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Modeling the Egyptian Goose (*Alopochen aegyptiaca*) Invasion; and Future Concerns

Percival Matzinger Marshall
University of Arkansas, Fayetteville

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Modeling the Egyptian Goose (*Alopochen aegyptiaca*) Invasion; and Future Concerns

A thesis submitted in partial fulfillment
of the requirements for the degree of
Master of Science in Biology

by

Percival Matzinger Marshall
Hobart and William Smith Colleges
Bachelor of Science in Biology and Philosophy, 2019

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University of Arkansas

This thesis is approved for recommendation to the Graduate Council.

Caleb P. Roberts, Ph.D.
Thesis Director

Jennifer Mortensen, Ph.D.
Committee Member

J.D. Willson, Ph.D.
Committee Member

ABSTRACT

In an increasingly interconnected world, the ecological and financial cost of invasive species is expected to continue to climb through the movement of exotic biota. Understanding the driving forces behind how a species invades, what environments promote their establishment, and what impacts they are likely to have on the invaded environment are all critical for management. Waterfowl, order Anseriformes, are one such category of invasive species of concern due to their popularity of accidental introduction, ease of movement, and propensity to affect both terrestrial and aquatic ecosystems. The Egyptian Goose (*Alopochen aegyptiaca*) is a native to the African continent that spread and established itself as a damaging invasive species in Europe in the 1700s and is now an incipient invader in North America. Much is unknown about the future of the invasion of the Egyptian Goose in North America. Understanding habitat suitability of the species can help predict areas where the species may invade in the future and highlight regions of immediate management concern. Furthermore, understanding how previous invasive waterfowl have influenced North America and how the Egyptian Goose has interacted both in its established invaded range and its native range, can help predict what could occur with the incipient invasion. The goal of this work is to 1. Establish concerns about the Egyptian Goose invasion through a literature review of the current and historical impacts of invasive waterfowl in North America 2. Model the invasion of the Egyptian Goose.

To establish the concerns about the Egyptian Goose invasion in North America, we performed a systematic literature review. We used the PRISMA 2010 guidelines for performing holistic and quality literature reviews as well as the 'litsearchr' package in R to improve the quality of search terms. Our results show that these species are significant reservoirs of multiple diseases, including *Escherichia coli* (*E. coli*), Avian Paramyxovirus-1 (Newcastle disease), and

avian influenza. Additionally, we found considerable gaps in the literature; particularly, field studies of newer invasive species and direct interactions with native avifauna. We found key gaps where the Egyptian Goose could pose a novel threat to North American ecosystems.

To understand the invasion of the Egyptian Goose, we utilized Species Distribution Modeling techniques through Random Forest Classified modeling in Google Earth Engine. The volume of historical and current distribution data from eBird, as well as the three distinct geographical locations, allowed for a robust test of adaptations of invading species. We found strong evidence to support the niche shift hypothesis for the Egyptian Goose. Suitable climate conditions strongly varied between continents with Africa and North America having similarly median annual temperatures (20.6°C and 20.7°C) while Europe had a significantly lower median annual temperature (11.0°C). Egyptian Geese showed increasing affinity for urban environments with invasion stage doubling from Africa to Europe and tripling from Africa to North America. The strength of the suitability of highly urbanized areas increasing with recency of arrival suggests that urban environments may be acting as foothold habitat for the Egyptian Geese.

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DEDICATION

I would like to dedicate this work to my niblings, Emerson and Quinn Van Raaphorst.

Conservation work is for the future; may yours be filled with the boundless curiosity you have now.

TABLE OF CONTENTS

INTRODUCTION.....	1
LITERATURE CITED.....	4
CHAPTER 1: Impacts of Invasive Waterfowl on North America: A Systematic Literature Review.....	
Review.....	8
ABSTRACT.....	9
INTRODUCTION.....	10
METHODS.....	12
RESULTS.....	13
DISCUSSION.....	16
LITERATURE CITED.....	20
TABLES.....	28
FIGURES.....	32
APENDEX A: Search Terms.....	35
CHAPTER 2: Egyptian Goose (<i>Alopochen aegyptiaca</i>) Invaded Habitat Supplemented by Urban Environments: A Case Study of Three Continents.....	
ABSTRACT.....	41
INTRODUCTION.....	42
METHODS.....	44
RESULTS.....	45
DISCUSSION.....	47
LITERATURE CITED.....	49
TABLES.....	54

FIGURES.....	55
CONCLUSION.....	60
LITERATURE CITED.....	62

INTRODUCTION

Globally, the cost of invasive species has been 1.288 trillion USD over the past fifty years (Zenni et al. 2021), and with more populations being established in an increasingly interconnected world, the cost is only estimated to grow. Anthropogenic activities, such as landscape modification and climate change further exasperate the problem by increasing the potential for non-native species to invade community ecosystems. As community compositions change with the new invasive species, both wildlife and human dynamics are put at risk. Direct competition and consumption by invaders threatens to reduce biodiversity in native communities (Keddy 2001, MacDougall and Turkington 2005, Carniatto et al 2013) which has the potential to have short-term destabilizing impacts. Invasive species have impacted human well-being via crop destruction (Magnall and Crowe 2002), competition with charismatic mega-fauna (Groom et al 2020), and environmental degradation (Vitousek et al 1997). Environmental changes; such as climate change (Abrahms 2021), habitat fragmentation (Amaja et al 2016), and the introduction of non-native wildlife (Baxter and Hart 2010) all have the potential to drive human-wildlife conflict well into the future. Understanding the driving forces behind the conflict opens up the possibility to make changes in how land is managed and lessen the tensions between the conflicting forces.

Waterfowl pose a unique relationship as potential invaders. Avian species are popular imports for food, feathers, and exotic collections (Abellán et al 2016) which increases their movement between nations. As semi-aquatic organisms, they interact with both terrestrial (Thompson et al 2017) and aquatic systems (Tatu et al 2006) allowing the potential for disturbance to be felt in either or both systems (Figuerola et al 2003). Their grazing patterns and dietary preferences often put them in conflict with grain farmers (Halse 1984, Magnall and Crowe 2001, Magnall and Crowe 2002). Some species are also put into conflict with native bird

populations as nest usurpers (Curtis et al 2007, Thompson et al 2017) which can threaten desirable native species. Waterfowl can also transmit disease between wild populations and farm animals (Shihmanter et al 1998, Thompson et al 2008, El-Zoghby et al 2011, Anis et al 2018) which can harm both environments. Conversely, as larger birds, they are prime targets for hunting both for sport (Magnall and Crowe 2001) and food (Geldenhuis et al 2013). This means that there are interests to introduce species for hunting purposes which can lead to escapees (USDA APHIS 2020) and the establishment of wild populations (Li et al 2021). Understanding the scope and modality of the problem with invasive waterfowl can identify which areas of potential concern are supported by data.

One of the leading theories as to why invasive species can gain a foothold into new habitats is the Niche shift hypothesis. The Niche Shift hypothesis, sometimes further differentiated into the Fundamental Niche shift and Realised Niche Shift, posits that due to the process of being introduced to a new range, an invasive species shifts its niche's density of occurrence or expands or retracts the limits of its niche (Bates & Bertelsmeier, 2021). These changes result from both smaller gene pools in the invasive populations and the unique environmental and community conditions that the species find themselves in. Changes can take the form of shifting mating behaviors due to nesting conditions (Matzek 2012), shortened mating seasons (Lensink 1998), new habitat occupancy choices (Rahel and Olden 2008), and migratory changes (Hellmann et al 2008). To test such a hypothesis, it is important to have established the conditions in both the native and invaded ranges.

The Egyptian Goose (*Alopochen aegyptiaca*), a native of the African continent, poses a unique model species to test the Niche Shift Hypothesis. It is currently an invasive species on two separate continents: North America and Europe. The European invasion is estimated to have

begun in the 1700s in England (Lensink 1998); and the North American invasion is estimated to have begun in California in 1967 (Renwick 1968), Florida in 1985 (Pranty and Ponzo 2014) and Arkansas in 2008 (Smith and James 2012). Given that the Egyptian Geese have a firmly established population in Europe, but they are still at the incipient invasion stage in North America, we have the opportunity to observe differences at different invasion stages.

Here, we sought to understand the incipient Egyptian Goose invasion in North America. Our goal was to understand the risks posed through a systematic literature review on invasive waterfowl as a whole and modeling current and suitable habitat based on the three ranges the birds are existing in. The objectives of my study were to 1) identify the impacts of invasive waterfowl on agroecosystems and wildlife in North America 2) identify knowledge gaps on the impact of invasive waterfowl in North America 3) Characterize how and to what degree Egyptian Geese distribution patterns differ between their native continent (Africa), an established invasion in Europe, and an incipient invasion in North America and 4) Predict likely invasion locations for the Egyptian Goose in North America. Chapter 1 of my thesis addresses the first two objectives and Chapter 2 addresses the second two. Both chapters are intended on being formatted with the intent to publish with Dr. Caleb Roberts, Dr. Jennifer Mortensen, and Dr. J.D. Willson.

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CHAPTER I

Impacts of Invasive Waterfowl on North America: A Systematic Literature Review

Percival Matzinger Marshall, Caleb P. Roberts, Jennifer Mortensen, and J.D Wilson

ABSTRACT

In an increasingly interconnected world, the ecological and financial cost of invasive species is expected to continue to climb due to the movement of exotic biota. In order to respond to the presence of invasive species, it is critical to understand what impacts they are likely to pose to a given area. Waterfowl are one such category of invasive species of concern due to their frequency of accidental introduction, ease of movement, and propensity to affect both terrestrial and aquatic ecosystems. Studies have been undertaken to understand the effects different invasive waterfowl species have had across North America, but the scope of current knowledge is uncertain due to lack of synthesis. Here we undertook a systematic literature review to understand the ecological impacts of invasive waterfowl in North America, while assessing the scope, distribution, and scale of studies on invasive waterfowl. Our results show that these species are significant reservoirs of multiple diseases, including *Escherichia coli* (*E. coli*), Avian Paramyxovirus-1 (Newcastle disease), and avian influenza. Additionally, we found considerable gaps in the literature. In particular, field studies of more recent invaders and their direct interactions with native avifauna are lacking. As current land-management choices are likely to continue to drive invasive waterfowl into urban spaces, so will the need for consideration of wildlife management options.

INTRODUCTION

Globally, the economic cost of invasive species has been 1.288 trillion USD over the past fifty years (Zenni et al. 2021). With more populations of invasive species being established in an increasingly interconnected world, the economic cost is only expected to grow. In North America alone, the current estimated annual cost of managing invasive species is 26 billion USD (Crystal-Ornelas et al. 2021) resulting from the varied negative impacts on human and non-human systems. These impacts range from direct infrastructure destruction, environmental degradation, restoration costs, and removal costs. Indirect competition with invaders, and depredation by invaders threatens to reduce biodiversity in native communities (Keddy 2001, MacDougall and Turkington 2005, Carniatto et al 2013) which can have short-term destabilizing impacts (Kelly et al 2013). Environmental changes, such as climate change (Abrahms 2021), habitat fragmentation (Amaja et al 2016), and the introduction of non-native wildlife (Baxter and Hart 2010) all have the potential to drive human-wildlife conflict well into the future. Understanding the forces driving conflict can inform management decisions.

As semi-aquatic and highly mobile organisms, both native and exotic invasive waterfowl, order Anseriformes, pose a unique suite of threats to socio-ecological systems due to their high reproductive rates, diet flexibility, and mobility (Blackburn et al 2009). Invasive waterfowl can transmit disease to humans, poultry, and native waterfowl populations (Shihmanter et al 1998, Thompson et al 2008, El-Zoghby et al 2011, Anis et al 2018). Invasive waterfowl can also negatively impact food security: for example, in Africa, where Egyptian Geese (*Alopochen aegyptiaca*) have spread beyond their ranges, can reduce grain harvests by around 67% (Halse 1984, Magnall and Crowe 2001, Magnall and Crowe 2002). Because they interact with both terrestrial (Thompson et al 2017) and aquatic systems (Tatu et al 2006), invasive waterfowl

impacts have the potential to be felt in either or both systems (Figuerola et al 2003).

Furthermore, impacts are not limited to non-native invasive species. Some native species also exhibit invasive tactics: Canada Geese (*Branta canadensis*) facilitate the spread of invasive plant species as their numbers explode across North America (Best 2007). Some invasive population can reduce native bird populations through competition for nesting locations (Curtis et al 2007, Thompson et al 2017).

Furthermore, avian species are popular imports for food (Geldenhuys et al 2013), feathers, hunting (Magnall and Crowe 2001, Geldenhuys et al 2013), and exotic collections (Abellán et al 2016) which increases their movement between nations, heightening the risk of novel invasions (USDA APHIS 2020, Li et al 2021). In North America, there are at least four designated invasive waterfowl species with established and expanding breeding populations outside their native range: Egyptian Goose (*Alopochen aegyptiaca*), Mute Swan (*Cygnus olor*), Muscovy Duck (*Cairina moschata*) and Canada Goose (*Branta canadensis*). Canada Geese are considered native invaders as their population levels have far exceeded historical level resulting in areas of complete population dominance (Simberloff et al 2011, Carey et al 2012). Studies over the previous 50 years have tried to understand the effects of these invasive waterfowl species have had across North America. This current scope of knowledge has been useful for practitioners in species-specific management scenarios. However, what the scope of current knowledge lacks is a synthesis of the current extent of impacts that could allow us to better predict risks of future invasions. Here, we conduct a systematic literature review on the ecological impacts of invasive waterfowl in North America, with a consideration on the scope, distribution, and scale of studies on invasive waterfowl. Specifically, our objectives are to 1)

identify the impacts of invasive waterfowl on agroecosystems and wildlife in North America, and 2) identify knowledge gaps on the impact of invasive waterfowl in North America.

METHODS

To perform a systematic review of the literature, we used the checklist outlined in PRISMA 2010's guidelines (Moher et al 2010) for performing holistic and quality literature reviews. Briefly, this includes specified practices and inclusions for each portion of the review as well as data availability for replication. This process involved: initial searches for computer assisted search term generation, secondary search with the generated search terms, and two stages of filtration.

We chose to use the Web of Science database for the initial and subsequent literature searches due to the character limit for search terms on other databases. The purpose of the initial search is to identify papers with useful terminology that allows for a more nuanced search in future steps. The selection of keywords can add additional biases into a literature review. Our initial keywords included: "waterfowl," "waterbird," "water bird," "game-bird," "impact," "effect," "harm," "benefit," "detriment," "nuisance," "affect," "influence," "competition," "exclusion," "alter," "aid," "control," "North America*," "United States," "America," "Canada," "Mexico," "invasive," "non-native," "alien," "pest," "introduced," "non-indigenous," "exotic," and "non-endemic." Results from the initial search were exported into RIS files for processing. The Exploratory search yielded 4387 papers for finding search-term matrices for use in the search term selection.

We refined the search terms using the 'litsearchr' package (Grames et al 2020) in R Statistical Software (R core team version 4.1.1, 2021). Litsearchr analyzes papers identified as potentially helpful based on initial searches. This dataset allows litsearchr to quickly scan for

common multi-word phrases that were aggregated with co-occurring tagged keywords. This gives a new list of search terms that is more likely to yield papers that are in line with the topic of the literature search (Grames et al 2019). We used both co-occurring keywords in the paper text with the minimum length of two words found in a minimum of ten of the sampled papers; and the list of tagged two-word keywords by the authors that occurred in a minimum of five papers. We exported the resulting list of 899 potential keywords for manual review and hand-sorting into categories based on perceived type: species, impact, location, etc. We then fed these categories back into the ‘litsearchr’ package to generate a new search term list with appropriate Boolean connectors. (See Appendix A for full search term list).

We used the newly generated list of search terms in Web of Science to generate the initial list of papers for our review. This resulted in 465 papers identified (March 2, 2022). We then applied our filtration processes. Papers had to take place in North America and either be written in or translated into English. Furthermore, the studies needed to discuss at least one impact of invasive or introduced species of waterfowl. The final count of papers that met all inclusion criteria was 45.

RESULTS

The 45 papers resulting from our systematic review (Table 2) contained research that was conducted between 1966–2021, with work ranging in duration from 1 to 39 years/seasons (median = 3, mean = 7.76). Topically, 19 studies focused on disease in invasive species/spread potential and 25 studies centered on ecological impacts (Figure 1.1A). Geographically, study locations were strongly skewed, with 30 studies conducted in the United States, 19 in Canada, and 3 in Mexico (Figure 1.1B).

A. Disease

Our systematic review revealed invasive aquatic avifauna in North America are significant reservoirs of multiple diseases, including *Escherichia coli* (*E. coli*), Avian Paramyxovirus-1 (Newcastle disease), and avian influenza (Figure 2.1). Several studies reported focusing on Canada Geese for avian influenza due to their high abundance and proximity to other avian populations. Eight of the nine studies (88.9%) on Canada Geese found no evidence to support that species as an important vector for avian influenza due to a combined total of 18 positive cases in over 12,000 cloacal, blood, and fecal samples (Deliberto et al 2009, Reeves et al 2013, Pederson et al 2009, Harris et al 2010, Belser et al 2013, Kistler et al 2015, Stallknecht et al 2020, Diskin et al 2020; Table 2). The one paper with conflicting results (Kistler et al. 2012) found a 15% antibody detection rate in 3205 cloacal swabs, across 9 US states (Georgia, Massachusetts, Minnesota, Mississippi, New Jersey, North Carolina, Pennsylvania, Washington, and West Virginia) with even higher rates in urban geese compared to rural geese. This work concluded that Canada Geese had a very high encounter rate with the virus but shed it quickly. For Mute Swans (*Cygnus olor*), all five studies demonstrated that this species is not a vector of avian influenza (Diskin et al 2020, Pedersen et al 2013, Stallknecht et al 2020, Pederson et al 2009, Deliberto et al 2009). Muscovy Duck (*Cairina moschata*) was the species most likely to be a vector of avian influenza. All three lab studies focusing on interactions between Muscovy Ducks and poultry found that the ducks were highly susceptible to avian influenza (Li et al 2018, Deliberto et al 2009), develop symptoms quickly, and rapidly spread the disease to other poultry species (Berhane et al 2016).

Bacterial and viral shed into water systems was supported by other studies of Canada Geese and Mute Swans. Fallacara et al. (2004) found that in Mute Swan fecal samples, 246 were positive for *E. coli* (72%), 146 were positive for *C. jejuni* (43%), and 8 were positive for *S.*

typhimurium (2%). They also found that all eight *S. typhimurium* samples were resistant to multiple antibiotics, including penicillin G, lincomycin, vancomycin, oxytetracycline, erythromycin, bacitracin, and cefepime. Nagamori et al (2022) found lower rates of *E. coli* shed (18%; 36 of 204 fecal samples) and half of the tested samples were antibiotic resistant. Tsung-Ta et al (2016) found a 20.8% positive rate in 77 fecal samples and a 7% positive rate in 71 water samples for Shiga Toxins; which are produced by *E. coli*. Navarro-González et al (2020) found that Canada Geese had standard Shiga Toxin positivity rates (12.5%; 2 of 16 samples) to their other sampled species (1369 total samples). Verma et al (2016) found 12 positive samples of toxoplasmosis in 169 (7.1%) sampled geese; including two novel strains. Pedersen et al (2013) found that Mute Swans are a highly important reservoir host for Newcastle Disease but not a strong host of Salmonella. In their 858 lethal blood samples, they found an active infection rate 8.7% with a 59.9% seropositive rate for Newcastle disease. Of the 459 samples they tested for Salmonella, they yielded 3 positive results. Psittacine beak and feather disease was found in Mute Swan chicks in Mexico indicating a possible new introduction point (Sánchez-Godoy et al 2010).

B. Ecology

As in the disease-related studies, Canada Geese received the most attention regarding ecological impacts. We found little evidence overall in the literature of direct impacts of invasive waterfowl on native avian species populations. The exceptions were four papers that correlated Mute Swan population expansion with native population declines (Figure 1.1A). Six studies showed this increasing population trend in Canada Geese (Erwin et al 1996, Austin and Pyle 2004, Costanzo and Hinderman 2009, McAlister et al 2017, Anderson et al 2017, Adde et al 2021) while three studies on Canada Geese showed conflicting results. Ryan et al (1998)

observed no crowding out effects of Canada Geese on grassland birds or ducks in breeding grounds; meaning that they did not observe direct competition effects of Canada Geese on other bird species for nesting locations. Messmer et al (2015) not only found no crowding out effects on other waterfowl species, but concluded that Mallards (*Anas platyrhynchos*) were able to out-compete Canada Geese in several habitats (temporary open water and emergent (seasonal or semi-permanent) wetland type). Mute Swan population trends were much more straight-forward, with aerial, breeding bird, and Christmas bird count surveys showing steady population growth in the Northwest and Midwest regions (Petrie and Francis 2003, Ellis and Elphick 2007, Costanzo and Hinderman 2009, Rees et al 2019). These studies, covering the 39 year period 1971-2000, also note declining populations of other waterbirds, such as the Black Duck (*Anas rubripes*), in the same areas. Muscovy Ducks have also seen population growth, alongside other resident exotics, while other native species were experiencing population declines (Wolff et al 2020). Egyptian Geese have seen establishment and population growth alongside the Canada Geese populations in the United States, but are underrepresented in the literature (Chesbro 2015).

DISCUSSION

The current state of invasive waterfowl research is missing a lot of key information. The majority of existing literature concerned Canada Geese with little having been done to understand the scope and effect of most of the present invasive waterfowl. Furthermore, Mexico and Western North America were underrepresented in research papers, indicating gaps in geographical focus of impact studies. Another lacking area of research is mechanistic studies as to how competitive exclusion is occurring in areas with invasive waterfowl. Many studies posit hypotheses as to how the invasive species are influencing population demographics: direct competition for nesting locations (Austin and Pyle 2004), the allee effect (Miller et al 2007,

Reiter et al 2013), and aggression (Groom et al 2020), among others. However, few are able to concretely determine more than local influence on other species. Larger-scale field observations are needed to more concretely determine the cause and outcome of these interactions with other water birds (Table 1.1).

Zoonotic outbreaks can devastate both commercial poultry production (Scott et al 2020) and lead to rippling effects through economies (Djunaïdi and Djunaïdi 2007). For example, the 2005 HPAI outbreak in Asia, Europe and Africa is estimated to have led to the deaths of over 200 million birds and more than 10 Billion in the Southeast Asian poultry industry (Beach et al 2007). These risks, coupled with fears for public health, have propelled the frequency of studies into zoonotic threats. Given that changing waterfowl community dynamics will likely change the disease ecology of the system (Anis et al 2018), these investigations indicate potential for novel threats on the horizon. Different species have different levels of susceptibility to various diseases and strains (Shihmanter et al 1998, Fereidouni et al 2009, Tseren-Ochir et al 2018). For example, increasing populations of Muscovy Duck (Scheibner et al 2019) and Egyptian Goose (El-Zoghby et al 2011), both known avian influenza vectors in their native ranges, are likely to change the nature of spread from wild to domestic birds (Thompson et al 2008, van den Berg et al 2008, Pérez Córdón et al 2009, El-Zoghby et al 2011, van Helden et al 2011). Field surveillance of the current breeding populations of Egyptian Goose and Muscovy ducks in North America are critically needed for appropriate risk evaluation (Table 1.1). The increasing populations of Mute Swans are also likely to increase the prevalence of Newcastle Disease and Psittacine Beak and Feather Disease. Both diseases have particularly detrimental effects to young poultry (Pass and Perry 1984, Seel et al 2000). Given the proximity of many of the invasive waterfowl species to

urban areas and agricultural habitat, these changing disease dynamics have the potential to affect poultry production (Plowright et al. 2017, Ayala et al. 2020, McDuire et al. 2021).

Invasive waterfowl proximity to economically valuable agriculture has been facilitated by anthropogenic urban developments. Historically, the green revolution swept across vast swaths of central North America (Allosso 2017) with many cereal grains being the staples in monocultures on scales previously unmet (Wolfe and Ceccarelli 2019). Cereal grains such as corn, barley, and wheat, are highly attractive to wildlife (Wiggers 1984, Cybluska et al 2020) and attract waterfowl species (Jordan 1953, Baguette and Van Dyck 2007, Henry et al 2016). This has led to conflict between crop-destroying wildlife (Hake et al 2010, Callaghan et al 2015) and the humans attempting to prevent the destruction (Halse 1984, Magnall and Crowe 2001, Magnall and Crowe 2002). In their native range, Egyptian Geese have been shown to consume up to 67% of cereal grains at all growth stages (Magnall and Crowe 2002). Field studies are needed to confirm similar behavior in North America (Table 1.1). At the same time, human populations have congregated into large urban centers, often at the expense of wildlife habitat (Matchett and Fleskes 2017). Inside urban centers, humans have also fostered their own green spaces, such as parks, golf courses, and nature trails. These pockets of green space attract Canada Geese, Mute Swans, and Egyptian Geese that would otherwise find urban centers inhospitable (Baxter and Hart 2010, Little and Sutton 2013, MacKay et al 2014, Atkins et al 2019, Groom et al 2020). Environmental restoration efforts have been undertaken to help offset habitat losses (Albrecht et al 2005, Brown et al 2008, Kettenring and Galatowitsch 2011) though often it is Canada Geese that are able to utilize newly restored habitat (Kettenring and Adams 2011, Gidoen et al 2015, Wong et al 2017). All of these factors have substantially changed the landscape in which these invasive species have taken root.

A changing landscape has fundamentally changed the conditions under which invasive waterfowl have been engaging with other species of waterbirds. Common nesting sites have seen sharp declines in other waterbird species, such as the American Coot. Invasive waterfowl aggression is particularly fierce near nesting locations (Gyimesi and Lensink 2012, Thompson et al 2017, Fattah et al 2021) and could be a contributing factor in declining water-bird species. Spatial competition has the potential to drive out desired avian species (Curtis et al 2007, Gidoin et al 2015, Callaghan and Brooks 2017) which could effectively reduce overall population levels of said species. Field observational studies are needed to confirm the type and extent of any competitive or territorial behavior invasive waterfowl are engaging in (Table 1.1). Furthermore, the potential resource use of the invaders have the potential to reduce food availability to other waterfowl species. Invaders such as Egyptian Geese (Edroma and Jumbe 1983, Halse 1984 MacKay et al 2014, Henry et al 2016), Canada Geese (Madsen and Mortensen 1987, Giroux and Bergeron 1996, Eaton et al 2017), Mute Swans (Tatu et al 2006), and Muscovy Ducks (West et al 2022) often have diets that overlap with other species in the area. These niche similarities often come at the expense of the native waterfowl species (Reynolds and Cumming 2016). Replication of behavioral studies in North America, such as Edroma and Jumbe's (1983), would bring greater clarity in how invasive waterfowl are interacting with the landscape and food resources (Table 1.1). Edroma and Jumbe's (1983) study involved daily observational record keeping of behaviors and environmental feature utilization to gather individual and flock behaviors. These local level community shifts have the potential to alter the resource makeup of the surrounding landscape. Differently fulfilled niches by waterfowl can favor different plant community makeups (Figuerola et al 2003, Tatu et al 2006)) which in turn influence the entire system (Idestam-Almquist 1998, Marklund et al 2002, MacDougall and Turkington 2005,

Yurkonis et al 2005, Wong et al 2017). Future gut and/or fecal studies into the potential of invasive waterfowl spreading invasive plant seeds are needed (Table 1.1).

Despite their impacts on local ecosystems, many invasive waterfowl species are viewed neutrally or even favorably by the general public. This has the potential to decrease effectiveness of their control once established. Mute Swans have been famously difficult to control due to public backlash for lethal removal programs which has led to the far less effective control method of nest destruction (Jager et al 2016). Canada Geese are viewed less favorably in the public eye yet the general public still finds lethal control unfavorably (Groom et al 2020). Any management that might want to tackle control measures has to grapple with public opinion on options. Additionally, as shown in this review, the land management choices that have facilitated and sustained invasive waterfowl lead to increased conflict between waterfowl and humans. This suggests that more effort needs to be put into either deliberate urban and suburban greenspace design or public outreach and education to reduce waterfowl presence in urban green spaces. As for invasive waterfowl species at lower densities (Egyptian Goose, Muscovy Duck etc.), there is still time to manage the incipient invasion.

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TABLES

Table 1.1. Research gaps in North American invasive waterfowl impacts literature.

TOPIC	GAP	EVIDENCE
DISEASE	Egyptian Goose + HPAI	Vector in native range (Anis et al 2017)
DISEASE	Muscovy Duck HPAI Field Surveillance	Lab Study (Berhane et al 2016) + Efficacy in other waterfowl (Diskin et al 2020)
COMPETITION	Observational Field Studies of Canada Goose breeding grounds	Higher nesting success rates in disturbed wetlands relative to other waterfowl (Lemelin et al 2007, 2010)
AGRICULTURE	Nuisance waterfowl use of grain fields	Research into rice production (Feaga et al 2015); Utilization elsewhere (Hake et al 2010; Magnall and Crowe 2002)
LANDSCAPE	Role of invasive waterfowl in facilitating invasive plant spread	Occurrences in Europe (García-Álvarez et al 2015) and Africa (Reynolds and Cumming 2016)

Table 2.1 A summary of the 45 North American Waterfowl studies resulting from our systematic literature search. Citations are sorted by species, then focus.

<i>Paper</i>	<i>Region</i>	<i>Study Species</i>	<i>Focus</i>	<i>Finding</i>
<i>Harris et al 2010</i>	Georgia, W. Virginia, Minnesota	Canada Goose	Avian Influenza	Not vector
<i>Kistler et al 2015</i>	Pennsylvania, NJ, Minnesota, Washington	Canada Goose	Avian Influenza	Not vector
<i>Reeves et al 2013</i>	Alaska	Canada Goose	Avian Influenza	Not vectors
<i>Kistler et al 2012</i>	Georgia, W. Virginia, Minnesota, Washington, NJ, NC, Penn., Mississippi, Mass.	Canada Goose	Avian Influenza	Possible vector
<i>Belser et al 2013</i>	North America	Canada Goose	Avian Influenza	Not a vector
<i>Fallacara et al 2004</i>	Ohio	Canada Goose	Bacterial Disease	<i>E. coli</i>
<i>Vogt 2018</i>	Ontario	Canada Goose	Bacterial Disease	<i>E. coli</i>
<i>Navarro-González et al 2020</i>	California	Canada Goose	Bacterial Disease	Shiga toxins
<i>Verma et al 2016</i>	Maryland	Canada Goose	Bacterial Disease	Toxoplasmosis
<i>Nagamori et al 2022</i>	Oklahoma	Canada Goose	Bacterial Disease	<i>E. coli</i>
<i>Lemelin et al 2007</i>	Quebec	Canada Goose	Competitive Exclusion	Success
<i>Lemelin et al 2010</i>	Quebec	Canada Goose	Competitive Exclusion	Success
<i>Ryan et al 1998</i>	North Dakota	Canada Goose	Competitive Exclusion	Unsuccessful
<i>Messmer et al 2015</i>	Ontario	Canada Goose	Competitive Exclusion	Competitively Excluded
<i>Nack and Anderson 2006</i>	Eastern Canadian Prairie	Canada Goose	Competitive Exclusion	Success
<i>Beaumont et al 2013</i>	Quebec	Canada Goose	Habitat Usage	Urban
<i>McAlister et al 2017</i>	USA	Canada Goose	Habitat Usage	Pasture

Table 2.1 (Cont.)

<i>Paper</i>	<i>Region</i>	<i>Study Species</i>	<i>Focus</i>	<i>Finding</i>
<i>McKinney et al 2015</i>	Rhode Island	Canada Goose	Habitat Usage	Prominent
<i>Feaga et al 2015</i>	Mississippi Alluvial Valley	Canada Goose	Habitat Usage	Aquaculture
<i>Austin and Pyle 2004</i>	Idaho	Canada Goose	Nesting	First to nest
<i>Miller et al 2007</i>	Alaska	Canada Goose	Nesting	Shrublands
<i>Issac-Renton et al 2010</i>	British Columbia and Washington	Canada Goose	Overgrazing	Supported
<i>Devault et al 2011</i>	USA	Canada Goose	Plane Strikes	Problem
<i>Adde et al 2021</i>	North America	Canada Goose	Population Growth	Exponential
<i>Erwin 1996</i>	Mid-Atlantic Coastal Region	Canada Goose	Population Growth	Exponential
<i>McAlister et al 2017</i>	North Carolina	Canada Goose	Population Growth	Steady Increase
<i>Anderson et al 2017</i>	North America	Canada Goose	Population Growth	Exponential
<i>Tsung-Ta et al 2016</i>	Lake Erie	Canada Goose	Shiga Toxins	Positive
<i>Stallknecht et al 2020</i>	Minnesota, Texas, Washington,	Canada Goose, Mute Swan	Avian Influenza	Not vectors
<i>Diskin et al 2020</i>	Mississippi Flyway	Canada Goose, Mute Swan	Avian Influenza	Not vectors
<i>Pederson et al 2009</i>	USA	Canada Goose, Mute Swan	Avian Influenza	Not vectors
<i>Costanzo and Hinderman 2009</i>	Virginia and Maryland	Canada Goose, Mute Swan	Population Growth	Exponential
<i>Deliberto et al 2009</i>	USA	Canada Goose, Mute Swan, Muscovy Duck	Avian Influenza	Not vector
<i>Ratti et al 2001</i>	South Dakota	Canada Goose	Habitat Usage	Restored Wetlands
<i>Chesbro 2015</i>	Arkansas	Egyptian Goose	Population Growth	Slow increase
<i>Berhane et al 2016</i>	British Columbia	Muscovy Duck	Avian Influenza	Vector
<i>Li et al 2018</i>	USA and Canada	Muscovy Duck	Avian Influenza	Vector

Table 2.1 (Cont.)

<i>Paper</i>	<i>Region</i>	<i>Study Species</i>	<i>Focus</i>	<i>Finding</i>
<i>Wolff et al 2020</i>	Puerto Rico	Muscovy Duck	Population Growth	Steady Increase
<i>Pedersen et al 2013</i>	Michigan, NJ, Rhode Island, NY, Indiana, Wisconsin, Mass.	Mute Swan	Avian Influenza	Not vector
<i>Weaver et al 2012</i>	Ontario	Mute Swan	Habitat Usage	Urban
<i>Petrie and Francis 2003</i>	Great Lakes	Mute Swan	Population Growth	Exponential
<i>Ellis and Elphick 2007</i>	North America	Mute Swan	Population Growth	Exponential
<i>Rees et al 2019</i>	North America	Mute Swan	Population Growth	Increasing
<i>Sánchez-Godoy et al 2020</i>	Mexico	Mute Swan	Psittacine beak and feather disease	Present

FIGURES

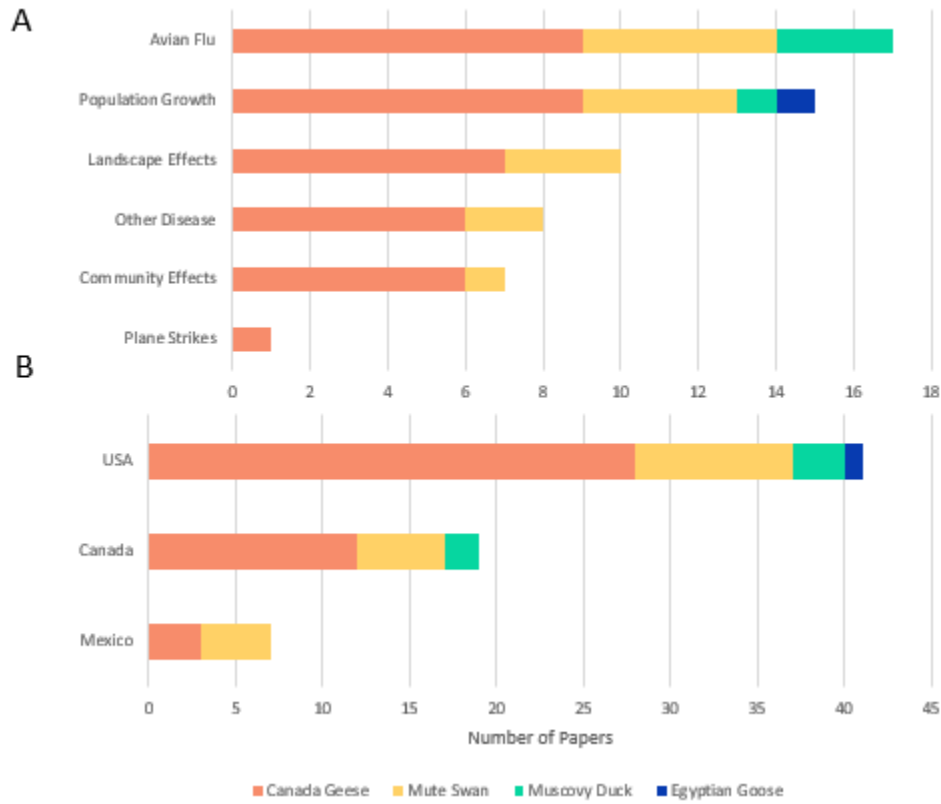


Figure 1.1. Impact topic (A) and geographical distribution (B) of the 45 systematic review papers on invasive waterfowl species in North America; broken up by study species.

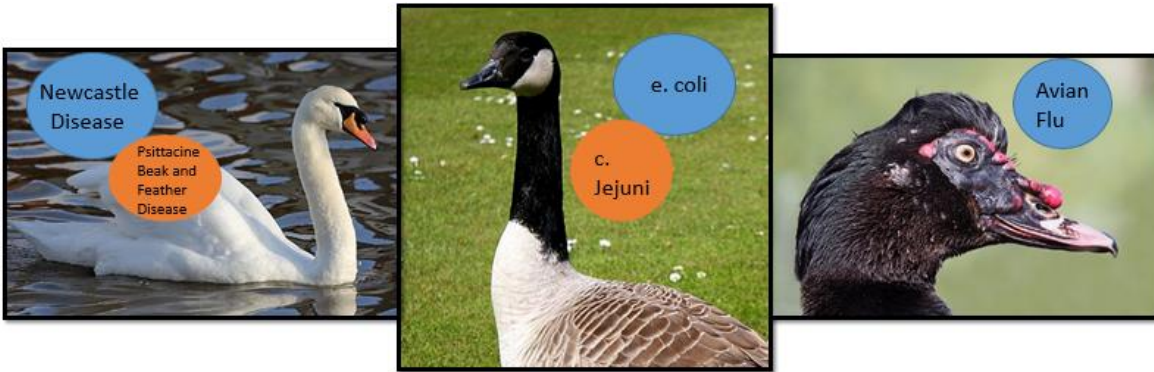


Figure 2.1. Most common zoonotic threats and their associated species (Mute Swan, Canada Goose Muscovy Duck).

APPENDIX 1: SEARCH TERMS

TS=((“aquatic birds” OR “avian species” OR “backyard poultry” OR “breeding female*” OR “breeding pair*” OR “breeding population*” OR “breeding waterbirds” OR “commercial poultry” OR “domestic birds” OR “domestic ducks” OR “domestic poultry” OR “domestic waterfowl” OR “game bird*” OR “grassland bird*” OR “invasive species” OR “marsh birds” OR “migrating birds” OR “migrating waterfowl” OR “migratory bird*” OR “migratory species” OR “migratory waterbirds” OR “migratory waterfowl” OR “national wildlife” OR “native plant” OR “native species” OR “natural hosts” OR “nesting birds” OR “sea duck*” OR “wading birds” OR “water bird*” OR “wetland bird*” OR “threatened species” OR “upland game birds” OR “wild bird*” OR “wild ducks” OR “wild mallards” OR “wild waterfowl” OR “wintering waterbirds”)

AND

(“american lineage” OR “american waterfowl” OR “anas spp*” OR “aythya ferina” OR “aythya fuligula” OR “breeding duck*” OR “caerulescens caerulescens” OR “canada geese” OR “canada goose” OR “chen caerulescens” OR “colinus virginianus” OR “common pochard” OR “cygnus cygnus” OR “cygnus olor” OR “dabbling duck*” OR “diving duck*” OR “geese anser” OR “muscovy duck*” OR “mute swan*” OR “pochard aythya” OR “wintering waterfowl” OR “Egyptian Goose” OR “Egyptian Geese” OR “Alopochen aegyptiaca” OR “Mandarin Duck” OR “Aix galericulata” OR “White-cheeked Pintail” OR “Bahama Pintail” OR “Anas bahamensis” OR “Phillipine Duck” OR “Anas luzonica” OR “Spot-billed duck” OR “Anas poecilorhyncha” OR “Blue-billed Teal” OR “Hottentot Teal” OR “Spatula hottentota” OR “Greylag Goose” OR “Greylag Geese” OR “Anser anser” OR “Swan Goose” OR “Swan Geese” OR “Anser cygnoides” OR “whooper swan” OR “bean goose” OR “Anser fabalis” OR “Bean geese” OR “Bar-headed Goose” OR “bar-headed geese” OR “Anser indicus” OR “Coscoroba swan” OR

“Coscoroba coscoroba” OR “ringed teal” OR “Callonetta leucophrys” OR “Black Swan” OR
“Cygnus atratus” OR “West Indian whistling duck” OR “Dendrocygna arborea” OR “white-
faced whistling duck” OR “Dendrocygna viduata” OR “Orinoco goose” OR “orinoco geese” OR
“Neochen jubata” OR “Ruddy shelduck” OR “Tadorna ferruginea” OR “common shelduck” OR
“Tadorna tadorna”)

AND

(“abiotic factors” OR “active surveillance” OR “adaptive harvest” OR “adaptive management”
OR “aerial survey*” OR “agricultural practices” OR “ambient temperature” OR “anthropogenic
disturbance” OR “climatic conditions” OR “cloacal swabs” OR “conservation concern” OR
“conservation efforts” OR “conservation measures” OR “conservation programs” OR
“conservation reserve” OR “conservation strategies” OR “control measures” OR “early
detection” OR “environmental change” OR “environmental conditions” OR “environmental
variables” OR “experimental infection” OR “experimentally infected” OR “fecal samples” OR
“genetic analysis” OR “genetic characterization” OR “geological survey” OR “global positioning
system” OR “growing season” OR “habitat change” OR “habitat loss” OR “habitat management”
OR “harvest management” OR “harvest rates” OR “human activit*” OR “human disturbance”
OR “human health” OR “human infection*” OR “human population” OR “hunting disturbance”
OR “hunting mortality” OR “hunting pressure” OR “hunting season” OR “immunosorbent
assay” OR “land management” OR “land use” OR “land-use change” OR “managed wetland”
OR “management actions” OR “management decisions” OR “management efforts” OR
“management implications” OR “management objectives” OR “management options” OR
“management plans” OR “management practices” OR “management strategies” OR
“management units” OR “monitoring program” OR “north american waterfowl management
plan” OR “phylogenetic analyses” OR “phylogenetic analysis” OR “population survey” OR

“predator control” OR “program mark” OR “protected area” OR “protected areas” OR “public health” OR “real-time pcr” OR “real-time reverse” OR “real-time rt-pcr” OR “recovery rates” OR “remote sensing” OR “reserve program” OR “retention time” OR “reverse transcription” OR “satellite transmitters” OR “sensitivity analysis” OR “sequence analysis” OR “serum samples” OR “simulation model” OR “site fidelity” OR “site selection” OR “stable isotope” OR “surveillance program” OR “total phosphorus” OR “trace element” OR “vegetation cover” OR “vegetation height” OR “virus isolat*” OR “water chemistry” OR “water depth” OR “water level*” OR “water management” OR “water quality” OR “water samples” OR “water temperature” OR “waterfowl habitat” OR “waterfowl hunt*” OR “waterfowl management” OR “waterfowl populations” OR “waterfowl production” OR “waterfowl survey*” OR “weather conditions” OR “wetland habitat” OR “wetland loss” OR “wetland management” OR “wetland restoration” OR “wetland use” OR “wetland vegetation” OR “wildlife habitat” OR “wildlife management”)

AND

(“agricultural fields” OR “agricultural lands*” OR “agricultural landscape” OR “alluvial valley” OR “aquatic ecosystem*” OR “aquatic habitat*” OR “atlantic coast” OR “atlantic flyway” OR “autumn migration” OR “boreal forest” OR “breeding area*” OR “breeding grounds” OR “breeding habitat*” OR “breeding range” OR “breeding sites” OR “british Columbia” OR “canadian prairie*” OR “central north” OR “central valley” OR “climate change” OR “coastal marsh*” OR “coastal wetland*” OR “eastern north America” OR “eastern united states” OR “emergent vegetation” OR “great lakes” OR “great plains” OR “home range” OR “illinois river” OR “joaquin valley” OR “lake erie” OR “lakes coastal” OR “lakes region” OR “long point” OR “managed wetlands” OR “marsh habitats” OR “migratory stopover” OR “mississippi alluvial valley” OR “mississippi flyway” OR “mississippi river” OR “national wildlife refuge*” OR

“natural reservoir” OR “natural resource*” OR “natural wetland*” OR “nature reserve” OR
“new jersey” OR “north America” OR “north Carolina” OR “north Dakota” OR “northern great
plains” OR “pacific coast” OR “pacific flyway” OR “permanent wetlands” OR “pothole region”
OR “prairie pothole” OR “prairie wetlands” OR “rainwater basin” OR “rice fields” OR “river
basin” OR “river delta” OR “river floodplain” OR “river valley” OR “sacramento valley” OR
“salt marsh*” OR “shallow lake*” OR “signaling pathway” OR “south Carolina” OR “south
Dakota” OR “southern Ontario” OR “stopover sites” OR “suisun marsh” OR “suitable habitat”
OR “surface water” OR “surrounding landscape” OR “united states” OR “upper Mississippi” OR
“western Alaska”)

AND

(“abundant species” OR “adult survival” OR “adverse effects” OR “adversely affect” OR
“annual cycle” OR “annual survival” OR “annual variation” OR “apparent survival” OR
“apparently healthy” OR “avian influenza” OR “bird communit*” OR “bird migration” OR “bird
populations” OR “bird use” OR “blood lead” OR “body condition” OR “body mass” OR “body
size” OR “breast muscle” OR “breeding birds” OR “breeding period” OR “breeding season*”
OR “breeding success” OR “breeding waterfowl” OR “brood parasitism” OR “brood rearing”
OR “brood size” OR “brood survival” OR “carrying capacity” OR “chain reaction” OR
“cleavage site” OR “clinical signs” OR “clinical symptoms” OR “closely related” OR “clutch
size” OR “community composition” OR “community structure” OR “conservation planning” OR
“conservation reserve program” OR “continental population” OR “control region” OR “cover
types” OR “daily survival” OR “demographic parameters” OR “density dependence” OR
“detection probabilit*” OT “differentially expressed” OR “digestive tract” OR “direct contact”
OR “disease control” OR “disease outbreaks” OR “disease virus*” OR “duck nests” OR
“duckling survival” OR “ducks wintering” OR “ecological factors” OR “ecological processes”

OR "economic losses" OR "ecosystem service*" OR "effective conservation" OR "effective management" OR "Egg production" OR "endangered species" OR "energetic carrying capacity" OR "energy expenditure" OR "environmental factors" OR "escherichia coli" OR "estimated survival" OR "female survival" OR "food availability" OR "food resources" OR "food web*" OR "foraging habitat" OR "gene expression" OR "gene flow" OR "genetic diversity" OR "genetic structure" OR "genetic variation" OR "genome sequence" OR "geographic distribution" OR "goose parvovirus" OR "growth performance" OR "growth rates" OR "h5n1 virus*" OR "habitat availability" OR "habitat characteristics" OR "habitat conditions" OR "habitat conservation" OR "habitat features" OR "habitat preferences" OR "habitat quality" OR "habitat requirements" OR "habitat selection" OR "habitat suitability" OR "habitat types" OR "habitat use" OR "harvest regulations" OR "hatch date" OR "hatching success" OR "hemagglutination inhibition" OR "higher levels" OR "higher survival" OR "highly pathogenic avian influenza" OR "highly pathogenic h5n1" OR "immune function" OR "immune response" OR "immune responses" OR "immune system" OR "incubation period" OR "indirect effects" OR "infected birds" OR "infectious disease" OR "influenza a" OR "influenza a virus" OR "influenza outbreaks" OR "influenza virus*" OR "innate immune" OR "internal genes" OR "invertebrate abundance" OR "invertebrate communities" OR "juvenile survival" OR "limiting factor" OR "lipid reserves" OR "local habitat" OR "local population" OR "local scale" OR "long-distance dispersal" OR "lower survival" OR "low-pathogenic avian" OR "mechanisms underlying" OR "migration patterns" OR "migration route*" OR "mortality rate*" OR "movement patterns" OR "nest density" OR "nest predation" OR "nest success" OR "nest survival" OR "nesting ecology" OR "nesting habitat" OR "nesting success" OR "nest-site selection" OR "newcastle disease" OR "Nutrient loading" OR "nutrient reserves" OR "organic carbon" OR "organic matter" OR

“oxidative stress” OR “pathogenic avian influenza” OR “percent cover” OR “population change”
 OR “population decline” OR “population dynamics” OR “population growth” OR “population
 growth rates” OR “population model” OR “population size” OR “population trends” OR
 “poultry farms” OR “poultry industry” OR “poultry markets” OR “poultry outbreaks” OR
 “poultry production” OR “predation rates” OR “predation risk” OR “provide critical” OR
 “provide evidence” OR “provide habitat” OR “provide important” OR “provide insight” OR
 “recent decades” OR “recent studies” OR “recent years” OR “related genes” OR “reproductive
 output” OR “reproductive performance” OR “reproductive success” OR “resource availability”
 OR “season survival” OR “seasonal patterns” OR “seasonal variation” OR “seed dispersal” OR
 “spatial distribution” OR “spatial scale*” OR “spatial variation” OR “species composition” OR
 “species distribution” OR “species diversity” OR “species richness” OR “spring migration” OR
 “subtype h5n1” OR “survival estimates” OR “survival probabilities” OR “survival probability”
 OR “survival rates” OR “target species” OR “temperate regions” OR “temporal patterns” OR
 “temporal trends” OR “temporal variation” OR “tested positive” OR “Transmission dynamics”
 OR “trophic level*” OR “upland habitat*” OR “upland nesting*” OR “vegetation structure” OR
 “viral infection” OR “viral shedding” OR “virus infection” OR “virus infections” OR “vital
 rates” OR “waterfowl wintering” OR “wetland availability” OR “wetland basins” OR “wetland
 characteristics” OR “wetland complex” OR “widely distributed” OR “winter survival” OR
 “wintering habitat”))

CHAPTER II

Egyptian Goose (*Alopochen aegyptiaca*) Invaded Habitat Supplemented by Urban
Environments: A Case Study of Three Continents.

Percival Matzinger Marshall, Caleb P. Roberts, J.D Willson, and Jennifer Mortensen

ABSTRACT

The prevalence of stationary versus non-stationary species-environment relationships is a fundamental question in landscape ecology. For invasive species in particular, understanding the ability to adapt and patterns of species' adaptations to novel environments is critical for effective management. The Egyptian Goose (*Alopochen aegyptiaca*) is native to the African continent. The species spread and established itself as a damaging invasive species in Europe in the 1700s and is now an incipient invader in North America. The volume of historical and current distribution data from eBird, as well as the three distinct geographical locations, allow for a robust test of invading species' changes. We used 21,449 occurrence records from eBird to construct Species Distribution Models (SDMs) using classified random forest models in Google Earth Engine. We found strong evidence in support of the niche shift hypothesis, which posits that invading species change or expand the conditions they are otherwise able to inhabit in novel environments. Suitable climate conditions for the Egyptian Goose strongly varied between continents. In Africa and North America, suitability was highest at median annual temperatures of 20.6°C and 20.7°C, respectively, whereas suitability in Europe was highest at a lower median annual temperature of 11.0°C. Egyptian Geese showed increasing affinity for urban environments: doubling from Africa to Europe and tripling from Africa to North America. The greater affinity for urban environments in recently invaded regions suggests that the urban areas may be acting as foothold habitat for the Egyptian Geese.

INTRODUCTION

Invasive species have contributed to the loss of half of the species that have gone extinct globally since 1500 CE and are entirely responsible for the loss of 20% of those species (Clavero and García-Berthou, 2005; Bellard et al., 2016). This makes invasive species one of the major contributors to changing landscapes. Humans have introduced thousands of species into new environments for food, labor, recreation, and aesthetics, as well as by accidental transportation (Hulme 2009). Furthermore, as global commerce and transportation increases, the frequency of introductions of non-native flora and fauna will continue to rise. Invasive species pose a threat to native species in regions that they are introduced into through interspecific competition (Groom et al 2020) and active niche displacement (Gidoín et al 2015). These disruptions can cause ripple effects through the invaded environments (Walsh et al 2016). In addition to their ecological impacts, invasive species cause economic losses to humans. Between damage to infrastructure (Booy et al 2017), agricultural interference (Magnall and Crowe 2001), and the costs to eradicate and control (Jardine & Sanchirico, 2018), invasive species are a costly problem to manage. Understanding the driving factors of invasion can inform strategies for preventing species invasions and consequent negative impacts of invasive species.

One of the leading theories as to why invasive species can gain a foothold into new habitats is the niche shift hypothesis. The niche shift hypothesis, sometimes further differentiated into the fundamental niche shift and realised niche shift, posits that due to the process of being introduced to a new range, an invasive species shifts its niche's density of occurrence or expands or retracts the limits of its niche (Bates & Bertelsmeier, 2021). A shift will move the overall range of habitable conditions (such as average temperature increase) whereas an expansion will encompass all previously habitable conditions plus additional conditions (e.g increased cold

temperature tolerance) and a contraction is a subset of the original niche conditions. These changes result from smaller gene pools in the invasive populations, and the unique environmental and community conditions that the species find themselves in. Changes can take the form of shifting mating behaviors due to nesting conditions (Matzek 2012), shortened mating seasons (Lensink 1998), new habitat occupancy choices (Rahel and Olden 2008), and migratory changes (Hellmann et al 2008). To test the niche shift hypothesis, it is important to have established the climatic and landscape conditions in both the native and invaded ranges.

The Egyptian Goose (*Alopochen aegyptiaca*), a native of the African continent, is a unique model species to test the Niche Shift Hypothesis. It is currently an invasive species on two separate continents, North America and Europe. The European invasion is estimated to have begun in the 1700s in England (Lensink 1998); the North American invasion is estimated to have begun in California in 1967 (Renwick 1968), Florida in 1985 (Pranty and Ponzio 2014) and Arkansas in 2008 (Smith and James 2012). That Egyptian Geese have a firmly established population in Europe, but are at the incipient invasion stage in North America, provides a unique opportunity to observe differences at different invasion stages.

Here, we test the niche shift hypothesis by comparing Egyptian Goose climatic and habitat associations between its native continent of Africa, an established invasion in Europe, and an incipient invasion in North America. Specifically, we hypothesize that invasive Egyptian Geese (1) have expanded their temperature associations relative to their native continent and (2) will occupy similar landscape habitats to their native continent. We test these hypotheses by using Species distribution models (SDMs) which allow for occurrence only data analyses with predictor variables (Araújo et al. 2019). The Egyptian Goose provides a novel opportunity to

apply SDMs across a spatial invasion with distinct progression points (native, established, and incipient).

METHODS

Data collection

We downloaded the eBird Basic Dataset (ebird 2021) on August 2, 2022 and imported observation records into R studio 4.1.1 (2021) for further processing. We retained records that contained media (photographs, videos, or audio recordings), were from the year 2000 or more recent, and were from terrestrial ecosystems on our continents of interest. We defined “North America” as containing Canada, Mexico, the United States, and Puerto Rico (Callaghan and Brooks 2017). We defined Africa using the established native range by the Audubon Society North American Bird Guide (add citation). The established invasion continent, as defined by Lensink (1998), demarks Europe. We excluded records from the Arabian Peninsula due to low sample size and this area’s unclear status as native or invaded (Fink et al 2022). We also excluded points from islands smaller than Puerto Rico to reduce environmental noise. This data filtering resulted in 10,725 eBird checklists (i.e., Egyptian Goose presence points) from North America, 6903 from Europe, and 3821 from Africa.

Analysis

We imported the filtered eBird data into Google Earth Engine (Gorelick et al 2017) to build our species distribution models. For each continent (native, established, and incipient), we followed Crego et al (2022) to develop models via random forest classifiers. Because this was a global analysis with a goal of comparing climatic and habitat associations across continents, we chose predictor variables that were available for all three continents. We assessed correlation between predictors and reduced variables when correlation coefficients were greater than 0.6. Our final predictor set included elevation (30 m resolution, data collected February 2000, Farr et al 2007), annual mean temperature, annual temperature range (1 km resolution, data from 1950–

2000, Hijamins et al 2005), crop cover, grass cover, urban cover, permanent water cover, and tree cover (100 m resolution, data from 2015-2019, Buckhorn et al, 2020). Presence points were masked off the study areas and pseudo-absences were generated for each model. The sum of generated pseudo absences was checked ensure a minimum of 10,000 pseudo absence points were generated in total for each model. For model training and validation purposes, we used a block repeated split-sample cross-validation technique to randomly partition data (Roberts et al 2017, Valavi et al 2019). We used ten runs per continental model in the random forest method for SDM creation, using a final average for a habitat suitability index. We assessed model performance using the Area Under the Curve of the Receiver Operator Characteristic (AUC-ROC; Fielding and Bell 1997) and the Area Under the Precision-Recall Curve (AUC-PR; Sofaer et al 2019). Using the metrics established by Liu et al 2016, we estimated the true positive, false positive, true negative, and false negative rates to generate the sensitivity, specificity, and precision of the model.

RESULTS

Model Performance:

The models performed well under both accuracy metrics (AUCROC and AUCPR). Africa performed the best (model-averaged AUCROC = 0.94, AUCPR = 0.92) with Europe (model-averaged AUCROC = 0.93, AUCPR = 0.85) and North America (model-averaged AUCROC = 0.93, AUCPR = 0.88) performing slightly lower but still well within the accuracy thresholds (Table 1.2). Sensitivity, specificity, and precision metrics for all three models were > 0.8 (Table 1.2) indicating accurate predictions for the habitat suitability index.

Climate

Climatic and habitat variable importance varied strongly across native, established invasion, and incipient invasion continents. Climate variables were the largest contributing factors for all three continental models (Table 1.2). The median annual temperature for areas with Egyptian Geese present were similar between the native continent (20.6°C) and incipient invasion continent (20.7°C), but it was nearly halved in the established continent (11.0°C) (Figure 1.2). In the available climate conditions for the continental models, Egyptian Geese found cooler temperatures to be more suitable in Africa whereas warmer temperatures were more suitable in Europe and North America. Egyptian Goose presence was predicted to be more common in areas with lower temperature variation across all three continents (Figure 1.2) with increasing tolerance for variation occurring from Africa to Europe to North America. High elevation was predicted to be positively associated on the African continent and negatively associated in North America and Europe (Figure 1.2, median elevation Africa = 954.0 m (SD 431), North America 24.9 m (SD 253), Europe = 104 m (SD 238)). Despite the high variance in mean elevation, elevation overall was a strong predicting variable for all three models (Fig. 3.2).

Habitat

For the land cover predictor variables, urban cover demonstrated the widest divergence between native and invaded continents. While Egyptian Geese presence was positively associated with urban areas for all three models, it was the weakest predictor for Africa (average 7.9%), doubled to 14.4% on average in Europe and tripled for North America to 26.8% (Figure 1.2). Crop lands were positively associated with Egyptian Geese presence in Africa and negative for North America and Europe while the reverse relationship was found for tree cover. Grasslands were negatively associated in North America but positive for Europe and Africa. Permanent water was the weakest, positive predicting variable for all three continents. The

aggregate habitat suitability index for all predictor variables shows the established native range (Figure 2.2A), suitable habitat in the established invaded continent (Figure 2.2B), and suitable habitat in the incipient continent (Figure 2.2C).

DISCUSSION

Our hypothesis was supported: we found strong evidence for niche shift between native and invaded continents. Highly conserved predicting variables, such as positive associations with water cover and moderate temperature conditions indicate a degree of niche conservation for the Egyptian Geese. The importance of moderate temperatures and unsuitability of highly variable regions indicate that some constraints exist for the total spread of this species. While Africa and North America had similar average annual temperatures in occupied regions, occupied areas of Europe were 8°C lower on average. This is in line with the freezes in the Netherlands in the 80s and 90s which killed off around two-thirds of the Egyptian Goose population (Lensink 1998). These results support the findings of Strubbe et al 2013 which found Egyptian Goose to be experiencing thermal niche expansion in Europe. With Europe being an established invasion that has already experienced climatic bottlenecks, the population has had decades longer to adapt to local conditions and to disperse outside of the source populations from the UK. The North American invasion is still incipient which suggests that more time could elapse to allow greater utilization of colder regions of the continent. This is supported by Liu et al 2020 who demonstrated that niche conservation was stronger in more recent invasions. Should the invasion continue, we would expect similar temperature-related shifts in the North American population. This prediction is supported by the greater tolerance for temperature variation in both invaded continents in comparison to the native continent.

These results highlight one of the exceptions to the meta-analysis conducted by Liu et al (2020) which demonstrated that most invasive species conserve their climatic niche. Their proposed reasoning behind why some species are able to niche expand are 1. Being introduced into similar climate and then rapidly expanding outward 2. The founder effect 3. Rapid evolution. In the case of the Egyptian Goose, all three of these factors may be at play. Higher climatic overlap between Africa and North American release points may have afforded the incipient invasion a foothold into the continent. The initial populations for both invaded regions were small (Renwick 1968, Lensink 1998, Pranty and Ponzo 2014) as most were brought in for food, feathers, and exotic bird collections (Abellán et al 2016, Smith and James 2012). In the established invasion, a population bottleneck from the severe winters may have also contributed to rapid evolution of the invasive species. Notably, the Egyptian Goose is a generalist species (Strubbe et al 2013) which a large native range; which would be at the greatest risk of showing a higher level of niche conservation than a specialist species with a small native range (Liu et al 2020). This further demonstrates the strength of the found climatic niche shift.

Contrary to our hypothesis, we also found strong evidence in support of land cover niche shifts. The models showed the greatest divergence in the landscape cover predictor variables. Higher affinity for trees, croplands and grasslands in the native continent when compared to both invaded continents indicates greater ability to exist across the majority of the range. The strength of the suitability of highly urbanized areas increasing with recency of arrival suggests that urban environments may be acting as foothold habitat for the Egyptian Geese. This concept is consistent with existing studies which indicate that highly disturbed urban landscapes leave empty niches for invasive species (Burton et al 2005) and furthermore act as food supplements (Groom et al 2020), havens from competitors (Kühn et al 2004) and predators (Ditchkoff et al

2006). For Egyptian Geese in particular, urban environments tend to provide these generalists very attractive habitat (Kornherr and Pütz 2022) which may allow them to persist into the novel environments. Affinity for urban environments is a trait Egyptian Geese share with other invasive waterfowl (Petrie and Francis 2003, Baxter and Hart 2010, Little and Sutton 2013, MacKay et al 2014, Atkins et al 2019, Groom et al 2020). This is further supported by grass cover continuing to be positively associated with the Egyptian Geese in Europe and a lower strength of the urban cover by comparison.

Overall, we have shown that the Egyptian Goose exhibits a niche shift. Furthermore, the ability to persist in these novel environments has been supported in no small part by urban environments. This has implications for any management strategies that could be enacted. If the urban environments are currently operating as source populations in the invaded continents and there is potential to further expand current suitable conditions in the native range, then it would be vital to focus efforts on the current source populations. We have further shown through model performance and adherence to the established native range indicate the applicability of Google Earth Engine SDMs using random forest model for invasive species. This provides more opportunities for future monitoring and management efforts.

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TABLES

Table 1.2: Accuracy Assessments of the Classified Random Forest Models.

	Africa		Europe		North America	
Run	AUCROC	AUCPR	AUCROC	AUCPR	AUCROC	AUCPR
1	0.94	0.93	0.93	0.82	0.93	0.82
2	0.95	0.93	0.94	0.76	0.94	0.80
3	0.93	0.90	0.91	0.87	0.90	0.87
4	0.94	0.93	0.96	0.90	0.96	0.83
5	0.94	0.91	0.91	0.84	0.90	0.89
6	0.94	0.90	0.91	0.92	0.91	0.92
7	0.93	0.92	0.90	0.85	0.90	0.89
8	0.95	0.94	0.91	0.88	0.91	0.89
9	0.95	0.91	0.98	0.81	0.98	0.98
10	0.93	0.92	0.94	0.88	0.92	0.91
Model Average	0.94	0.92	0.93	0.85	0.93	0.88

FIGURES

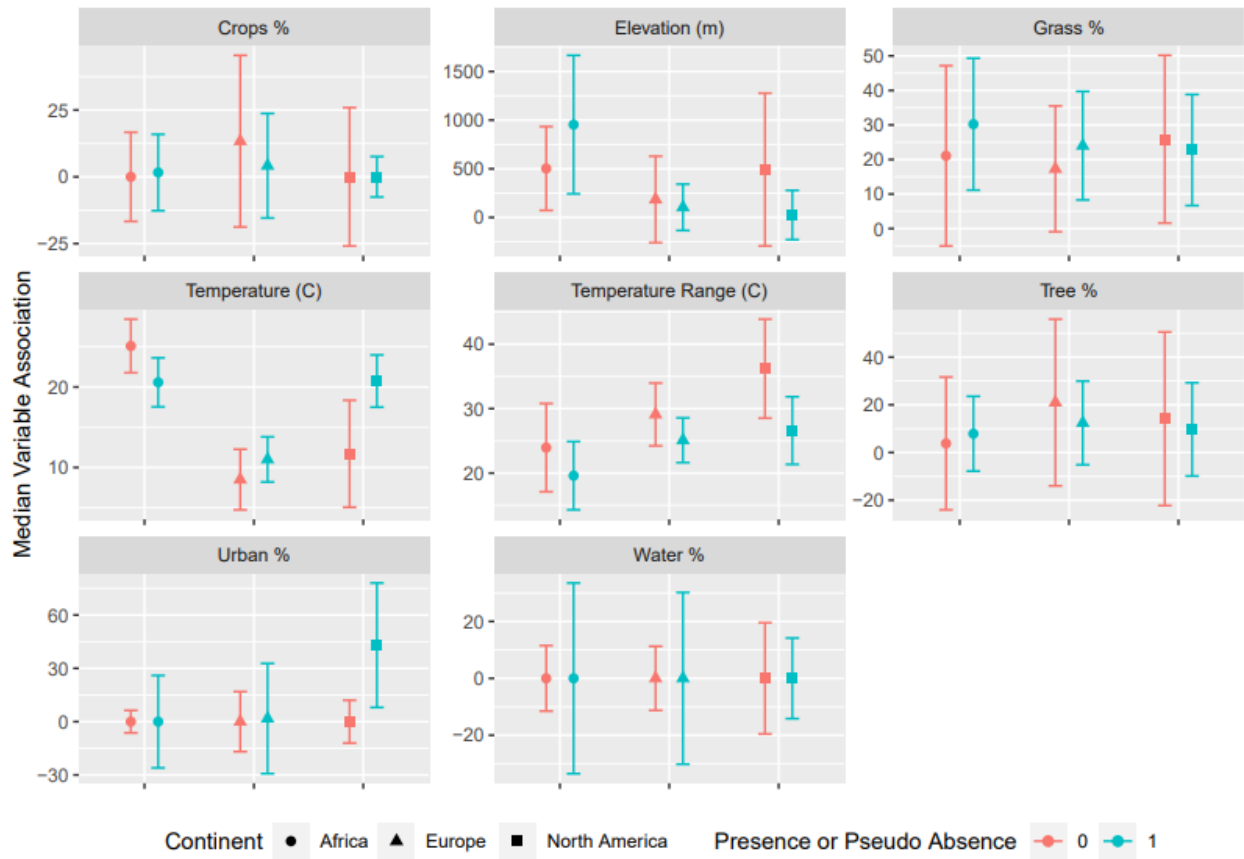


Figure 1.2. Predictor variable association with Egyptian Goose presence (Blue) or pseudo-absence (Red) across their native continent (Africa), their established continent (Europe), and their incipient invasion (North America). Error bars represent standard deviation.

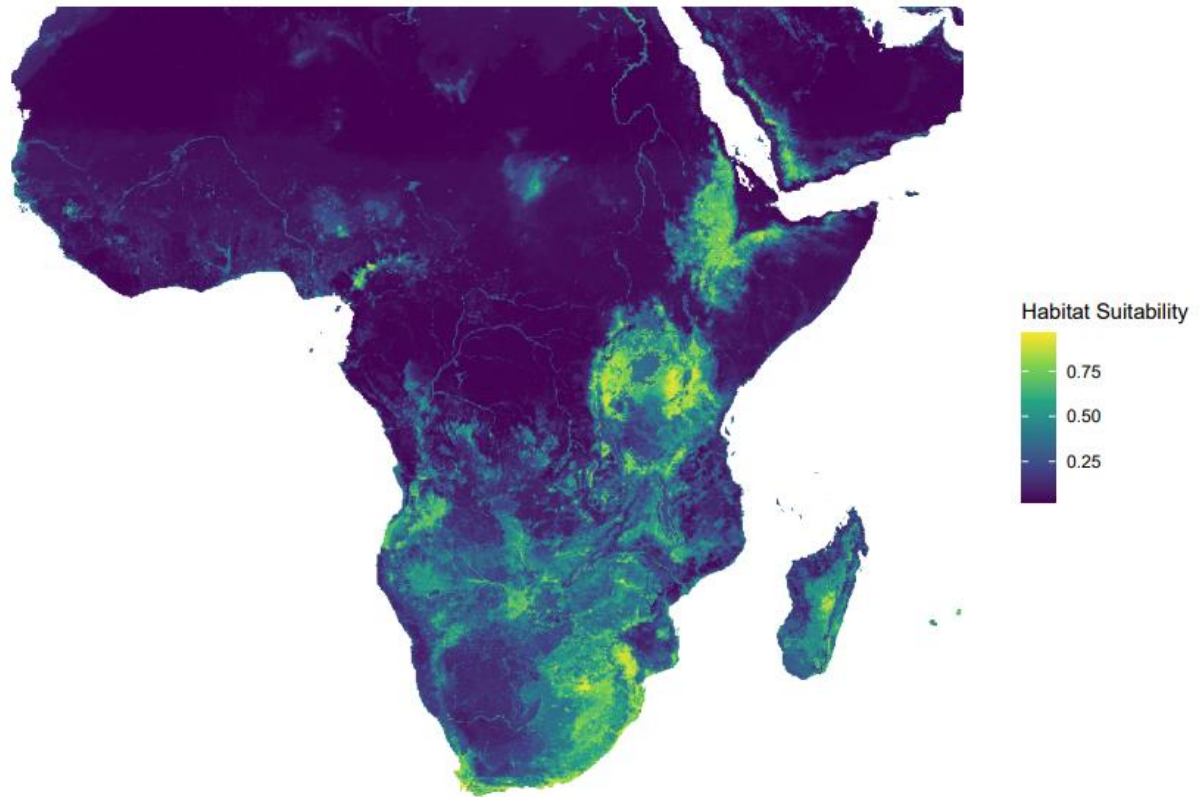


Figure 2.2A. African Habitat Suitability Model for the Egyptian Goose. Yellow indicates highest suitability.



Figure 2.2B. European Habitat Suitability Model for the Egyptian Goose. Yellow indicates highest suitability.

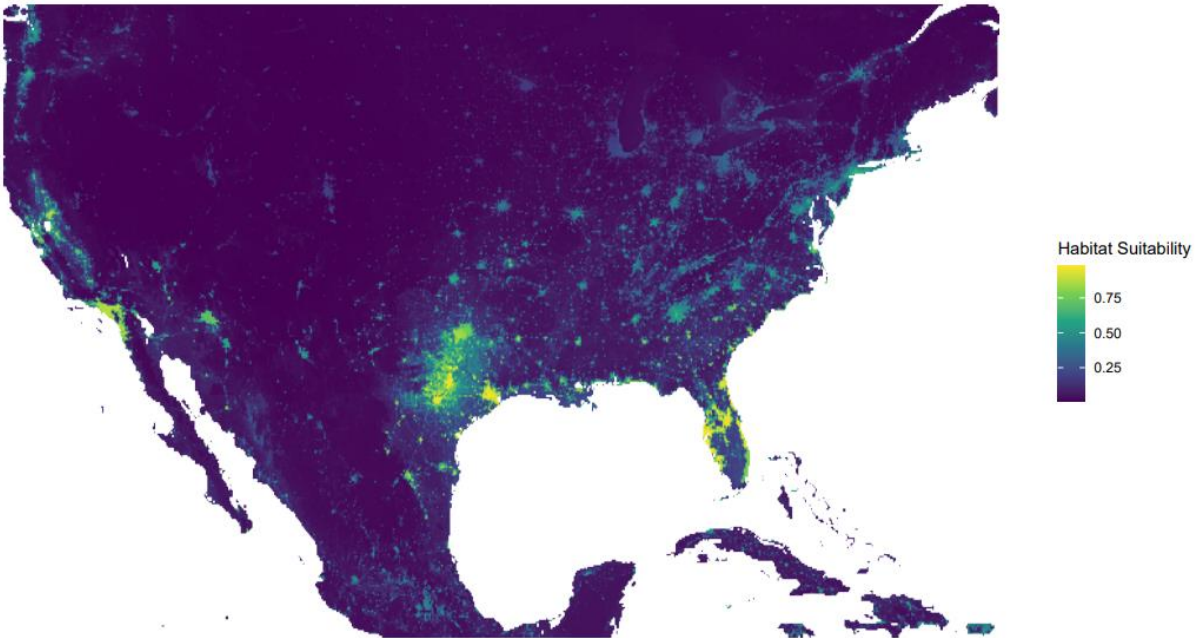


Figure 2.2C. North American Habitat Suitability Model for the Egyptian Goose. Yellow indicates highest suitability.

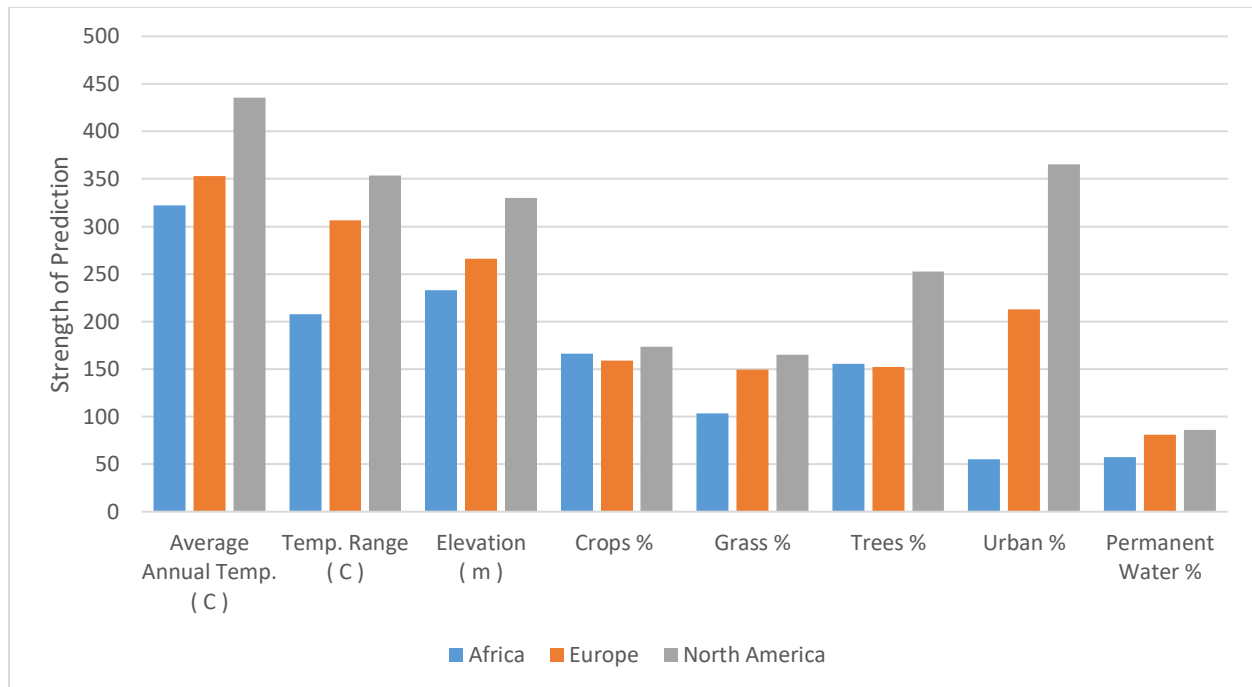


Figure 3.2. Relative Strength of the habitat predictor variables for Egyptian Goose presence in Africa, Europe and North America.

CONCLUSION

We have shown that the Egyptian Goose is a highly adaptable species with strong evidence in support of the niche shift hypothesis. In an established invasion, they are able to expand the thermal conditions they are able to persist in (Lensink et al 1999). Furthermore, we have shown that urban environments are acting as a foothold for the Egyptian Goose to establish populations in novel environments. This provides the groundwork for management. If these urban centers are acting as source populations for the rest of the Egyptian Goose populations, then they are the areas to target for any wildlife management operations (Stevens and Falk 2009). The Egyptian Goose population is still relatively low in North America for now (Chesbro 2015) but should their population gain the same potential as the European established invasion (Lensink 1998), management may have to change course to harm reduction.

We have also shown that despite large gaps in the North American invasive waterfowl literature, there are aspects of the Egyptian Goose invasion that are a cause for concern. Other aquatic invasive avifauna, Mute Swan and Canada Geese, are not strong vectors of avian influenza (Diskin et al 2020, Stallknecht et al 2020). However, the Egyptian Goose is a vector of avian influenza and has a history of contracting new strains before poultry outbreaks in its Native Range (Anis et al 2017). With the Egyptian Goose population increasing in North America, there is potential for the disease ecology conditions to change and increase the threat of avian influenza on the continent (Fereidouni et al 2009, Tseren-Ochir et al 2018). Furthermore, their potential to negatively influence wildlife through competition and aggression (Gyimesi and Lensink 2012, Thompson et al 2017, Fattah et al 2021) make the Egyptian Goose a strong candidate for further study and management in North America. Our study highlights the role humans have played in the facilitation of this invasion as well as avenues for potentially managing the current outcomes.

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