

BULLETIN
OF THE
TEXAS ORNITHOLOGICAL SOCIETY

Vol. 54 No. 1-2 December 2021



ECOLOGY, BEHAVIOR, AND REPRODUCTION OF INTRODUCED MUTE SWANS (*CYGNUS OLOR*) IN TEXAS

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ABSTRACT.—Natural history of the Mute Swan (*Cygnus olor*) in Texas is lacking. A citizen-science invasive bird project was developed to collect observational data on the ecology, behavior, and reproduction of the Mute Swan in Texas. The highest frequency of Mute Swan sightings occurred in San Antonio, Austin, Dallas-Fort Worth metroplex, Tyler metropolitan area, and Houston. The most frequently reported habitat was freshwater lakes, wetlands and other water bodies, with most swans found in water. Swimming and foraging were the most common behaviors. Swans were sympatric with other aquatic bird species in nearly one-fourth of all observations. Mean flock size was 3.0 (mode = 1-2, range = 1-15). Some swans were permanent residents while others displayed short, seasonal movements. Swans commonly re-nested in previous locations, and cygnets hatched between early May - June. Very limited information is also provided on the Black Swan (*C. atratus*) in Texas. We compare and contrast our finding with other studies of Mute Swans, both in their native and invasive ranges, and also discuss whether they are currently an environmental threat in Texas.

INTRODUCTION

Invasive species pose potential threats to native ecosystems, and an understanding of their natural and life histories is needed for effective conservation (Blackburn et al. 2014). Given the potentially volatile nature of the effects of invasive species, such populations should be managed properly, and this requires working knowledge of the life history and ecological niche of introduced species (Clout and Williams 2013).

The Mute Swan (*Cygnus olor*) is native to Eurasia, ranging from the British Isles to Inner Mongolia (Cramp and Simmons 1977), with considerable expansion since the early twentieth century (Gayet et al. 2020). It is an invasive species to North America from multiple introductions, inhabiting coastal ponds, slow-moving rivers (Kear 2005), and an increasing number of artificial waterbodies in residential areas (Gayet et al. 2020).

There are a variety of factors responsible for the successful invasion of Mute Swans. With the ability to upend in deeper water than other waterfowl (O'Brien and Askins 1985), the Mute Swan has a distinct foraging advantage over many native species. Overgrazing (Cobb and Harlan 1980) and subsequent abandonment of foraging sites

by native species (Allin et al. 1987) have become concerns. Furthermore, the Mute Swan is known to graze agricultural lands (Sears 1989) and is thus a potential nuisance to farming activity. Due to its potential effects on recreational and natural landscapes, further study on the behavior and environmental impacts of the Mute Swan is required. For populations in Texas, much of this information is still unexplored. Herein we document natural and life history aspects of the Mute Swan in Texas, specifically the ecology, behavior, and reproduction of this species.

METHODS

A questionnaire was designed to gather data on Mute Swans. The questionnaire was posted on the website of the Houston Museum of Natural Science (hmns.org/files/invasivebirds.doc) and internet list-servs, and was also distributed to local birdwatching clubs and annual birdwatching festivals. The questions were straightforward, requiring only minimal knowledge on Mute Swans to answer them. The front page of the questionnaire also included images of the invasive species to aid in identification.

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Mute Swans at Barton Creek. Photo Vincent O'Brien

The collected email responses to the questionnaire varied in detail. Some responses were complete, while others had many questions unanswered. Responses with multiple missing components were considered incomplete and were not included in the analyses. Photographs documenting the specimen and surroundings of the sighting were often attached along with the returned questionnaires. To ensure accuracy, responses were reviewed by checking photographs and ground-truthing certain sites before they were entered into a database.

In addition to the responses for the questionnaire, publicly available data sets from eBird (i.e., Texas sightings, 1988-2020) were also included for the distribution analysis of this study. Data that were not complete with locality or known to have non-flighted swans (pinioned, tendon- or wing-clipped) were discarded. For multiple sightings at the same location, only the earliest sighting was included.

Data for White Rock Lake (Dallas) were excluded from mean flock size computation

because the number of swans was a strong outlier in the normalized distribution of the data points.

RESULTS

Distribution

Breeding Mute Swans, initially established for ornamental purposes, were first recorded in the United States along the lower Hudson River in 1910 (Baldassarre 2014). Mute Swans were later imported for recreational activities, zoos, and as a potential deterrent towards Canada Geese, with the population in Texas likely being established by swan escapes or releases after such introductions.

Mute Swans were observed in 736 unique locations in Texas (Fig. 1). Distribution was clustered around Austin ($n = 239$), Houston ($n = 142$), Dallas-Fort Worth metroplex ($n = 105$), San Antonio ($n = 61$), and Tyler metropolitan area ($n = 25$). Approximately one-half of all sightings at unique locations before 2000 were reported in Austin ($n = 8$). Although the exact source of introduction

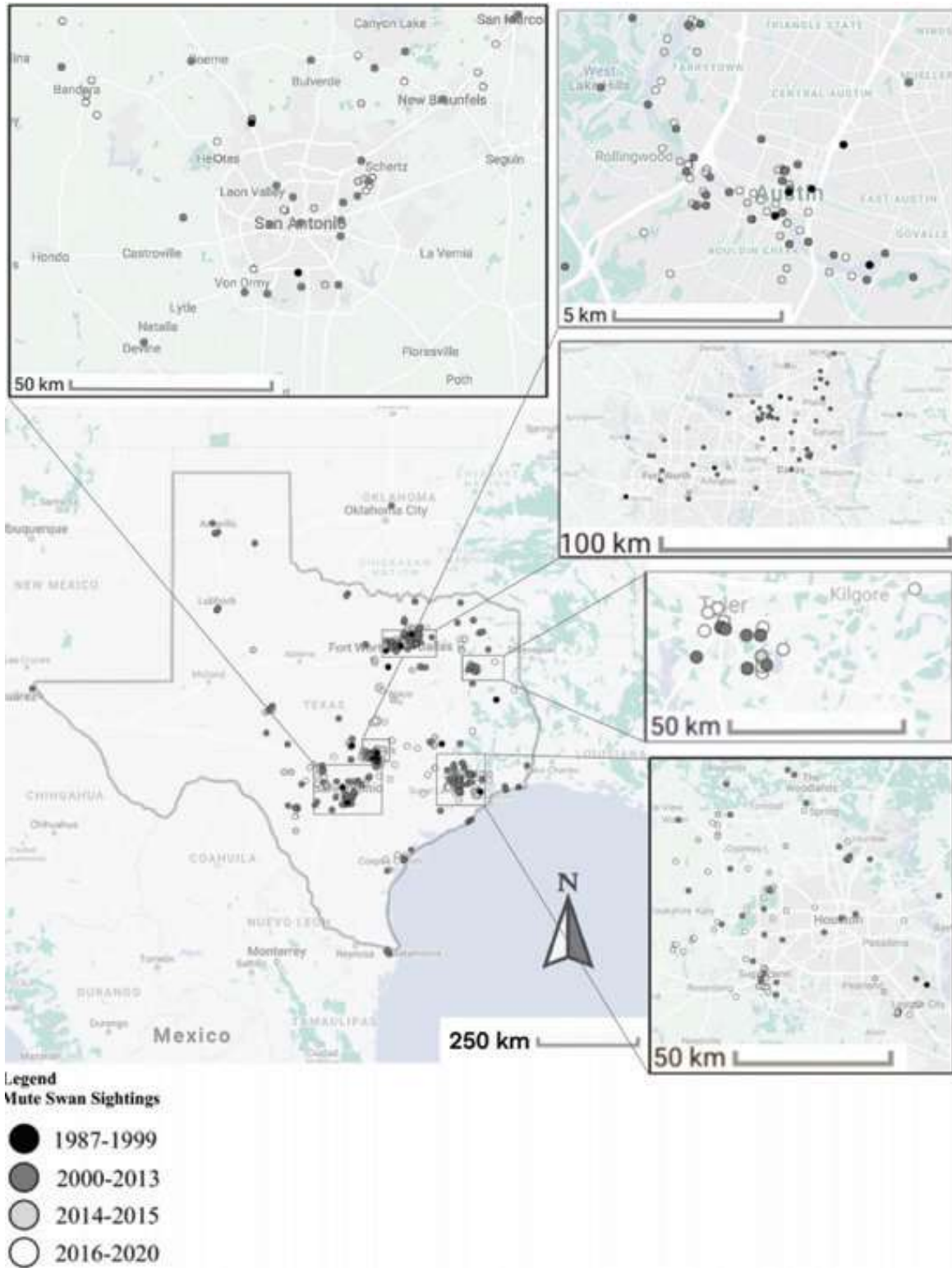


Figure 1. Distribution of Mute Swans in Texas.

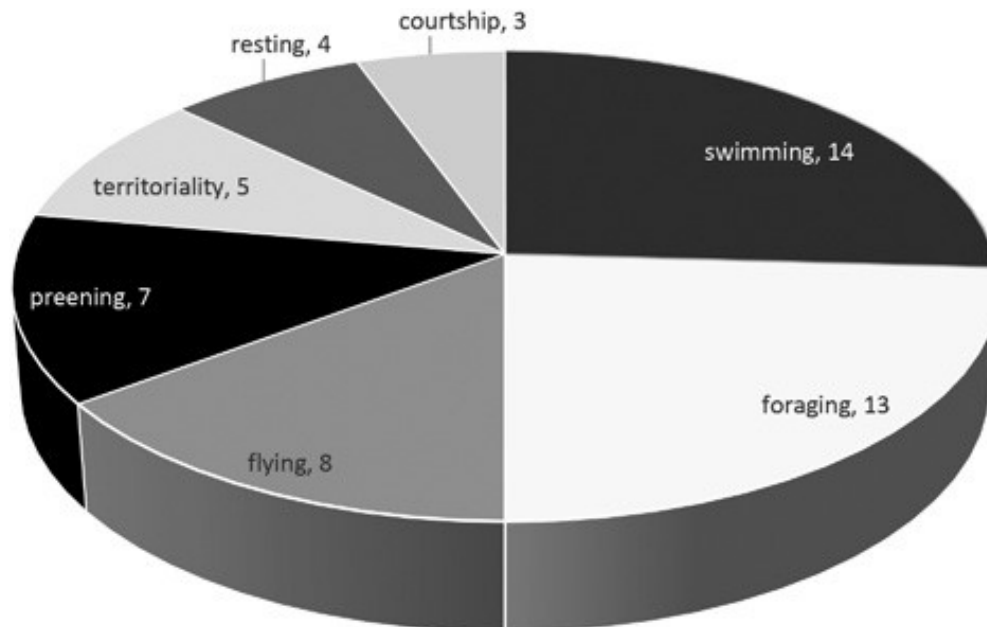


Figure 2. The most common behaviors of Mute Swans in Texas. Numbers represent # of records of each respective behavior.

remains unknown, it was likely around Austin, where the highest frequency of sightings occurred before (and after) 2000. Several recent sightings after 2013 were reported west of all five distribution clusters, suggesting that Mute Swans are expanding in the state. For example, approximately 50% and 72% of all reported sightings in San Angelo and Kerrville, respectively, occurred after 2015.

Habitat

All habitats were comprised of large freshwater bodies of water ($n = 30$), these were primarily freshwater lakes and wetlands (80%, $n = 24$), or similar habitats, including ($n = 1$ each): water treatment plants, bayou oxbows, flooded gravel pits, flooded pastures, reservoirs, and canals connecting two lakes. Water bodies varied from pristine and spring fed, to next to a major construction zone with illegal dumping of trash (e.g., old furniture).

Vegetation ranged from little with vast open water, to areas with punctuated aquatic vegetation, including reed beds ($n = 5$) containing rushes, grasses, sedges, Cattails (*Typha sp.*; $n = 4$), emergent Seep (*Baccharis salicifolia*) and Button willow (*Cephalanthus occidentalis*; $n = 2$), dead trees ($n = 1$), and islands with Sycamore (*Platanus occidentalis*) and Willow (*Salix sp.*) trees ($n = 2$). Water bodies were surrounded by irrigated

farmland, park, grassland, brushland, or woodland. Swans were most often recorded in the water (79%) as opposed to on land (6%), with 15% of the cases on both land and water during the observation.

Behavior

Swan behaviors (Fig. 2; from most to least frequently recorded) included: swimming (26%), foraging (24%), flying (15%), preening (13%), territoriality (9%), resting (7%), and courtship (6%).

Very little information was recorded regarding diet. Swans ate algae ($n = 1$), fed on vegetation at the bottom of a lake ($n = 1$), and ate bread and grain products when offered supplemental food by humans in 17% of reports.

Interspecific interactions

Swans were sympatric with other aquatic bird species in nearly one-fourth (23%, $n = 11$) of all observations, including White Pelicans (*Pelecanus erythrorhynchos*), several species of cormorants, herons, egrets and ibis, seven species of wild ducks, several breeds of introduced and domestic ducks, American Coots (*Fulica americana*), and Forster's Terns (*Sterna forsteri*). However, in most cases these species were not necessarily in close association with the swans. Swans did coexist with Black-

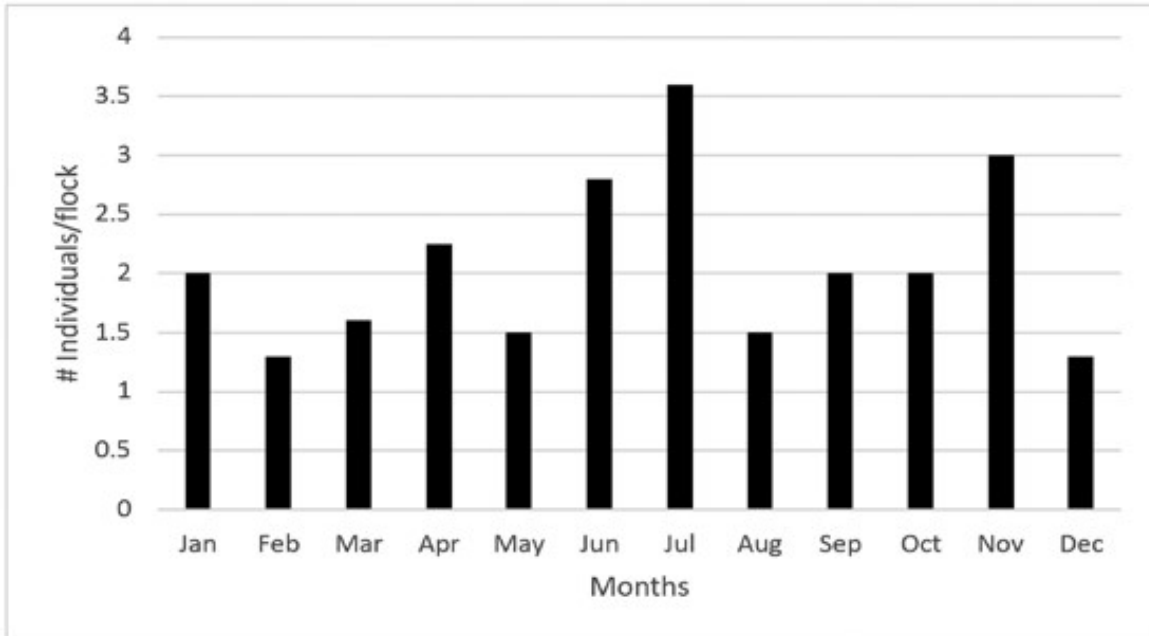


Figure 3. Mean flock size of Mute Swans in Texas per month.

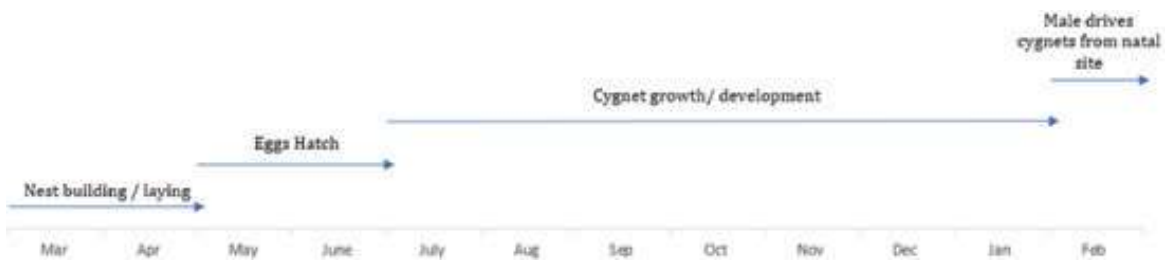


Figure 4. Annual reproductive cycle of Mute Swans in Texas.

bellied Whistling Ducks (*Dendrocygna autumnalis*; $n = 4$) and invasive Egyptian Geese (*Alopochen aegyptiaca*; $n = 2$), but would become aggressive towards whistling ducks and large catfish when food was being provided by humans ($n = 1$).

Flock dynamics

Overall mean flock size was 3.0 (mode = 1-2, range = 1-15, $n = 43$). Much larger populations were found at White Rock Lake (Dallas), with 30-40 birds typically present, and a peak Christmas Bird Count (CBC) in December of 61 birds. The highest flock sizes occurred during summer (June-July) reflecting the addition of offspring, and the lowest occurred during the winter (December, February; Fig. 3).

Seasonality and movements

Some populations of swans display short, seasonal migrations, and others (primarily solitary individuals) were permanent residents, as swans were observed throughout the calendar year (Fig. 3). Local seasonal migration was apparent because certain populations in the same region were present only at a certain site October - February, and present at two other sites February/March–October. Swans left at least one site during a drought in 2011 that rendered their pond uninhabitable.

Reproduction and life cycle

Courtship of bonded male-female pairs involves head-bobbing and intertwined necks ($n = 1$). Nest building takes place from early March–April ($n = 4$; Fig. 4). Parents attempt to re-nest annually

in the same vicinity, as long as the nesting area is not flooded (n = 3). For example, a 2013 nest was built 27 m from the 2012 nest because the old nesting ground was flooded. At the same site in 2016, the first nest built in March was flooded, so the second nest was built the following month 30 m from the first attempted site. The nest is 2.5 m in diameter, located on shore 3 m from water (n = 3), and is made of long, dead grasses and tall reeds, often built on top of short grass (n = 2).

Clutches of 4-8 eggs (mean = 5.6, n = 3) are typically laid an average of 1.5 days apart, with incubation commencing upon completion of the clutch (n = 1), by both parents (n = 2), from March-April (n = 7; Fig. 4). Non-developing eggs are rolled out of the nest by the parents (n = 1).

The number of cygnets hatching ranges 1-8 (mode = 2-3, mean = 3.4, n = 7) between early May (n = 5)-June (n = 5; Fig. 4). Newly hatched cygnets remain in the nest up to three days, whereupon the parents take them to the water to drink, returning to the nest nightly to sleep for the first week of life (n = 1).

Males with nests/cygnets are aggressive to intruders (n = 2). For example, when people approach the bank with a nest/cygnets, the male swims over quickly and leaps onto the bank, vocalizing and wing-flapping (n = 3), while the female stays in the water feeding with the cygnets (n = 1). Although cygnets are full-sized beginning in July (n = 1), they remain grey in color until post-winter molt to white plumage (n = 4).

Survivorship data was provided for 2012-17 at Converse North Park. Cygnet survivorship was 100% during 2012-14, and in 2017 a single cygnet disappeared at three weeks of age, probably due to predation. Although eight cygnets hatched in 2013, five had injuries due to fishing hooks/line. None hatched despite three attempts during 2015-16 due to heavy rains (see above); adults aborted attempts and abandoned the inundated nest after 3 weeks.

Males drive offspring from the natal site in February (n = 3; Fig. 4) to prepare for the breeding season, as a territory of ~1.25 Ac. (0.50 Ha) is required for a breeding pair (n = 1). The young typically range within 1.5 km of their natal pond when dispersing, and individuals flying further often return to the natal area ultimately (n = 1).

Mortality is due to vehicular collision (n = 2 adults), utility line electrocution (1 adult), coyote

(1 adult female incubating eggs), and unknown predators (3 cygnets, 1/night serially). Raccoons (*Procyon lotor*) predated 1-2 eggs from nests (n = 1). One adult flew to a new residential pond, where a dog (*Canis familiaris*) attacked it and broke its wing (n = 1).

Black Swans (*Cygnus atratus*)

Black Swans were reported at three locations: 15 May 2010 in Bacliff (north of highway 646), 17 and 24 March 2005 in Beaumont (Highway 69 @ Washington), and 12 October 2017 in La Vernia. In all three cases they were also associated with freshwater bodies (e.g., lake or drainage ponds with numerous canals), were swimming (n = 2) or flying over (n = 2, probably the same individual in Beaumont), and were in groups ranging 1-3. Reports from eBird appear to be captive birds without flying ability, rather than the feral situations mentioned above.

DISCUSSION

Comparisons with Mute Swans in their native range.

Throughout their native range in north and central Eurasia (Cramp and Simmons 1977), Mute Swans are described as having high ecological plasticity (Fouque et al. 2007) due to their lax habitat, breeding, and dietary requirements. In their native range Mute Swans occupy a wide variety of wetland habitats, frequently making use of artificial bodies of water. They have flexible requirements for nesting sites (Gayet et al. 2011), eat a wide range of plant material (Berglund et al. 1963), and supplement their feeding by grazing on agricultural crops and habituating to artificial food (Bailey et al. 2008), sometimes leading to competition among conspecifics (Sears 1989). Although fully wild populations are mainly migratory, particularly in areas with colder winters, regions of their native range with partial migrants or sedentary populations experience higher population growth (Snow and Perrins 1998).

Plasticity in Mute Swans was also observed in this study. In Texas, habitats varied in water quality, vegetation, and level of human development, with only a large body of water being the main requirement. Mute Swans were commonly found coexisting with humans, as 17% of the reports

documented supplemental feeding, with swans even occasionally becoming aggressive towards other species while being fed. Any migration observed was limited to short and local seasonal movements and only seen in some populations.

Within their native range, Mute Swans are also gregarious outside of the breeding season, particularly during fall and winter. However, the smallest flock sizes in the Texas study occurred during the winter, with most winter months averaging ≤ 2 birds/flock. Conversely, the largest flocks in Texas occurred in the summer and reflected the addition of offspring. Similar to their native range, nesting commenced in early March, and territorial behavior during the breeding season was also observed. In some areas of Europe, Mute Swans do not exhibit breeding aggression, believed to be due to their recolonization of previous habitats and occupation of once-vacant niches (Posya and Sorjonen 2000). Similarly, some Mute Swans in the Texas study lacked agonistic behavior when sympatric with other species.

Although there is a potential for overgrazing in locations with high densities of Mute Swans within their native range, flock sizes in Texas averaged three birds and generally did not suggest such ecological impacts.

Comparisons with Mute Swans in their invasive range.

Mute Swans have successfully established populations outside of Europe in Japan, Morocco, South Africa, Australia, and New Zealand (Lever 1987), in addition to North America. In North America, Mute Swans occur most frequently in British Columbia, California, and Michigan (Baldassarre 2014), with significant increases occurring within the Atlantic Flyway (Allin 1993), lower Great Lakes, and Atlantic and Pacific Coasts (Petrie and Francis 2003). Overall, the trends of Mute Swans in Texas are similar to those of other introduced populations, with smaller populations and flock sizes in Texas.

Within much of their invasive range, Mute Swans are non-migratory, prefer to remain on their breeding grounds throughout the year (Snow and Perrins 1998), and tend to form multiple local populations, as they do not disperse widely. This explains the visible population clusters around five locations in Texas (Fig 1), with individual sightings more dispersed outside of these clusters. Invasive

Mute Swans are generally either sedentary or short-distance migrants as dictated by weather severity, and occasionally migrate within their breeding range (Brewer et al. 1991), similar to our findings in Texas.

In North America dominant predators of Mute Swans include raccoons and dogs, both documented in this study. Although predation is a driving cause for population declines in New Zealand (Seabrook-Davidson 2013), the numerous sightings in Texas suggest that predation did not contribute to population decline in this study.

In Japan and Australia, Mute Swan numbers are low and there are no recorded negative impacts (Rees et al. 2019). In those areas and other regions of North America with smaller populations of Mute Swans (e.g., Texas), the potential for overgrazing is also low. Conversely, in Connecticut (Chasko 1986), certain locations within the Chesapeake Bay (Tatu et al. 2006), and some mid-continental American wetlands (Stafford et al. 2012), Mute Swans had significant impacts on plant communities by either reducing plant cover or below-ground biomass. A source for the high magnitude of grazing is high density of birds (Wood et al. 2012), with overgrazing also being more pronounced in smaller ponds (Chasko 1986). Thus, given that Texas Mute Swans occupy larger bodies of water with a low mean flock size, overgrazing is not currently an issue in Texas.

Are invasive Mute Swans a threat to the environment in Texas?

Mute Swans raise many potential and realized environmental and socioeconomic concerns within their invasive range. Ecological concerns include overgrazing and reduction of plant biomass (Stafford et al. 2012), competition with native species (Gyimesi et al. 2011), and their ability to transport avian influenza viruses (EFSA Panel on Animal Health and Welfare 2017). Socioeconomic effects also exist, including but not limited to crop damage (Rowell and Spray 2004) and reduction in the quality of recreational areas from swan feces and territorial attacks (Hindman and Tjaden 2014).

Among these concerns, small flock and population sizes in Texas limit overgrazing potential and fecal contamination, although large flocks of up to 61 individuals have been recorded at White Rock Lake (1.93 mi.²/5 km²) and are a potential source of concern if populations continue to grow.

Aggression to humans remains a potential concern, and agonistic behavior exhibited by male swans towards humans has been documented in Texas, although not frequently and with no serious injury. Mute Swans were also aggressive towards other waterfowl and fish species; however, this was restricted to a single circumstance during supplemental feeding. As such, agonistic and territorial behavior are potential threats in Texas and may increase in frequency should populations expand.

CONCLUSION

Holistically, given their high ecological plasticity, abundance of well-suited habitats, and trends of increased sightings in recent years, Mute Swan numbers will likely continue to grow and thrive in Texas. Moreover, the observed interactions between this species and humans in their invasive range raises questions about the potential for more frequent and aggressive encounters. As such, further study on the expanding ranges and flocks of Mute Swans is warranted, with an emphasis on the increasing numbers in current population clusters. We document the life history of Mute Swans in Texas and compare our observations with studies conducted in both the natural and invasive range of this species. Although few harmful ecological or environmental effects have been observed currently, the potential for greater impacts and exacerbated threats posed by Mute Swans is a cause for concern in Texas and North America.

ACKNOWLEDGMENTS

We are indebted to the many volunteers who took the time to painstakingly report and submit their observations for this project. Special thank goes to Betty Burkett and Maggie Wegner for their detailed observations of reproduction and life cycle at the Lakes on Eldridge in west Houston.

CITATIONS

- ALLIN, C. C. 1993. "Mute Swan mid-summer Mute Swan survey report for the Atlantic flyway". Providence: Rhode Island Dept. Environ. Mgmt., Div. Fish and Wildl.
- ALLIN, C. C., G. G. CHASKO AND T. P. HUSBAND. 1987. "Mute Swans in the Atlantic flyway: A review of the history, population growth, and management needs". *Trans. Northeast. Sect. Wildl. Soc.* 44:32-47.
- BAILEY, M., PETRIE, S.A. AND BADZINSKI, S.S. 2008. "Diet of mute swans in Lower Great Lakes Coastal Marshes". *Journal of Wildlife Management* 72: 726--732.
- BALDASSARRE, G. 2014. *Ducks, Geese and Swans of North America*. Revised and Updated Edition. Vol. I. John Hopkins Univ. Press.
- BERGLUND, B. E., K. CURRY-LINDAHL, H. LUTHER, V. OLSSON, W. RODIIE AND G. SELLERBERG. 1963. "Ecological studies on the Mute Swan (*Cygnus olor*) in southeastern Sweden". *Acta Vert.* 2:167-288.
- BLACKBURN, T. M., F. ESSL, T. EVANS, P. E. HULME, J.M. JESCHKE, I. KÜHN, S. KUMSCHICK, Z. MARKOVÁ, A. MRUGAŁA, W. NENTWIG, J. PERGL, P. PYŠEK, W. RABITSCH, A. RICCIARDI, D. M. RICHARDSON, A. SENDEK, M. VILÀ, J. R. U. WILSON, M. WINTER, P. GENOVESI, AND S. BACHER. 2014. "A Unified Classification of Alien Species Based on the Magnitude of their Environmental Impacts". *PLoS Biology* 12: e1001850.
- BREWER, R. G., A. MCPHEAK, AND R. J. ADAMS JR. 1991. *The Atlas of Breeding Birds of Michigan*. Michigan State Univ. Press.
- CHASKO, G. 1986. "The impact of Mute Swans on waterfowl and waterfowl habitat." *Wildl. Invest.: Waterfowl Res. and Surv.*
- CLOUT, M. N. AND WILLIAMS, P. A. 2013. *Invasive Species Management: A Handbook of Techniques*. Oxford Univ. Press.
- COBB, J. S. AND M. M. HARLAN. 1980. "Mute Swan (*Cygnus olor*) feeding and territoriality affects diversity and density of rooted aquatic vegetation". *American Zoology* 20:882.
- CRAMP, S., AND K. E. L. SIMMONS. 1977. *The Birds of the Western Palearctic*. Volume 1. Ostrich to Ducks. Oxford Univ. Press.
- EBIRD. 2021. eBird: An online database of bird distribution and abundance [web application]. eBird, Cornell Lab of Ornithology, Ithaca, New York. Available: <http://www.ebird.org>.
- EFSA PANEL ON ANIMAL HEALTH AND WELFARE. 2017. "Scientific opinion on avian influenza". *EFSA Journal* 15: 4991.
- FOUQUE, C., GUILLEMAIN, M., BENMERGUI, M., DELACOUR, G., MONDAIN-MONVAL, J.-Y. AND SCHRICKE, V. 2007. "Mute swan (*Cygnus olor*) winter distribution and numerical trends over a 16-year period (1987/1988-2002/2003) in France". *Journal of Ornithology* 148: 477-487.
- GAYET, G., GUILLEMAIN, M., MESLÉARD, F., FRITZ, H., VAUX, V. AND BROYER, J. 2011. "Are Mute Swans (*Cygnus olor*) really limiting fishpond use by waterbirds in the Dombes, eastern France". *Journal of Ornithology*. 152(1): 45-53.
- GAYET, G. G., M. GUILLEMAIN, E. C. REES, K. A. WOOD AND M. W. EICHHOLZ. 2020. Chapter 31: Mute Swan (*Cygnus olor*, Gmelin, 1789). Pp. 232-242 In: *Global trends and impacts of alien invasive birds* (Downs, C.T. and L.A. Hart (Eds.)). CABI, Wallingford, UK.

- GYIMESI, A., DE VRIES, P.P., DE BOER, T. AND NOLET, B.A. 2011. "Reduced tuber banks of fennel pondweed due to summer grazing by waterfowl". *Aquatic Botany* 94: 24-28.
- HINDMAN, L.J. AND TJADEN, R.L. 2014. "Awareness and opinions of Maryland citizens toward Chesapeake Bay Mute Swans *Cygnus olor* and management alternatives". *Wildfowl* 64: 167-185.
- KEAR, J., ed. 2005. *Ducks, Geese and Swans*. Oxford Univ. Press.
- LEVER, C. 1987. *Naturalized birds of the world*. Essex, U.K: Longman Sci. and Tech.
- O'BRIEN, M. AND R. A. ASKINS. 1985. "The effects of Mute Swans on native waterfowl". *Connecticut Warbler* 5:27-31.
- PETRIE, S.A. AND FRANCIS, C.M. 2003. "Rapid increase in the lower Great Lakes population of feral mute swans: a review and a recommendation". *Wildlife Society Bulletin* 31: 407-416.
- POYSA, H. AND SORJONEN. 2000. "Recolonization of breeding waterfowl communities by the whooper swan: vacant niches available". *Ecography* 23: 342-348.
- REES, E.C., CAO, L., CLAUSEN, P., COLEMAN, J., CORNELLY, J., et al. 2019. "Conservation status of the world's swan populations, *Cygnus sp.* and *Coscoroba sp.*: a review of current trends and gaps in knowledge." *Wildfowl*, Special Issue No. 5: 35-72.
- ROWELL, H. AND SPRAY, C. 2004. "Mute swan *Cygnus olor* (Britain and Ireland population) in Britain and Northern Ireland". *Waterbird Review Series*, The Wildfowl and Wetlands Trust/Joint Nature Conservation Committee.
- SEABROOK-DAVISON, M. 2013. Mute swan. In: Miskelly, C.M. (ed.) *New Zealand Birds Online*. Available at: <http://nzbirdsonline.org.nz/species/mute-swan>.
- SEARS, J. 1989. "Feeding activity and body condition of Mute Swans *Cygnus olor* in rural and urban areas of a lowland river system". *Wildfowl* 40: 88-98.
- SNOW, D.W. AND PERRINS, C.M. 1998. *The Birds of Western Palearctic: Concise Edition, Vol. I: Non-Passerines*. Oxford Univ. Press.
- STAFFORD, J.D., EICHHOLZ, M. W. AND PHILLIPS, A.C. 2012. "Impacts of Mute Swans (*Cygnus olor*) on submerged aquatic vegetation in Illinois River Valley Backwaters". *Wetlands* 32: 851-857.
- TATU, K.S., ANDERSON, J.T., HINDMAN, L.J. AND SEIDEL, G. 2006. "Mute swan's impact on submerged aquatic vegetation in Chesapeake Bay". *Journal of Wildlife Management* 71: 1431-1439.
- WOOD, K.A., STILLMAN, R.A., CLARKE, R.T., DAUNT, F. AND O'HARE, M.T. 2012. "Understanding plant community responses to combinations of biotic and abiotic factors in different phases of the plant growth cycle". *PLoS One* 7, e49824.