2,000 mute swans statewide by 2030 (Michigan Department of Natural Resources 2012). Concomitantly, the Mississippi Flyway

Council also outlined flyway-wide abundance goals of fewer than 4,000 mute swans by 2030. Management in Michigan prior to 2011 primarily focused on addressing human-wildlife conflict although some larger removal efforts occurred. Conflict resolution typically resulted in oiling eggs, removing of nest material, or culling of individuals. The Wildlife Services division of the U.S. Department of Agriculture Animal and Plant Health Inspection Service (USDA APHIS) began receiving additional funding from the Great Lakes Restoration Initiative (GLRI) in 2011 to increase mute swan surveillance and intensify their culling efforts (Marks 2015). The additional funding provided by the GLRI and sustained funding from the Michigan DNR allowed for a more robust statewide culling program which removed over 9,700 individuals since 2011 (Arsnoe and Duffiney 2018). However, the mute swan population in Michigan appears to have stabilized despite an initial decrease in abundance (MDNR, unpublished data). Population stabilization and increased difficulty in accessing areas to remove mute swans prompted research to estimate Michigan-specific demographic parameters and understand regional movement for sub-adult and adult swans. It was unknown if removal levels achieved 2011 – present were sufficient to meet the long-term goal; however, results from this research suggest that removal rates were insufficient in all years except in 2012 when 2,628 mute swans were culled (17% of the 2012 estimated population; Marks 2015, MDNR, unpublished data). Our study of demographics and movement across the full life cycle of the mute swan has improved demographic models and has also provided practical in-field guidance for mute swan management.

Overview of pertinent results from demographic and movement study

Our investigation of mute swan nesting ecology found productivity varied across Michigan with density of nesting pairs. Mean clutch size in Michigan (7.0 eggs/pair) was higher

than in other areas of native and introduced ranges; however, mean productivity was lower especially when considering sites with many pairs and saturated nesting cover (Chapter 3). Reduced cygnet survival was related to variation in territory quality for saturated sites as a result of high competition for characteristic territories (Chapter 3). Survival for immature and adult non-breeding swans (Chapter 4) was similar to values reported for other areas of their range (Watola et al. 2003). Importantly, juvenile and breeding adult survival (Chapter 4) was slightly lower than values reported in the literature (Watola et al. 2003). Slightly lower values for adult survival resulted in a large change in the population growth rate (λ) when comparing a native-parameterized model to a Michigan-specific model especially since survival and probability of continuing to breed for adult breeding swans was most elastic in our demographic model (Chapter 5). Our density-dependent matrix population model allowed comparison of management scenarios aimed at reaching the long-term goal established by the Michigan DNR given the estimated abundance in 2018 and observed demographics from this study.

Management scenarios to reach long-term abundance goal

Demographic modeling suggests that a 26% reduction in survival across all life stages is needed to reduce mute swan abundance to goal levels by 2030. This will require removal of at least 17% of the annually estimated population; however, annual removals must be distributed across 3 primary life stages (32% juvenile, 35% non-breeding swan, and 33% breeding swan) to be effective. A total of at least 12,760 swans would need to be removed before 2030 with annual removal goals listed in Table 5.2. It is important to note that agencies tasked with mute swan management in Michigan should consider annual removal goals listed in Table 5.2 to be conservative minimums since they assume complete additive mortality for those life stages.

Stochasticity in demographic rates could also result in slight variation in the number of swans that need to be removed yearly to reach the long-term goal (Ellis and Elphick 2007).

We also found that increased management effort is needed if only one swan life stage is targeted for removal or if egg and nest destruction was the chosen management method. An estimated 20,445 juvenile swans (i.e., fledged swans not yet 1 year old) would need to be removed from 2018 – 2029 to achieve the long-term goal. This would require annual fall and winter culling of at least 50% of the juveniles statewide. About 40% of non-breeders would need to be removed annually (12,188 total removed non-breeders 2018 – 2029) to achieve the same goal. At least 60% of breeding swans (10,036 total removed breeding swans 2018 – 2029) would need to be removed annually for mute swan abundance in Michigan to be fewer than 2,000 mute swans by 2030. The long-term abundance goal could only be met through reduction in breeding productivity if at least 94.5% of all mute swan nests and eggs were destroyed annually in Michigan (15,748 nests and approximately 110,237 eggs destroyed 2018 – 2029). Further, the inefficiency of egg and nest destruction is highlighted in the fact that about 61% of the total eggs destroyed would not have produced a fledged cygnet anyway. It is impossible for managers to know which eggs will produce fledged cygnets during incubation; therefore, all eggs must be destroyed regardless of potential fate. Watola et al. (2003) evaluated the use of clutch size reduction in reducing overall abundance but found partial clutch removal to be ineffective at reducing ultimate productivity and overall mute swan abundance.

Simulations of our density-dependent matrix population model showed that the population of mute swans in Michigan stabilizes when mean statewide breeding productivity is near 1.6 fledglings per pair (22.8% egg to fledge survival; mean clutch size of 7). Further, we have shown that there is spatial variation in productivity throughout Michigan that results from

differing nesting pair densities and competition for characteristic nesting territories. These two findings suggest that productivity within areas where density dependence is strongest (i.e., where characteristic nesting cover is saturated, and pairs are nesting in suboptimal cover) is not contributing to overall population growth in Michigan. At least 81% of all eggs produced in these areas fails to yield a fledged cygnet during our study. Areas where mean productivity is near 1.6 fledglings per pair are contributing to overall population stability but may not be contributing to growth. Conversely, breeding pairs in areas where nesting cover is abundant, pair density is low, and productivity is in excess of 1.6 individuals per pair are contributing to overall population growth in Michigan.

Practical considerations for future management

Egg and nest destruction

Observed density-dependence in breeding productivity and low elasticity for egg to fledge survival in demographic modeling shows that destruction of nests and oiling of eggs is inefficient at reducing overall mute swan abundance. However, egg oiling and nest destruction remain useful management tools to locally reduce summer cygnet abundance, limit aggression by nesting pairs, and to retain support for the management program by concerned citizens. If nest destruction operations must only focus on some nests within a given area, nests in typical nesting cover or those which have been present for multiple years should be prioritized for destruction as those are the most likely to produce fledged cygnets. Nests that are being targeted for egg oiling and nest destruction should be checked between 20 – 30 April when most breeding females are

incubating and at least a week prior to our observed mean hatch date of 12 May. Low-level surveys in fixed-wing aircraft are invaluable at locating nests for such operations.

Life stage-specific removal of mute swans

The long-term statewide abundance goal of fewer than 2,000 mute swans in Michigan by 2030 can be achieved if removal efforts target all juvenile or adult life stages. Targeting swans by life stage allows different management objectives to be met year-round since some stages (e.g., juveniles and breeders) are harder to target during some seasons. Flocks of non-breeding swans can be accessed in summer once they settle on large inland bodies of water or on waters of the Great Lakes (typically by 15 July) to complete their annual flight feather molt. Non-breeding swans begin to move from molting areas by the end of August. Juvenile swans and breeding pairs are most readily accessible when ice coverage forces them to regional wintering sites (typically late December). Removals in these areas should be conducted before breeding females start returning to nesting territories in mid-February. Mean displacement from nesting location for breeding females was about 11 km; therefore, winter culling efforts targeted at breeding females will likely need to occur at inland wintering concentration sites in addition to waters of the Great Lakes. It is important to note that targeting mute swans during periods of widespread ice coverage may have lethal or sublethal impacts on non-target species like native waterfowl that also congregate in those regions during periods of ice coverage; however, the magnitude of impact to native species is unknown.

Although our demographic model is spatially invariant and assumes that life stage-specific removals have a uniform effect on survival and reproduction statewide, our knowledge of mute swan distribution and density dependence in breeding productivity can further leverage the effectiveness of life stage-specific culling. The current goal of the Michigan DNR is to

reduce abundance to fewer than 2,000 individuals by 2030 (Michigan Department of Natural Resources 2012). This damage management approach is preferable to complete eradication in the short term since immigration is possible from nearby mute swans in Ontario and could hinder efforts for complete removal (Bomford and O'Brien 1995). Therefore, removal of breeding swans will be most effective at reducing overall abundance when conducted in areas where breeding productivity is above average. Removal of juvenile and non-breeding swans will also be most effective at reducing overall abundance when in proximity to areas of unoccupied typical nesting cover. Conversely, removal of breeding pairs that nest in areas of saturated nesting cover may not cause an overall reduction in local productivity due to effects of density dependence in productivity. We suggest that culling efforts, especially for breeding swans, should first be focused in regions where regional density is low to maximize reduction in breeding output and reduce the ease of which non-breeders can occupy unfilled characteristic nesting territories. We acknowledge that targeting removals in areas with fewer total swans is likely to increase the cost per swan removed; however, fewer total swans would need to be removed using this strategy due to density-dependent productivity and potential immigration from other established populations (i.e., Ontario). A management strategy such as this would temporarily leave breeding pairs intact in areas such as southeast Michigan where breeding productivity is likely low and competition for nesting territories are high. Additionally, developed inland lakes and wetland areas of southeast Michigan are likely not of highest conservation priority for other wetland-dependent species at this time. However, culling mute swans in high-quality wetlands and stopover areas used by migrating waterfowl in these regions should remain a priority under this strategy. A spatially stratified culling approach such as this, which temporarily leaves breeding mute swans in high-density areas of southeast Michigan could

also serve as a physical buffer to dispersing swans from adjacent regions where mute swans are present but widespread management programs are not being performed (i.e., Ontario).

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