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PERSPECTIVES AND PARADIGMS

A complete history of the establishment of Japanese sika deer on the Delmarva Peninsula: 100 years post-introduction

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Abstract While many non-native species immediately express their negative qualities which encourage their management (even attempted eradication), some have long lag periods before the population begins to grow out of control. Sika deer have been problematic in many places where they were introduced as novelties or games species through hybridization or aggressive interactions with native deer. In attempt to better manage these species we need to know their native ecosystem. We provide evidence through summarized literature of the manner in which sika deer arrived on Delmarva from Yakushima Island in Japan via a multi-generational stopover in the United Kingdom. We also add morphological and genetic support that confirm the origins and help describe the path of introduction of sika deer to Maryland. We also summarize the growth and change in population size(s) over the last 100 years. This historic understanding is an essential part of coping with the persistent growth of a large, aggressive herbivore that is currently being managed as a game species. We summarize the possible impacts of sika deer including the displacement of native white-tailed deer. The management of this species needs to be carefully observed as they continue to spread throughout the critical saltmarsh of the Delmarva Peninsula.

Keywords Additional ungulate · *Cervus nippon yakushimae* · Founding invasion · Serial bottlenecks

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Introduction

Sika deer found on the eastern shores of Maryland and Virginia, and in Delaware (here after: Delmarva) are increasing in number and expanding in range. To date, there is a paucity of publications regarding sika deer on Delmarva, and fewer reference their introduction to the United States. We conducted a thorough review of literature to determine the history behind the introduction of sika deer, and the implications their introduction may have on the current population. The competitive interactions that this species has with the native white-tailed deer directly affect management decisions of both species, and are confounded by the economic benefits that are associated with having a unique, large game species in the region.

The introduction of sika deer in the United States happened several times (at different locales), with several different subspecies; the first was into Maryland. For a short period after their introduction in 1916, (Flyger 1959, 1960) there was confusion about which species of deer was actually introduced (Flyger

1960; Presnall 1958). The initial population of 4 or 5 individuals (Flyger 1960) has grown to an estimated 12,000 today (2013: Unpublished data, T. B. Eyler, Maryland State Deer Biologist). Sika deer are a popular game animal but in some areas can also be an overabundant crop pest (Hiroshi et al. 2009; Takatsuki 2009). As the sika deer population continues to grow there are serious concerns about the effects they will have on native species and the habitats they live in (Flyger and Warren 1959; Feldhamer and Armstrong 1993; Takatsuki 2009; Kalb et al. 2013; Chollet et al. 2015). Past sika deer management regulations have either been based on what we know about other native and introduced populations of sika deer from literature, or on regulations that pertain to white-tailed deer.

Founding introductions

From Japan to the British Isles

In the early 1800's a German harbor officer, Jacob Gerhard Gotthold Jamrach took notice to the exotic wildlife that was coming into the Hamburg port. He started a business of buying, selling and showing some of these animals in St. Pauli, Germany. The thriving business was moved to London, where it was taken over by his son Charles Jamrach in 1841 (Simons 2014). In 1863, the German portion of the business was sold to Carl Hagenbech, who became one of Charles' greatest rivals for acquiring exotic wildlife (Rothfels 2002; Simons 2014), and can be credited with the introduction of sika deer into Germany and Austria in 1893 and 1907 (Pitra et al. 2005) and for providing some individuals to Woburn Abbey, England (Banwell 2009). Jamrach became known as a "man who could get things" (Robertson 1901). His passion brought him to collecting exotic animals of all types, especially items from Japan which were in high demand due to the Japonism culture (decorating with or in a Japanese style) that had taken hold in England (Simons 2014). The wealthy of England, the United Kingdom, and all of Europe came to Jamrach for stocking their exotic game farms, parks, and zoos with wildlife. One proprietor of Jamrach's was the 7th Lord Powerscourt, who in 1860 purchased (for around £15 per head [todays value would be about $800 per head]: Robertson 1901; Ratcliffe 1987) 3 female and 1 male Japanese sika deer for his estate in Enniskerry, County Wicklow, Ireland (Powerscourt 1884). This purchase and transport of Japanese deer was a great credit to the abilities of Jamrach when we consider that Japanese ports had just opened to western trade (by threat of force from British, French and US) the same year after having been closed for over 200 years.

The herd in Wicklow increased rapidly and Lord Powerscourt made gifts of the deer throughout Ireland and England (Powerscourt 1884). At the time there were also red deer and sambar deer (*Cervus unicolor*) intermingling with the sika deer. Ratcliffe (1987) questions the genetic integrity of all stocks which were founded from the herd in Wicklow as suspected of having some mixed genes. One destination of the small Japanese deer was Woburn Abbey in England (still a popular historic site and animal zoo), where the 11th Duke of Bedford (Herbrand Russell: 1858–1940) collected several deer species including five subspecies of sika deer (Bedford 1949; Banwell 1995; Swanson and Putman 2009) over several year period from 1893 to 1897 starting with Japanese sika deer (Lowe and Gardiner 1975; Ratcliffe 1987). While the Duke can be credited with the preservation of Peré David's deer which more than likely would have been extirpated without his influence; we also can attribute several introductions of non-native deer to other counties to him (Bedford 1949). The sika deer populations that are now firmly established in both New Zealand and on the Delmarva Peninsula were started from gifts of deer made by the Duke (Banwell 2009; Feldhamer and Demarais 2009). In addition to the missing information regarding the transportation of individuals from Wicklow (by whom and exact numbers and dates), there was a substantial period of time when the multiple subspecies (Banwell 1993; Goodman et al. 2001) of sika deer from the Japanese Islands were all considered to be a single subspecies (Lowe and Gardiner 1975; Ratcliffe 1987) *C. n. nippon*. This lack of differentiation in literature makes distinction of many historical documents ambiguous without specific details regarding source locations or morphology.

The 12th Duke of Bedford provided documentation that his father attempted on several occasions to create hybrids for specific traits and that he was also careless with species isolation. In 1941, all of the remaining deer of the smaller species of sika deer were lost to disease or culled from the Abbey (Bedford 1949). Morphological and genetic characteristics of the sika deer in New Zealand show that these deer were

established not from pure stock, but from some form of sika–sika, or sika-red deer hybrids (Glover 1956; Banwell 1993, 1995, 2009; Swanson and Putman 2009). Glover (1956) also references the hybridization of sika deer in England, and compares the smaller subspecies of sika deer in England into those in America (suggesting they are of a similar lineage).

From British Isles to the United States

In the late 19th and early 20th centuries in U.S. there was an extreme shortage of wild game animals, especially on the heavily populated east coast. Market hunting had reduced wild deer populations in Maryland to such low numbers that hunting seasons were closed and restocking efforts were undertaken. The lack of wildlife as food sources inspired some (including members of the U.S. Department of Agriculture) to consider game farming, especially deer farming as a source of meat (Lantz 1908, 1910). Sika deer were, and still are, considered a tasty and easily managed species for farming (Powerscourt 1884; Lantz 1910).

Prior to their removal from the Park at Woburn Abbey, a gift of 5 sika deer was made to Clemment Henry (or a middleman who gave them to Mr. Henry shortly after receiving them) in Maryland (Flyger 1960; Feldhamer and Demarais 2009). These deer were kept as pets until their release into the wild in 1916 onto James Island, a small island located south of the Choptank River inlet in the Chesapeake Bay (Fig. 1). James Island was 185 acres at the time, however, due to sea level rise and nature weather events, James Island is now split into 3 smaller islands totaling about half the total landmass. In 1920, Dr. Charles Law from Berlin, Maryland purchased 4 or 5 sika deer from a man in Cambridge (most likely Clemment Henry); he kept these and they reproduced. Sika deer on James Island were successfully reproducing because Mr. Law purchased only a portion of the deer that were released to James Island.

Maryland population establishment and growth

A split in the Maryland population

Around 1924, a Boy Scout troop purchased up to a dozen deer (presumably the entire stock) from Mr. Law in Berlin, MD and kept them in Ocean City, MD (Fig. 1) as a tourist attraction (Flyger 1960). There was an amusement park run by Dan Trimper in Ocean City and he may also have been the leader of the Boy Scout troop (Presnall 1958). As the novelty of these deer wore off, the Boy Scouts released them across the Ocean City inlet (<300 m) to the north end of Assateague Island (Fig. 1). The released deer quickly expanded to the entire barrier island, but by 1958 the population was still only 60–100 individuals (Presnall 1958; Flyger 1960). The USFWS (2011) report that in 1943 sika deer had dispersed the entire length of Assateague Island and by 1963 their numbers were estimated at 1300. Sika deer quickly spread to neighboring Chincoteague Island and maintained a population of 1000 there until the 1990's (USFWS 2011).

Population control

Once established, the sika deer in Maryland had several large swings in population size. First, in 1957 a large fire on James Island destroyed the majority of the understory causing the indirect death of many sika deer by starvation. Between those killed in the fire and those that died of starvation, more than 160 deer perished (Flyger and Bowers 1958; Flyger 1959). Christian et al. (1960) conclude that this large population decline on James Island was the result of physiological derangements brought on by high population densities, however, the do not mention the fire or its potential influences on the population. Hayes and Shotts (1959) concluded that the die off was a result of malnutrition and pine oil poisoning as a result of overconsumption of pine without other resources available on the island. Regardless of the cause the population at the time was between 270 and 300 animals (Flyger and Bowers 1958; Flyger and Warren 1959; Christian et al. 1960) concentrated on James Island with a few individuals visiting or establishing permanent home ranges on the mainland, resulting in >50% mortality.

Harvest of sika deer began on James Island and Taylor's Island (actually mainland Dorchester County) as early as 1938 (Flyger and Warren 1959) but was sporadic through the early 1960's with only a few harvested annually (Flyger and Davis 1964). Harvest of white-tailed deer resumed, but was limited in the 1930's through 1960's. During these years, the

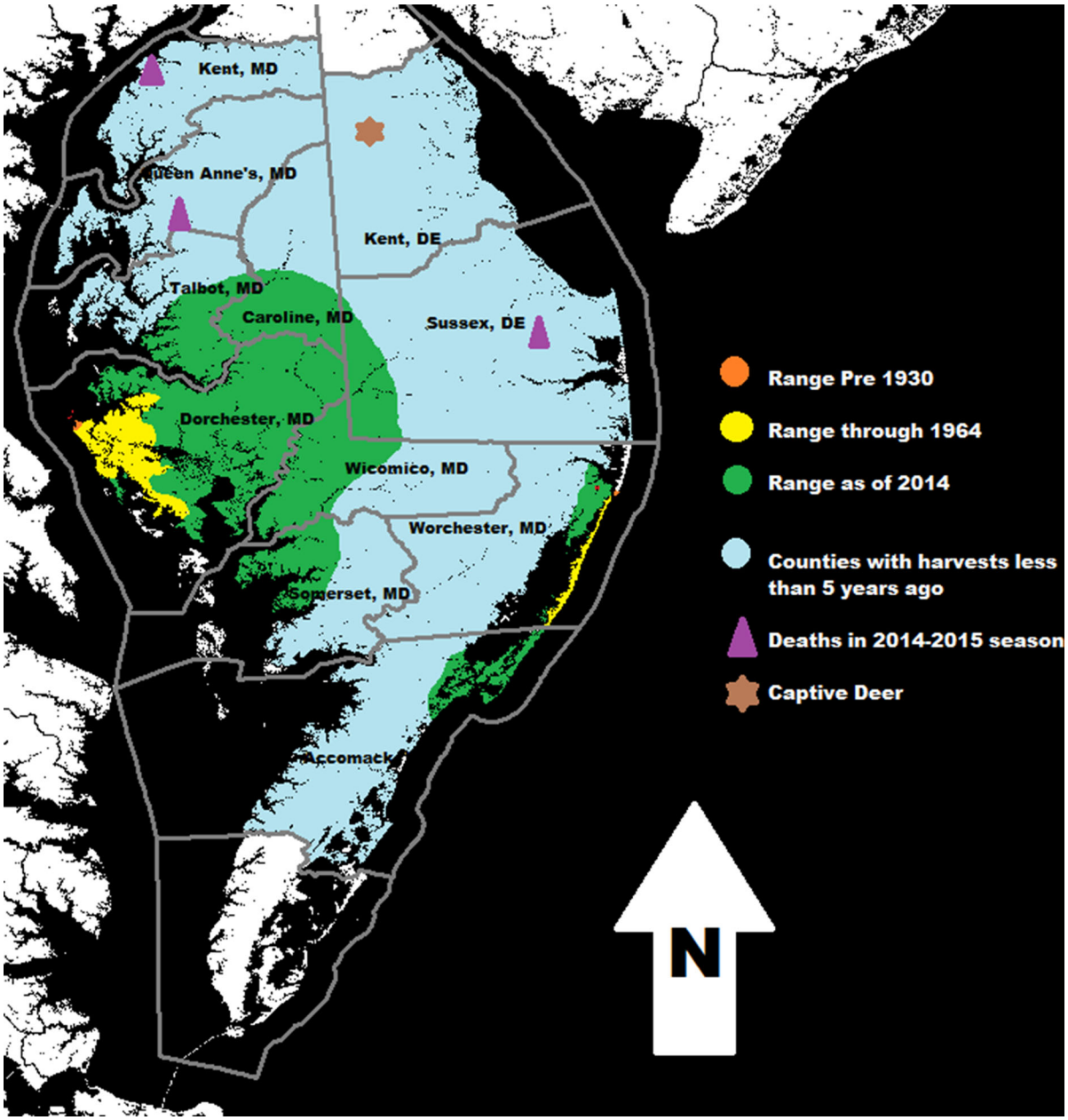

Fig. 1 Change in distribution of sika deer on the Delmarva Peninsula over 100 years. Harrington Delaware shows where captive sika deer are held. Islands in red show the location of the initial sika deer release in Maryland (James Islands). Area labeled in *yellow marked* according to Flyger and Davis (1964). *Blue triangles* show the location of sika deer deaths known from 2014 season that are considered far outside the current sika deer range

few sika deer harvested were taken under a standard, non-specific deer tag (Flyger and Davis 1964; Eyler and Timko 2014). Flyger and Davis (1964) estimated the geographic range of sika deer in the early 1960's to be about one third of the way across Dorchester County (Fig. 1), or about 10 linear miles. Sika deer harvest on Assateague began in 1964 when the population was estimated to have grown to 1300 (USFWS 2014). Sika deer were so abundant that they had created a clear browse line around the island. The harvest of sika deer helped to reduce the population to an estimated 600 deer by 1990 (USFWS 2014).

As the spread of sika deer continued and the harvest of sika deer increased, sika deer harvests needed to be separated from white-tailed deer harvests to collect information for management decisions. Sika deer were distinguished from white-tailed deer as a large game animal in 1973 and harvest regulations actually allowed more sika deer to be harvested than white-tailed deer in Dorchester County (Feldhamer et al. 1978). After sika deer harvest was separated from white-tailed deer harvest, Dorchester County averaged 415 sika deer harvests per year for the first 5 years (1973–1977: Feldhamer et al. 1978). In comparison from 2009 to 2013, Dorchester County harvested an average of 2397 sika deer per year (Eyler and Timko 2010, 2011, 2012, 2013, 2014). In addition to the thousands harvested in Dorchester County, sika deer are now harvested annually in Caroline, Somerset, Talbot, Wicomico, and Worchester Counties. Outside of Maryland, sika deer from the same initial introduction in 1916 are harvested in neighboring states Virginia and Delaware.

Support for the Maryland origins

Molecular support

The first study to attempt to determine the lineage (which of 14 different subspecies) of Maryland's sika deer was not conducted until 2002 (however see Cook et al. 1999 for use in classification). Six sika deer from across the extent of their range at the time were sampled for mitochondrial DNA haplotypes. Dr. Jesus Maldonado from the Smithsonian Institute amplified a section of the control region of mitochondrial DNA. He found all six of the sampled deer shared the same haplotype (and matched 8 sample sequences from Cook et al. 1999) which fit into the *C.n. yakushimae* cluster which had been very clearly defined in Japanese literature (J. Maldonado, personal communication). The *yakushimae* subspecies of sika deer are the smallest subspecies of sika deer and are native to two small islands in the very south-eastern portion of the Japanese Island chain (Fig. 2), Yakushima Island and Kuchinoerabujima Island (Tamate et al. 1998; Nabata et al. 2004; Koda et al. 2008).

A more in-depth look into the genetic variation of sika deer on the Delmarva Peninsula is needed and could provide insight into historic hybridizations. Current work with highly variable microsatellite markers shows an extreme lack of polymorphism and heterozygosity in Delmarva sika deer tissue samples. We observed 11 alleles across 10 loci in Assateague samples (N = 29), 14 alleles across 10 loci in Dorchester samples (N = 53), compared to 28 alleles across the same 10 loci in samples from Yakushima Island Japan (N = 14). There were more alleles found in the Dorchester samples compared to Assateague samples. This suggests that the transfer of deer from Dorchester to Assateague did not carry all the genetic diversity of the population through the Maryland population split. While there were 12 alleles shared between Maryland and Yakushima, there were also 2 unique alleles in the Dorchester that were not observed in Yakushima samples suggesting that not all the genetic information found in Maryland was exclusively from Yakushima sika deer. A lack of polymorphic enzymes was also observed in sika deer by Feldhamer et al. (1982) who tested between 25 and 40 individual sika deer from Maryland across 10 enzymes and found no polymorphism or heterozygosity. These data support both the severe bottleneck of sika deer on Delmarva, and the hybridization between several subspecies/species that we know occurred in the UK.

Increases in the severity of bottleneck and/or founder events should theoretically increases the intensity of genetic drift, and decreases adaptation

Fig. 2 Islands of Japan highlighting the Capital city, Tokyo and the Island of Yakushima, the origin island for the sika deer that were introduced to the UK in the late 1800's and then from there, to the Delmarva Peninsula in 1916

through natural selection which should cause problems with reproduction and survival due to susceptibility to disease (O'Brien et al. 1985). Due to the serial nature of several events the sika deer on Delmarva express extremely low genetic variability however, there is no evidence that the populations are affected by this lack in variation.

Kirpatrick and Jarne (2000) point out that recessive mutations (likely to cause disease and disorders) are often purged from populations that are founded from few individuals. Lacy (1997) suggests that all small populations of mammals that persist post-bottleneck events are/should be affected by inbreeding; sika deer of Delmarva may challenge this assumption. Delmarva sika deer low genetic diversity parallels (on a smaller scale and location) examples observed in red deer in Bavaria (Kuehn et al. 2003) or sika deer in Japan (Nabata et al. 2004) where cervids have survive and proven successful after extensive population declines and bottleneck events (Allendorf et al. 2008).

Sika deer that are on the eastern shore have not only survived, they have been highly successful, and in some cases shown high resistance to disease and parasitism (Davidson and Crow 1983). Some of the introduced sika deer success may be attributed to some degree of hybridization in past generations (Tompkins et al. 2006) although we did not detect any clear genetic enrichment. Sika deer on Delmarva appear to be well adapted to their environment, but given the way the population has changed over the years since their introduction, this is most likely a coincidence of a generalist herbivore rather than the evolution of the fittest adapting to the new environment.

Physiological support

Weight of Delmarva sika deer add supporting information regarding sika deer arriving from Yakushima, Japan by way of the United Kingdom. On the native island of Yakushima, body weight for an adult male is about 40 kg (88 lbs.: Takatsuki 1990; Koda et al. 2008). Today, harvest weights of sika deer on Delmarva are comparable to the Yakushima sika deer, between 27 and 37 kg (60 to 80 lbs: Eyler and Timko 2014) with large adult males reaching 50 kg (110 lbs) dressed weights (Personal communication, A. Jolicoeur, Farm Manager at Tudor Farms LLC). However, after their initial establishment on the Delmarva Peninsula, there are reports of deer harvested with dressed weights between 58 and 68 kg (125–150 lbs: Flyger and Warren 1959). These larger weights could be reflective of some introgression of genes from some of the larger subspecies of sika deer or red deer that were still in the population from their historical lineages in the United Kingdom. These data also suggest that there was more variation in weight of sika deer 50 years ago, prior to the fire of 1957.

Antler characteristics of sika deer on the Delmarva Peninsula also suggest a mixed sika lineage. The antlers of Yakushima sika deer usually have 4 points with a max of 6 (3×3: Takatsuki 1990). Larger subspecies of sika deer in the Japanese Islands are known to carry antlers of 8 points (Takatsuki 1990; Bartoš 2009), while mainland sika deer and red deer can commonly carry much larger antlers, 10–12 and 12–16+ respectively (Bartoš 2009; Winans 1913). Sika deer on the Delmarva Peninsula typically carry 4–6 points, but 7 and 8 points are observed (Eyler and Timko 2014). The mixture of larger subspecies genes into the population due to hybridization at Woburn Abbey (Bartoš 2009) could have led to the antler characteristics that we see today on the Delmarva Peninsula.

Implications and management

Understand how Delmarva sika deer will impact their communities is critical to the native ecosystem (Simberloff et al. 2012). Personal communications of observations, harvests, and road kills, show that sika deer are continually progressing (from both Dorchester and Assateague) towards the center of, and north along the peninsula. The continued growth of the population leads to additional concerns, one being the presence of a population of farmed Manchurian (a distinguishable subspecies) sika deer held in captivity in Harrington, DE (approximately 80 km north-east of the Dorchester County). To date, there are no confirmed sightings or harvests of wild sika deer close to Harrington but the chance of further admixture if these captive deer were to interbreed with the wild sika deer is cause for concern. The realistic probability of escapees from the farmed deer breeding with wild type sika deer on Delmarva are still remote, but we predict that this chance will increase as wild sika deer continue to expand northward up the peninsula (sika deer escaping captivity is well documented in several

other States: Feldhamer and Demarais 2009). The biological and ecological consequences of such a hybridization could be profound for the Delmarva region. An introgression of genes from larger sika deer, and an increase in allelic diversity could result in an even more adapt species with an existing competitive advantage over native white-tailed deer (Feldhamer and Armstrong 1993; Bartoš 2009).

There are also concerns about the impact of sika deer resource use. Sika deer are a large herbivore with a diet that includes a broad range of plant species, many that are found in white-tailed deer diet (Keiper 1985). Since their introduction, scientists and wildlife professionals have been interested in investigating the competition that sika deer have with white-tailed deer (Flyger and Warren 1959; Keiper 1985; Feldhamer and Armstrong 1993). One of the most obvious and concerning problems of sika deer is the displacement of native white-tailed deer because of their high degree of niche overlap in geographic area, dietary resources, and spatio-temporal activity (Flyger 1959; Keiper 1985; Eyler 2001; Kalb et al. 2013). The direct cause of the change in white-tailed deer range is not fully understood yet, but it is clear that there sika deer are taking over some areas. There are portions of Dorchester that prior to 1970 had thriving white-tailed deer communities and annual harvest, that now have only sika deer and harvest equivalent numbers (Feldhamer and Demarais 2009).

In addition, the impact sika deer have by consuming different plants than native deer is also important and should be investigated. Current sika deer populations are concentrated in both the Chesapeake and Delaware Bay areas; they spend more time in the salt marsh habitat eating plants that white-tailed deer do not consume, or consume in very low quantities, that are important parts of this critical ecosystem (Bertness 1999) such as cattail (*Typha* spp.), cord grass (*Spartina* spp.), reed grass (*Phragmites* spp.), sedges (*Carex* spp.) and rushes (*Juncus* spp.) (D. M. Kalb, Unpublished data). The high population densities of sika deer that exist in some areas cause concern about how their diet on these species is impacting the marshes of Delmarva (Takatsuki 2009).

The implications of invasive deer species can reach beyond their diet use or any direct measure, and may not be realized for several generations (Chollet et al. 2015). Uncontrolled herbivory is already understood to have devastating impacts on the salt marsh community. The periwinkle (*Littoraria irrorata*) was shown to decimate salt marsh grass in the absence of a predator (Silliman and Bertness 2002). Nutria (*Myocastor coypus*) have caused extensive damage due to their herbivory habits both here in Maryland as well as in Louisiana both of which currently have extensive eradication efforts in place (Southwick Associates 2004; Hogue and Mouton 2012). There are few predators of sika deer on Delmarva, other than human harvest.

Sika deer on Delmarva provide a unique resource. They are an additional game species to hunters which draws upwards of 5000 hunters annually (Eyler and Timko 2014). While Maryland's economy benefits from having sika deer, they are not native and harm the wildlife and the habitats where they are found. Like other exotics on the eastern shore (nutria, mute swan [*Cygnus olor*], and snakehead [*Channa argus*]); the presence of sika deer needs to be balanced against the negative effects that result from invasive species. For these others (nutria and snakeheads) the benefit does not appear to influence management and there are state-wide attempts at eradication. There is little hope that even if the desire to eradicate sika deer was accepted (there is little chance of agreement from all stakeholders), that it would be feasible (Feldhamer and Demarais 2009). Sika deer have established a foothold in a highly inaccessible portion of the state. The range of sika deer is continually expanding and only time will tell if harvest regulations (2014–2015 season will increase from 2 sika deer to allow 3 sika deer to be harvested per weapon, no more than one antlered) will curtail this expansion. A more clear understanding of the maximum expansion edge of sika deer have expanded to is also necessary. With observations and harvested sika deer coming from counties as far north as Kent MD and Kent DE, regulations need to be implemented that will allow hunters in these northern areas to harvest sika deer, slowing their spread.

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