

Density dependence in productivity of a North American Mute Swan *Cygnus olor* population

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Abstract

Mute Swans *Cygnus olor* were first introduced to North America in the late 19th century and were brought to Michigan, USA, by humans in 1919. Numbers in Michigan remained low throughout the 20th century but began to grow rapidly in the early years of the 21st century, reaching 17,520 by 2013. The Michigan Department of Natural Resources (MDNR) produced a policy in 2012 to have fewer than 2,000 Mute Swans state-wide by the year 2030; however, estimates of demographic parameters and information on patterns of density dependence are needed to identify the annual control level needed to achieve long-term goals. A research partnership between the MDNR, the Wildlife Services section of the US Department of Agriculture Animal and Plant Health Inspection Service, and Michigan State University was formed to investigate the patterns of density dependence in the Michigan population of Mute Swans. Nesting pair density and productivity were surveyed in 2016–2018 using fixed-wing aircraft. Extent of nesting habitat was quantified to assess the relationships between the number of nesting pairs and nest site availability. Mean productivity for nesting pairs was low (1.4 fledglings/pair) and decreased with increases in the number of nesting pairs. Productivity was inversely related to estimated saturation of characteristic nesting habitat ($\beta = -0.979$, s.e. = 0.439). Mute Swan pairs nested in non-characteristic habitat on sites with many nesting pairs where characteristic nesting habitat was saturated. These results suggest that habitat-mediated density dependence in productivity is occurring for Mute Swans in Michigan. As such, demographic modelling and in-field management of Mute Swans in Michigan should take into consideration the demonstrated relationships between productivity and nesting pair densities.

Key words: habitat heterogeneity hypothesis, interference hypothesis, invasive species, Michigan, nest spacing.

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

Density dependence is typically evident within, and operates through, the main demographic variables (*e.g.* birth, death and emigration rates) and could be regulated by intraspecific competition for resources (Newton 1998). A density-dependent effect on reproductive effort has been found for several territorial waterbird species (Sedinger *et al.* 1998; Lebeuf & Giroux 2014), and this may operate through several mechanisms (Ferrer & Donazar 1996). Lack (1966) and Fretwell and Lucas (1969) proposed that overall productivity would decrease while variation in reproductive success between individuals would remain stable with increasing density. They hypothesised that increased agonistic interactions would accompany increased density and, therefore, would reduce mean

territory quality for all individuals regardless of a characteristic territory's quality at lower densities. This would result in a homogenisation of territories where all become equally poor at high densities, even though some are high quality territories at low pair densities. Negative density dependence in productivity could also be explained by heterogeneity in habitat quality on breeding territories (Kadmon 1993). This theoretically would result in a population in which productivity declines with increased density, but where variation between individuals in their breeding performance increases rather than remains equal, as proposed by Lack (1966). Variation in individual reproductive success relating to habitat heterogeneity follows the hypothesis that the best habitats are filled first (Hildén 1965; Ferrer & Donazar 1996; Rodenhouse *et al.* 1997; Lovette & Fitzpatrick 2016). Ferrer and Donazar (1996) summarised and investigated these two 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 the quality of territories and the quality of 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 & Saari 2003).

Mute Swans *Cygnus olor* employ two breeding strategies across their introduced and native ranges. Most populations exhibit a territorial nesting strategy where nest sites, brood-rearing habitat, and food resources are defended aggressively by the pair, resulting in relatively low pair densities. Colonial-breeding populations also exist, however, where nesting habitat is abundant, intraspecific aggression is low and pairs nest at high densities with normal productivity (Perrins & Ogilvie 1981). Nummi and Saari (2003) conducted a longitudinal study (1976–1998) to analyse reproductive parameters for Mute Swans introduced to a Finnish archipelago. They hypothesised that breeding success would differ between territories of varying quality, with quality measured as the length of time it has been occupied. Clutch size, brood size and fledged young per pair were inversely related to the number of breeding pairs in their introduced population. Several cygnets were found with crushed skulls in high density areas, which is evidence for IH; however, sites occupied for the longest number of years (*i.e.* were of highest quality) produced more young, and variation in brood size increased with density (Nummi & Saari 2003). These results, much like those of Ferrer and Donazar (1996), predominantly provide support for HHH, and accounts published elsewhere in the scientific literature (Lack 1954; Sedinger *et al.* 1998) likewise indicate that the dynamics of the brood-rearing phase becomes increasingly important for birds as densities increase (Ferrer *et al.* 2008).

Mute Swans were first introduced to North America along the Atlantic coast in the late 19th century to grace urban ponds

and large estates (Baldassarre 2014). A pair of Mute Swans was translocated to Michigan's Charlevoix County from an estate in Iowa in 1919 because of the aggressive behaviour of the pair (Gelston & Wood 1982). Population growth was slow throughout the 20th century; however, the population increased to an estimated 17,520 individuals in 2013 (D. Luukkonen, unpubl. data), making it the largest population of Mute Swans in North America. In 2012, the Michigan Department of Natural Resources (MDNR) formalised management goals and objectives for Mute Swans in the state (Michigan Department of Natural Resources 2012), with a long-term goal of there being no more than 2,000 Mute Swans in Michigan by the year 2030 estimated through their annual breeding waterfowl surveys. This policy did not outline levels of control needed to accomplish that goal, however, due to uncertainty over the demographic parameters affecting trends in numbers for this introduced population. Furthermore, there were no empirical data to examine the role of density in influencing breeding productivity for Mute Swans within North America, although it has been demonstrated for an introduced population in Europe (Nummi & Saari 2003). It has previously been suggested that density dependence was likely occurring for introduced Mute Swan populations established for more than three decades (Ellis & Elphick 2007); investigation of density dependence therefore was considered timely for the well-established sub-populations in Michigan, and a study was initiated to assess density dependence on productivity for Mute Swans in the state. Here we present results of

an analysis of Mute Swan productivity at different breeding densities within the swans' core breeding range in Michigan, and also investigate nesting density in relation to habitat characteristics, to inform future population modelling and management actions.

Methods

Study area

The state of Michigan, USA, is naturally separated by Lake Michigan and Lake Huron into two landmasses commonly called the Upper Peninsula and Lower Peninsula. This research focussed on Mute Swans within their core breeding range in Michigan, which is found in the Lower Peninsula (Michigan Department of Natural Resources, unpubl. data). Spring density of all Mute Swans was estimated in 2011–2015 and was overlaid with hydrography data (Center for Shared Solutions and Technology Partnerships 2015) in a geographic information system (GIS; ArcGIS 10.3.1) to identify waterbodies that might harbour breeding pairs. The Lower Peninsula was stratified using township boundaries outlined in the United States' Public Land Survey System (PLSS; Center for Shared Solutions and Technology Partnerships 2015) and by running a query in the 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. The mean shoreline distance for these townships (mean = 40 km; a coarse proxy for nesting habitat potential) was taken as an estimate of where Mute Swans were likely to occur in the Lower Peninsula during the next breeding season (*i.e.* 2016). Fifteen preliminary study sites (6×6 km

each) were identified using these methods (Fig. 1). Fixed-wing aircraft (Cessna 185) were used to survey preliminary study areas for Mute Swan presence and nesting habitat in December 2015 and April 2016. Five study sites were chosen based on presence of, and access to, ≥ 5 breeding pairs within a 36 km² area: Tobico (43°41'29"N, 83°56'21"W in Bay County), Juno (41°48'31"N, 86°0'40"W in Cass County), Wabasis (43°07'06"N, 85°22'45"W in Kent County), Oakland Pontiac (42°41'14"N, 83°26'49"W in Oakland County), and St. Clair (42°37'21"N, 82°40'56"W in St. Clair County), to investigate density dependence in breeding productivity during 2016–2018 (Fig. 1). One additional site, Clam (44°56'30"N, 85°14'25"W, in Antrim County; also covering a 6×6 km area), was included in this investigation for 2017–2018 to ensure that complete latitudinal variation was being accounted for in analysis of Mute Swans breeding across Michigan's Lower Peninsula (Fig. 1).

Land cover composition varied across our four inland (Clam, Juno, Pontiac, Wabasis) and two Great Lakes 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 open water (Lacustrine Limnetic Unconsolidated Bottom Permanently Flooded habitat, L1UBH; US Fish and Wildlife Service 2015). Natural shoreline consisted of characteristic Mute Swan nesting habitat (Palustrine Emergent, PEM; US Fish and Wildlife Service 2015) such as Broad-leaved Cattail *Typha latifolia*, bulrushes *Schoenoplectus* sp., Narrow-leaved Cattail *Typha angustifolia*, Common Reed

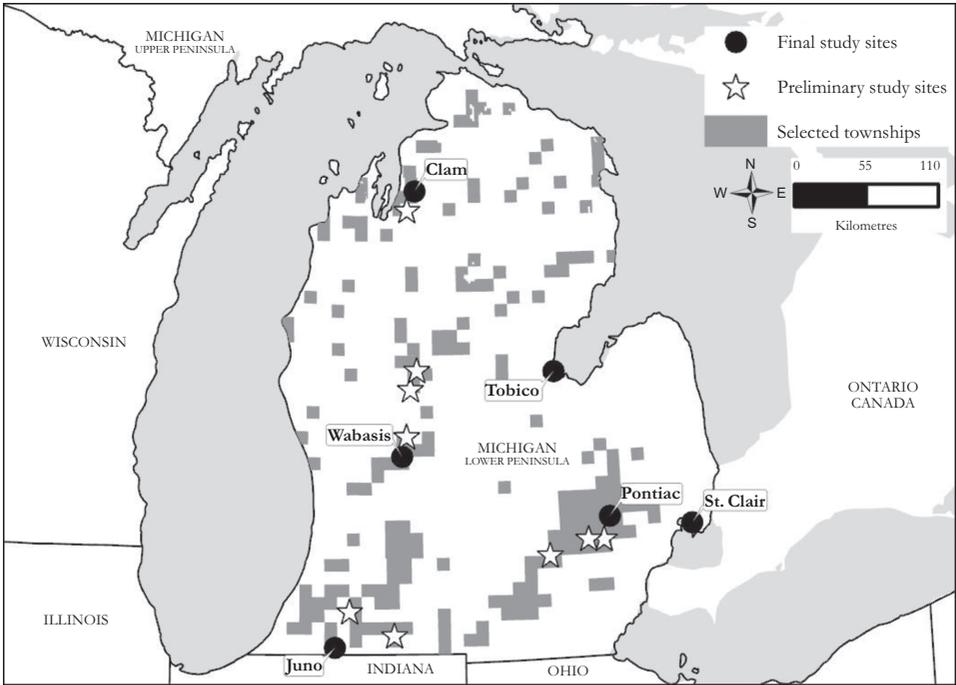


Figure 1. Preliminary and final study sites located across the Lower Peninsula of Michigan, USA, within selected public land survey system (PLSS) townships which had a high likelihood of breeding pair presence (*i.e.* ≥ 40 km of shoreline).

Phragmites australis, or woody vegetation (Buttonbush *Cephalanthus occidentalis*, willow *Salix* sp., ash *Fraxinus* sp., maple *Acer* sp., Cottonwood *Populus deltoides*, and oak *Quercus* sp.). The Tobico study site contained areas of Broad-leaved Cattail and Narrow-leaved Cattail (Palustrine Emergent Persistent Semi-permanently Flooded habitat, PEM1F) and open water (Palustrine Aquatic Bed Intermittently Exposed habitat, PABG; US 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 or Lacustrine Limnetic Unconsolidated

Bottom Permanently Flooded habitat, L2UBH) but also included large areas of freshwater wetlands with emergent vegetation (*e.g.* Broad-leaved Cattail, bulrushes, Narrow-leaved Cattail, and Common Reed) and small developed islands (< 5 ha each) that contain seasonal human dwellings (*i.e.* cottages) dispersed within the matrix of open water and emergent vegetation.

Nesting pair density

Annual aerial surveys of nesting Mute Swans were conducted (12 April–1 May) to detect actively nesting pairs within study sites and determine GPS coordinates of all

observed nests for sites (2016 $n = 5$; 2017–2018 $n = 6$). The aircraft circled all wetlands and waterbodies to ensure complete coverage of all potential swan nesting habitat. This approach was preferable to a fixed-transect design since a complete census of all nesting pairs within site boundaries was needed rather than a calculated estimate of pair density. Two observers worked together, with one on each side of the aircraft, to detect incubating females on the large (≥ 1 m) conspicuous nests (Conover & Kania 1999) against the backdrop of senesced emergent vegetation. Cooper (1979) and Kear (1972) estimated that incubation recesses for female Trumpeter Swans *Cygnus buccinator* and Mute Swans were < 30 min daily and that females and males typically remained near nests; therefore, the detection probability for nests with a breeding pair of swans was likely close to 100% during the low-level (*c.* 100–150 m above ground level) aerial surveys. The flight route of the aircraft was recorded using a cellphone application (Strava, Inc.) which recorded GPS fixes at 1 sec intervals, whilst flight observations were recorded using wing strut-mounted video camera systems in 2016–2017 (MotoCam 360) and also in 2018 (GoPro Hero 4 Silver) to confirm the physical location of nesting pairs and ensure that all nesting habitat was surveyed. All nests detected were recorded directly onto physical orthophotographs, which contained aerial imagery and identified all waterbodies and wetlands within the study area. The location data recorded on orthophotos were later transferred to a GIS.

Management of Mute Swans continued throughout the state of Michigan during the

years of this research, but management did not occur within or adjacent to study sites with the exception of two sites in 2018. Removal of Mute Swans by the Wildlife Services section of the US Department of Agriculture Animal and Plant Health Inspection Service (USDA APHIS) at these two sites (Juno and St. Clair) during incubation (3 May 2018 and 30 April 2018, respectively) was at the request of waterfront residents. Although Mute Swan removals were not designed or implemented through this research, the removals were coordinated with USDA APHIS so that they did not have an adverse impact on the ongoing Mute Swan study. Aerial surveys were flown prior to and after removals to ensure that the numbers and locations of nesting pairs within the study sites were known. All estimates of the number of nesting pairs, productivity and nesting habitat saturation levels presented in this manuscript account for the removal of nesting pairs during incubation at these two sites during 2018. The numbers of nesting pairs therefore did not include pairs removed through Mute Swan management efforts and, likewise, productivity (number of fledged cygnets per pair) did not include pairs removed during culling. Michigan State University (MSU) Institutional Animal Care and Use Committee (IACUC) granted an animal-use exemption for MSU personnel throughout this project because in-field research efforts were led by staff of the Wildlife Services section of USDA APHIS.

Breeding productivity

Aerial surveys were used to determine breeding productivity per pair near the time

of 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. White (*i.e.* adult or leucistic-morph cygnets) and grey swans were counted and approximate locations for each of the pairs and broods were recorded on orthophotographs, with the data then transferred to a GIS. Boats were used to confirm brood size and the colour morph ratio (*i.e.* by counting leucistic-morph cygnets separately from their parents). The number of fledged cygnets per site was compared to the total number of nesting pairs, to derive an estimate of productivity that included failed nests and failed broods.

Nest spacing

Median distance to the closest conspecific nest was determined for all nests detected within study site boundaries, for each year from 2016–2018 inclusive. A GIS was used to determine the Euclidean distance between Mute Swan nests for pairs residing on the same waterbody ($n = 143$ comparisons). Mute Swans are nearly fully aquatic (Sousa *et al.* 2008) and are likely not directly influenced by the presence of pairs on adjacent waterbodies during the nesting period. Our methods for measuring nest spacing therefore ensured that we only included comparisons that were biologically relevant. Nest spacing measurements were summarised for each year, with sites pooled to understand the typical conspecific nest spacing for Mute Swans rather than variation in spacing potentially related to pair densities on specific sites.

Saturation of nesting habitat

Mute Swans in North America typically nest in dense vegetation adjacent to water (Baldassarre 2014), for instance in cattail, bulrush and Common Reed beds (Ciaranca *et al.* 1997). A GIS and recent (2014–2016) high-resolution (< 1 m per pixel) orthophotographs taken during April (when no leaves were on the trees to obstruct assessment of water area) were used to digitise the transition between open water and other cover types (*e.g.* emergent herbaceous vegetation, forests, developed land). We then conducted in-field surveys on all sites during the 2018 nesting season to record whether or not characteristic nesting habitat was present at the boundary of open water and other cover types.

Using information from the in-field surveys, digitised line features representing the transition to open water were then grouped into two categories: areas with adjacent characteristic nesting habitat and areas adjacent to other cover types. A new line feature was created that contained all the segments where characteristic nesting habitat was immediately adjacent to open water. Equally spaced points (10 m spacing) allocated along polylines of nesting habitat were used to represent potential nest locations for the nesting pair saturation analysis (Fig. 2). These points were created to discretize the continuous line feature into locations where hypothetical nests could be located and allow us to space potential nest locations in relation to our observed nest spacing, for assessing the maximum number of pairs that could potentially nest on each site given the distribution of nesting habitat.

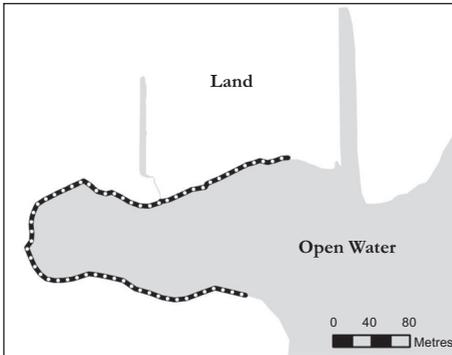


Figure 2. Example determination of potential nesting locations (white circles, spaced at 10 m intervals) within characteristic nesting habitat for Mute Swans (black line) at the transition of open water and adjacent habitat types for focal waterbodies in the Lower Peninsula of Michigan, USA.

The maximum number of nesting pairs (*i.e.* saturation) was estimated for the six study sites, from the distribution of characteristic nesting habitat and the spacing of conspecific nests recorded during the surveys. The methods used to determine saturation levels for the nesting habitat were conceptually similar to the approach used by Downs *et al.* (2008) who estimated nesting carrying capacity for territorial Sandhill Cranes *Grus canadensis*. Our estimates of saturation assumed that Mute Swans space their nests optimally in characteristic habitat, to obtain the highest possible number of nests in their breeding areas. In reality, Mute Swans do not necessarily space their nests optimally in this manner; however, this method provides a liberal estimate of nesting pair saturation, to which the actual number of nesting pairs can be compared. Sites where pairs establish nesting territories

outside of characteristic nesting habitat and where observed saturation ratios are close to or ≥ 1 indicate that the nesting habitat is likely at saturation level.

Comparison of observed breeding productivity among sites

The functional relationship between productivity (*i.e.* the number of fledglings per nesting pair) and the number of nesting pairs was examined for evidence of density dependence. A linear regression was conducted in Program R (R Development Core Team 2018) to examine the relationship of productivity to: (i) the number of nesting pairs, and (ii) the ratio of observed pairs to numbers estimated at saturation (*i.e.* the saturation ratio). Three competing models: 1) intercept only, 2) number of nesting pairs per site, and 3) nesting habitat saturation ratio, were ranked using Akaike's Information Criterion corrected for small sample sizes (AIC_c; Anderson & Burnham 2002). This approach was used to assess whether adjusting the observed number of nesting pairs on each site by the extent of characteristic nesting habitat (*i.e.* calculating an ecological density) better explained the relationship between the number of nesting pairs and productivity recorded per pair.

Results

A total of 228 pairs of Mute Swans with nests were detected within the study site boundaries during 2016–2018 (Table 1). The median distance to the closest conspecific nest was 418.1 m ($x \pm \text{s.d.} = 495.1 \pm 388.7$ m, range = 22.6–2959.2 m). The mean number of nests and number of fledged

Table 1. Reproductive parameters during 2016–2018 for Mute Swans nesting on six equal-sized study areas (36 km² each), ordered by increasing latitude in the Lower Peninsula of Michigan, USA.

Study area	2016			2017			2018			Pooled mean			Estimated saturation		
	Pairs	No. fledglings/ pair		Pairs	No. fledglings/ pair		Pairs	No. fledglings/ pair		Pairs	No. fledglings/ pair		Pairs	Saturation ratio	
Juno	21	1.6		20	1.3		10 ^a	1.5		17.0	1.5		17	1.0	
St. Clair	25	0.9		19	1.2		6 ^a	2.4		16.7	1.0		67	0.2	
Pontiac	31	1.0		25	0.9		22	0.4		26.0	0.8		32	0.8	
Wabasis	9	2.6		9	2.1		7	1.0		8.3	2.3		40	0.2	
Tobico	7	2.7		5 ^a	1.8		5	2.6		5.7	2.3		31	0.2	
Clam	–	–		5	0.6		2	1.0		3.5	0.6		6	0.6	
All sites	93	1.4		84	1.2		52	1.1		76.3	1.2		193	–	

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

young per pair in 2016–2018 ranged from 3.5–26.0 nests per site and 0.6–2.3 fledglings per pair (Table 1).

The most parsimonious model in the analysis comparing productivity to nesting pair abundance included a fixed effect for the ratio of observed nesting pairs to estimated saturation ($\hat{\beta} = -0.979$, s.e. = 0.439) and this provided a slightly better fit to the data (linear regression: $F_{1,15} = 4.972$, adjusted $R^2 = 0.199$, $P < 0.05$; Table 2, Fig. 3a) than the next competing model (linear regression: $F_{1,15} = 4.507$, adjusted $R^2 = 0.180$, $P > 0.05$, n.s.; Fig. 3b) which contained a fixed effect for the number of nesting pairs ($\hat{\beta} = -0.039$, s.e. = 0.018) The site with the lowest number of nesting pairs (Clam) also fledged the fewest young (Table 1).

Nesting pairs were not spaced optimally in relation to characteristic nesting habitat (Figs. 4 & 5). Over a quarter of nests on sites where the number of pairs was near estimated saturation occurred in non-characteristic nesting habitat (Clam, 28.6%; Juno, 39.2%; Pontiac, 39.7%; Fig. 4)

whereas pairs almost exclusively nested in characteristic habitat on less saturated sites (11.8% and 8% of nests in non-characteristic cover at Tobico and Wabasis, respectively; Fig. 5). Given the expansive beds of Common Reed at the St. Clair study site, all nests at St. Clair were considered to be in characteristic cover. The number of nesting pairs provided a suitable approximation of pair saturation (*i.e.* saturation ratios) for four of the six sites (Juno, Pontiac, Wabasis and Tobico); however, interpretation of pair saturation changed at two sites (Clam and St. Clair) on using saturation ratios instead of the observed number of nesting pairs (Table 1). St. Clair had a low saturation ratio (Table 1) despite its high number of nesting pairs because of the large amount of characteristic habitat present at the site. Clam had few nesting pairs, but also had a paucity of well-spaced characteristic nesting habitat, resulting in a site that was near saturation even though the observed number of pairs was low (Table 1).

Table 2. Model selection for linear regression of the parameters influencing productivity during 2016–2018, for Mute Swans breeding in Michigan, USA. k = number of parameters in model, AIC_c = Akaike's Information Criterion adjusted for small sample sizes, ΔAIC_c = difference between AIC_c of best fitting and current model, and w_i = Akaike's weight.

Model	β	s.e.	k	AIC_c	ΔAIC_c	w_i
Saturation ratio	-0.979	0.439	2	38.085	0	0.486
Number of pairs	-0.039	0.018	2	38.486	0.401	0.398
Null model	1.506	0.179	1	40.952	2.867	0.116

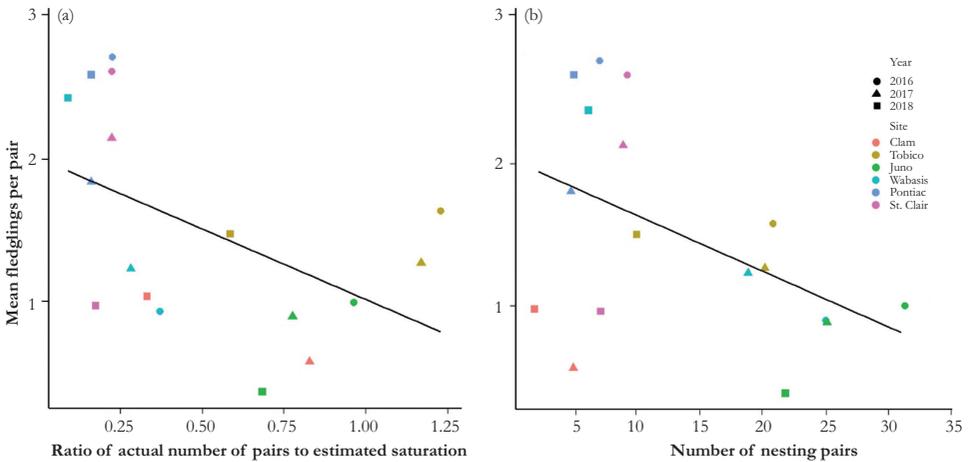


Figure 3. Mute Swan productivity in relation to (a) the estimated nesting pair saturation ratio ($y = -0.979x + 1.997$; adjusted $R^2 = 0.199$), and (b) the number of pairs per site ($y = -0.039x + 2.032$; adjusted $R^2 = 0.180$), recorded during 2016–2018 for six equal-sized study sites in the Lower Peninsula of Michigan, USA.

Discussion

Effects of density dependence in territorial avian species typically first become evident through aspects of the birds' breeding success, such as hatching success (Lebeuf & Giroux 2014), growth of young (Sedinger *et al.* 1998), productivity (Wood *et al.* 2016), 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 & 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 affects 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). The approach used in this study looked for the presence of density dependence, and the mechanism by which this process is acting on nesting Mute Swans within Michigan's Lower Peninsula.

There was evidence for density dependence in breeding productivity for Mute Swans in the study area. Mean productivity declined as the number of breeding pairs approached the estimated saturation level (*i.e.* as the saturation level approached 1; Fig. 3a). The range in observed

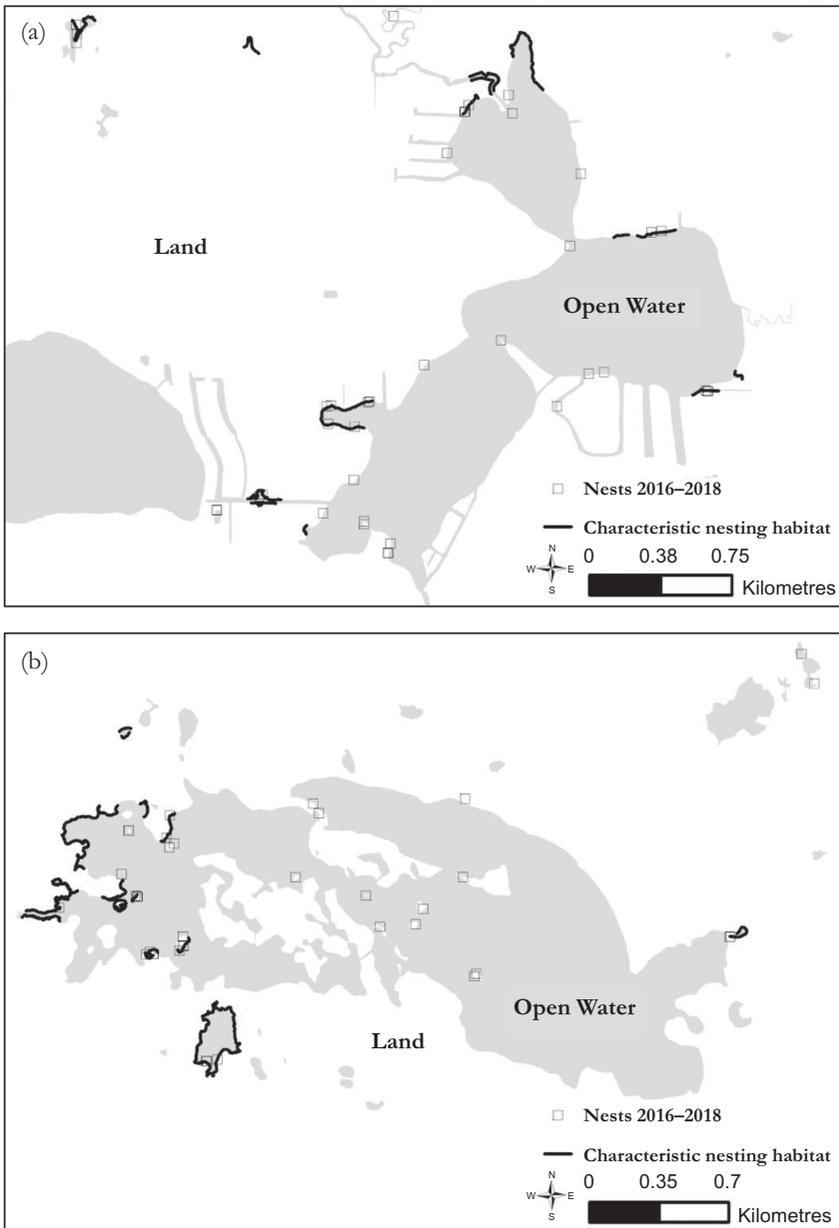


Figure 4. Mute Swan nest locations during 2016–2018 within characteristic and non-characteristic nesting habitat at select waterbodies in (a) the Juno site in Cass County, Michigan, USA, and (b) the Pontiac site in Oakland County, Michigan, USA, where nesting pairs established territories outside of their characteristic nesting habitat and were found to have low productivity.

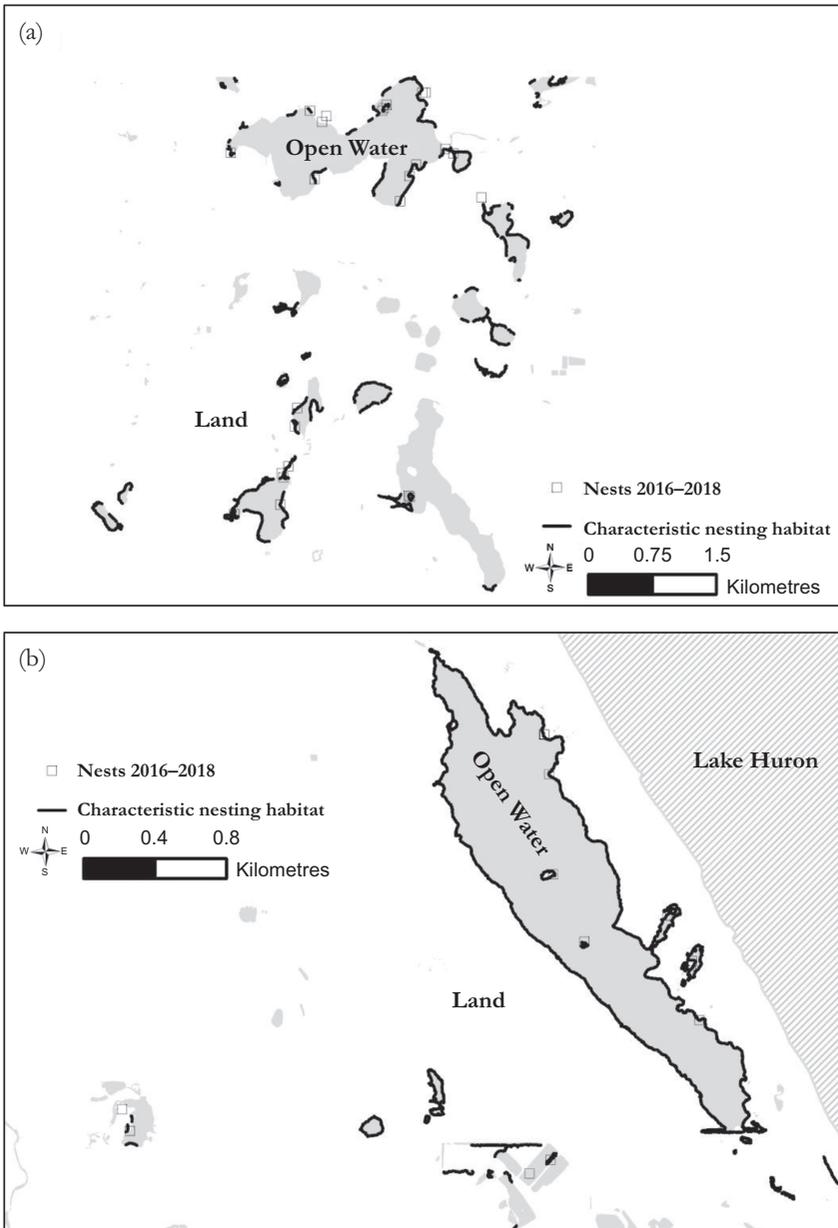


Figure 5. Mute Swan nest locations during 2016–2018 within characteristic and non-characteristic nesting habitat for select waterbodies in (a) the Wabasis site in Kent County, Michigan, USA, and (b) the Tobico site in Bay County, Michigan, USA, where most nesting pairs used territories in characteristic nesting habitat and were found to have higher productivity.

nesting density (0.1–0.7 nesting pairs/km²) was similar to values estimated in early (≤ 0.1 nesting pairs/km²) and late (0.6 nesting pairs/km²) stages of establishment for an introduced Mute Swans population in part of a Finnish archipelago, where the density of nesting pairs during the later years of the study was the highest recorded for a non-colonial population in Europe (Nummi & Saari 2003). Similar extreme nesting densities and low productivity were observed on two inland sites and one Great Lakes coastal site (Table 1) in Michigan's Lower Peninsula; however, the site with the fewest pairs also produced the fewest young. This site (Clam) was near saturation of characteristic nesting habitat despite the low number of nesting pairs (Table 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 also was not close to our estimate of its nesting habitat saturation level (Table 1). This may be due to its uniqueness among the study sites (*i.e.* as an open water site located in the largest freshwater delta in North America with extensive Common Reed beds), which could potentially have other extrinsic factors limiting cygnet survival not encountered at the inland sites nor captured in this analysis (*e.g.* storm surges or cooler water temperatures). Additionally, the estimated saturation level using these methods may be biased high if other factors become limiting before nesting habitats become saturated. The estimated saturation density for nesting at St. Clair was 1.86 pairs per km² (Table 1), which is 3 times higher than any reported Mute Swan pair density outside of colonial populations (Nummi & Saari 2003). St. Clair

therefore was considered a high-density site on the basis that its observed density of nesting pairs is near the maximum density reported in the literature (Nummi & Saari 2003). Further, nesting pair density was reduced on the St. Clair site under permit by the Wildlife Services section of USDA APHIS to reduce human-wildlife conflict during the final year of investigation. Nesting pairs that remained fledged more cygnets per pair and utilised larger areas during brood-rearing than in previous years (Knapik 2019). This suggests that density impacts were realised at observed nesting pair density in previous years even though it was below the estimated saturation level. Optimisation methods used to estimate saturation of characteristic nesting habitat aligned well with the observed number of nesting pairs and productivity at the other sites (5 of 6 total sites; Table 1).

The spatial comparison of the number of nesting pairs to characteristic nesting habitat provided insights into the mechanism by which density is influencing breeding productivity, with the results generally supporting the HHH hypothesis (Andrewartha & Birch 1954; Kadmon 1993; Rodenhouse *et al.* 1997). Pairs almost exclusively nested in characteristic nesting habitat on sites with few nesting pairs and unfilled characteristic nesting habitat remained (*e.g.* at Wabasis, Tobico and Clam; Fig. 5) whereas pairs filled characteristic nesting habitat and nested, presumably, in suboptimal areas on sites at or near estimated saturation (*e.g.* at Juno, St. Clair and Pontiac; Table 1, Fig. 4). Additionally, mean brood survival was lower (0.58 ± 0.03 ; Knapik 2019) in Michigan when compared

to other introduced populations (Conover & Kania 1999), despite a normal mean brood size at fledging for pairs that fledged young (3.1 cygnets/pair; Knapik 2019). This means that pairs which fledged young successfully did so with brood sizes comparable to other areas of their introduced range (Conover & Kania 1999), although the overall mean breeding productivity across sites (1.4 cygnets/pair; Table 1) was lower than for introduced populations in low-density nesting areas elsewhere (Reese 1975; Conover & Kania 1999; Nummi & Saari 2003). These findings lend further weight to the HHH, which expects an increased variance in mean brood size produced per pair (Andrewartha & Birch 1954; Rodenhouse *et al.* 1997) rather than a uniform reduction in the number of fledged young across all pairs (Lack 1966). Of note, it cannot be claimed that agonistic interactions (*i.e.* IH) had no effect on productivity because both HHH and IH can occur simultaneously (Ferrer & Donazar 1996; Krüger *et al.* 2012); however, observed patterns provided more support for HHH rather than for IH among the Mute Swans in Michigan.

Not all factors that potentially influence productivity could be controlled for the analyses. The effects of individual and territory quality could not be separated in this short-term study because not all nesting individuals within sites were uniquely marked; however, there were 10 instances at sites with the highest densities of nesting pairs where territories and even the nest mounds of neck-collared swans breeding in characteristic nesting habitat were taken over by new pairs in the year following the dissociation of a nesting pair (*i.e.* through

the death of a mate; R. Knapik, unpubl. data). The surviving members of these pairs joined the nonbreeding flocks and did not nest again for the remainder of the study (R. Knapik, unpubl. data), signalling high competition for territories in characteristic habitat. Therefore, it could not be assumed that unmarked individuals observed on territories were constant among years. The presence or abundance of nonbreeding flocks could also have influenced productivity through agonistic interactions or competition for food resources, although breeding pairs successfully excluded nonbreeding flocks from areas around their territories especially after hatching of cygnets (R. Knapik, pers. obs.). Birkhead *et al.* (1983) demonstrated that inexperienced pairs had slightly lower breeding productivity than experienced pairs, but with inexperienced pairs still producing 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.

The evidence provided here for habitat-mediated density dependence in the breeding productivity of an introduced North American Mute Swan population is similar to findings reported for an introduced population in a Finnish archipelago (Nummi & Saari 2003). Further, this research demonstrated that the strength of density dependence in breeding productivity varied spatially within Michigan, influenced by the number of nesting pairs and coverage of characteristic nesting habitat. This research continues to suggest that density-mediated breeding productivity

can occur and should be considered when developing demographic models for Mute Swans in North America or when designing in-field management guidelines.

Targeted removal of breeding pairs should focus on areas where this activity is likely to be most effective. These are the lakes and wetlands where the number of breeding pairs is low but characteristic nesting habitat (*i.e.* cattails, Common Reed, or bulrushes next to shallow open water) is abundant. Our results indicated that pairs in these habitats were the most productive and, although we recognise that targeting low density areas increases the costs needed to remove each swan in the short term, ultimately the long-term management costs should be lower because fewer total swans would need to be removed (Ellis & Elphick 2007). Post-removal surveillance of these areas should be undertaken to ensure that pairs do not return, since swans coming into the area will likely have high breeding productivity while nesting pair density is low and nesting habitat is abundant (Table 1; Nummi & Saari 2003).

Our evidence for habitat-mediated density dependence in breeding productivity also has implications for lethal management options targeted during the incubation stage, such as egg oiling. Oiling Mute Swan eggs during incubation is a highly effective method for preventing hatching (Hindman *et al.* 2014), but it is not effective at reducing the overall population in the short term (Ellis & Elphick 2007; Watola *et al.* 2003; Wood *et al.* 2013; Hindman *et al.* 2014; Knapik 2019). Nevertheless, it is a method that can have a local impact, reduce the numbers of cygnets each summer (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 focus on lakes and wetlands with few pairs or on pairs that have a 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 habitat (Fig. 4) will be inefficient because many pairs would not have fledged young anyway. We suggest that management aimed at achieving long-term population goals in Michigan, or in other introduced populations, take into consideration patterns of habitat-mediated density dependence on Mute Swan breeding productivity.

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Photograph: Adult Mute Swan with cygnet in Michigan, USA, by Randall Knapik.