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Natural history of *Amblyomma maculatum* in Virginia

Robyn M. Nadolny[1,2] and **Holly D. Gaff**[1,3]

[1]Old Dominion University, Department of Biological Sciences, Norfolk, VA USA

[2]U.S. Army Public Health Center Tick-Borne Disease Lab, Aberdeen Proving Ground, MD USA

[3]University of KwaZulu-Natal, School of Mathematics, Statistics, and Computer Sciences, Durban, South Africa

Abstract

The Gulf Coast tick *Amblyomma maculatum* Koch is increasingly relevant to medical and veterinary communities as human infection rates of *Rickettsia parkeri* rise, the risk of introduction of *Ehrlichia ruminantium* increases, and the range of this tick expands into the densely populated Mid-Atlantic region of the United States. We report on the results of five years of field surveillance to better describe the ecology of *A. maculatum* in newly established populations in southeastern Virginia. We document habitat preferences, host preferences, and the phenology of the adult human-biting life stage. We discuss key ecological factors needed for *A. maculatum* establishment and the influence of the successional process and anthropogenic activities on the persistence of *A. maculatum* populations in Virginia.

Keywords

Amblyomma maculatum; invasions; range expansions; succession; ticks

INTRODUCTION

The Gulf Coast tick, *Amblyomma maculatum*, is an aggressive, human-biting tick of increasing medical and veterinary significance (Paddock and Goddard, 2015). It is a known vector of several emerging pathogens including *Rickettsia parkeri*, the agent of Tidewater spotted fever (Paddock et al., 2004). Human infection with *R. parkeri* results in an eschar-associated febrile illness that is milder than the more familiar Rocky Mountain spotted fever caused by the related *Rickettsia rickettsii* (Paddock et al., 2008). Veterinary pathogens transmitted naturally or experimentally by this tick include *Hepatozoon americanum*, the principal agent of American canine hepatozoosis (Baneth, 2011), *Rickettsia felis*, the agent of feline rickettsiosis, *Leptospira pomona*, causal agent of leptospirosis in livestock, and *Ehrlichia ruminantium*, the agent of heartwater in ruminants (Stromdahl and Hickling, 2012). In addition, *A. maculatum* is often infected with spotted fever group rickettsiae of unknown pathogenicity, including "*Candidatus* Rickettsia andeanae" and other newly described organisms (Paddock et al., 2010; Jiang et al., 2012). In addition to carrying various microbes, *A. maculatum* is a relatively large tick, and bites can cause inflammation, edema, abscesses, and predisposition to myiasis, anemia, and secondary infections, especially in livestock (Paddock et al., 2010; Teel et al., 2010; Jiang et al., 2012). As the effects of these pathogens on human and animal health have become better understood over the last decade, there has been a renewed interest in understanding the ecology *A. maculatum* in order to prevent disease (Paddock and Goddard, 2015).

The historical range of *A. maculatum* throughout the Caribbean, South and Central America is extensive, including records from Mexico, Jamaica, Belize, the West Indies, Columbia, Venezuela, and Peru (Teel et al., 2010; Paddock and Goddard, 2015). The southern extent of the range of *A. maculatum* is in question because of the morphological similarity of *A. maculatum* to the closely related *A. tigrinum* and *A. triste* (Estrada-Peña et al., 2005). In the early 1900s, *A. maculatum* was common along the Gulf Coast of the U.S. from Louisiana to Texas, invading into the coastal Atlantic region up through South Carolina in the mid-1900s (Teel et al., 2010). After the 1950s, the distribution of *A. maculatum* drastically changed, as the cattle industry facilitated the establishment of this tick in Kansas and Oklahoma in the 1950s-1980s (Teel et al., 2010; Paddock and Goddard, 2015). Researchers in Arkansas collected over 200 *A. maculatum* between 2006 and 2009, and now consider *A. maculatum* to be established in that state (Trout et al., 2010; McAllister et al. 2016). Between 2009 and 2011, *A. maculatum* populations reached sufficient levels to be considered established in North Carolina, having previously been known only from sporadic records (Harrison et al., 2010; Varela-Stokes et al., 2011). Newly established *A. maculatum* populations have also recently been discovered in southeastern and northern Virginia (Fornadel et al., 2011; Wright et al., 2011), Delaware (Florin et al., 2014), and Kentucky (Pagac et al., 2014). Incidental collections of individual ticks reported nearly everywhere further north are generally along migratory bird flyways; migrating birds and an expanding white-tailed deer population have been suggested as hosts that may be implicated in the continued expansion of this tick (Paddock and Goddard, 2015).

Human infections with *R. parkeri* are reported everywhere this tick is found (Sumner et al., 2007; Jiang et al., 2012; Paddock and Goddard, 2015). However, newly established populations of this tick, especially in Mid-Atlantic states, have tended to exhibit higher infection prevalence than populations found in areas where these ticks have long been established (Paddock et al., 2010; Sumner et al., 2007; Cohen et al., 2009; Jiang et al., 2012; Trout et al., 2010; Wright et al., 2011; Fornadel et al., 2011; Varela-Stokes et al., 2011; Ferrari et al., 2012). Some of the first cases of *R. parkeri* infection were described in Virginia, which has only had established *A. maculatum* populations for a short while, indicating this tick can start spreading disease as soon as it arrives (Paddock et al., 2004; Whitman et al., 2007). Recent evidence suggests that spillover of *R. parkeri* to other common tick species, including the lone star tick (*Amblyomma americanum*), may occur in areas invaded by *A. maculatum* (Gaines et al., 2014; Henning et al., 2014; Wright et al., 2015). As this tick continues to expand its range, understanding the ecological mechanisms by which new populations arise and persist is critical to protecting human and animal health. Here, we describe the results of five years of field surveillance on newly established populations of *A. maculatum* in southeastern Virginia, and discuss implications for the continued expansion of *A. maculatum* into the Mid-Atlantic.

MATERIALS AND METHODS

Collection of questing ticks

Questing *A. maculatum* were collected from public and privately owned lands throughout southeastern Virginia from for five years from 2010 to 2014. Fifteen sites representing a variety of woodland, grassland, successional, and anthropogenically disturbed habitats were sampled weekly during the summer months and at least monthly throughout the rest of the year (Fig. 1). All transects were marked with surveyor's flags so that the same transect was walked during each sampling event. In order to determine the area sampled at each site, GPS coordinates were taken along each transect. ArcGIS 9.3 (www.esri.com) was used to draw a line connecting the GPS points from each transect and to draw a 2m buffer around the line.

Ticks were collected using $1m^2$ white denim flags attached to wooden dowel rods swept over the ground and through low vegetation. All ticks found clinging to the flag material were removed from the flag with forceps and placed in containers labeled with the time and date of collection, as well as the sampling location, temperature, and other weather data. Ticks were frozen at −20 C until morphologically identified (Keirans and Durden, 1998) ; they were then stored frozen at −80 C. Only sites where more than six adult ticks or multiple life stages were collected within a single collection period were considered to represent established populations (Fish and Howard, 1999).

Collection of ticks from hosts

Host-targeted sampling techniques were employed from 2010 to 2014, including collection of ticks from large mammals at hunt check locations during the fall of each year, collaboration with veterinarians to collect ticks from companion animals, serendipitous sampling of road-killed mammals, small mammal live-trapping, avian sampling using mist-nets, and opportunistic hand-capture of reptiles at flagging sites (ODU IACUC # 11-012, 13-018, 13-008). In addition, ticks found crawling on or attached to humans throughout southeastern Virginia were submitted periodically to the Old Dominion University Tick Research Team between 2011 and 2014 as a result of local outreach and educational programs.

Large wild mammals were sampled for ticks through collaborations with local hunters, game managers, and state biologists, and through checking road-killed animals for ticks. Any ticks found on dead mammals were removed with forceps, places in vials, and returned to the laboratory where they were frozen at −20 C until processing. Domesticated animals were sampled through collaborations with veterinarians with practices in southeastern Virginia. If any ticks were found on an animal patient, ticks were removed, labeled, and frozen until they could be forwarded to the Old Dominion University Tick Research Team for identification and processing.

Small mammal communities were sampled at two primary flagging sites with established populations of *A. maculatum*, CHS and CH2. These sites represented mid to late successional habitats adjacent to the Great Dismal Swamp National Wildlife Refuge in the City of Chesapeake, Virginia, and were dominated by grasses and forbs with mixed coniferous and deciduous trees that were 5–15 years old. Transects or grids of modified Fitch live traps (Rose, 1994) were laid at each site. Trapping was conducted monthly or quarterly from 2010 to 2014. Traps were baited with birdseed and sunflower seeds, set in the evening, and checked for three consecutive mornings. Trapped mammals were examined for ticks, and any ticks were removed using forceps, placed in vials, and returned to the laboratory to be frozen until identification and processing. All mammals were handled according to the guidelines set forth by the American Society of Mammalogists (Sikes and Gannon, 2011).

Avian hosts were sampled from 2013 to 2014 at a subset of the flagging sites (Fig. 1) through weekly or bi-weekly mist netting, conducted as previously described (Heller et al., 2016). Starting in 2013, local reptiles were sampled at the weekly flagging transect sites, with an emphasis on collecting ticks from native lizards, snakes, and turtles. Reptiles were captured using standard collection techniques, including the implementation of artificial cover objects and visual encounter surveys, and examined for ticks before being released (McDiarmid et al., 2012). Ticks were removed from reptiles with forceps and placed in vials, before being returned to the laboratory and frozen until identification and processing.

Molecular methods and identification

All ticks collected from flags and from hosts were identified to species using morphological characters (Clifford et al., 1961; Keirans and Durden, 1998). If morphological identification was impossible because of uncertain morphological characters or damage to the specimen, a fragment of the 16S mitochondrial rRNA gene was sequenced using previously established methods (Nadolny et al., 2015) to determine tick species. While adult *A. maculatum* are morphologically distinct from other U.S. ticks in the genus *Amblyomma*, immatures can be difficult to tell apart from other *Amblyomma* and *Dermacentor* species, especially when engorged. Unengorged immatures from flags and engorged immature ticks from hosts were identified via restriction fragment length polymorphism (RFLP) assay and/or sequencing of the 16S mitochondrial gene (Fornadel et al., 2011).

RESULTS

Questing adult *A. maculatum* ticks were collected from eight of 14 sites sampled from 2010–2014 (Fig. 1, Table 1). Of those sites where *A. maculatum* was collected, four yielded sufficient numbers of adults within a single sampling period to be considered populations (Fig. 1). Adults were collected only during the warmer months, from April through September, with peak activity in June (Fig. 2). While immature *A. maculatum* were infrequently collected on flags, a small number were collected over the five years (Table 2). *Amblyomma maculatum* immatures were flagged almost exclusively immediately after grassy fields had been mowed at sites where large numbers of adults were regularly collected. Larvae and nymphs were sporadically collected from spring through late summer, however, insufficient numbers of immatures were collected to establish a clear phenology of these life stages in Virginia.

Amblyomma maculatum adults were collected from a variety of habitat types over the five years (Table 1), but all of the most productive sites where *A. maculatum* could be reliably collected were characterized by open habitat, including mowed fields (YRK, HAM, and parts of VB1) and old fields undergoing ecological succession to forest (CHS and CH2). Sites with large swaths of open habitat had the highest densities of *A. maculatum* per m^2 (Fig. 3), and maintained those populations of *A. maculatum* over multiple years (Table 1).

Sites where populations of *A. maculatum* were established did not maintain static numbers of ticks from year to year (Table 1, Fig. 3). In particular, the largest population of *A. maculatum* at the CHS site reached peak abundance in 2011, with decreasing numbers each subsequent year, indicating the decline of this population. This decline corresponded with the progression of ecological succession, and the closure of the canopy at that site. Another site, CH2, yielded increasing numbers of *A. maculatum* in the two years it was sampled, indicating that this population may be undergoing an increase in *A. maculatum* numbers, similar to the first few years of sampling VB1 and CHS. This site is earlier in the successional process, and will not undergo canopy closure for several more years. While numbers of *A. maculatum* were fewer at VB1 (Table 1), *A. maculatum* were the most densely populated tick at this site (Fig. 3). The VB1 site is a nature preserve that comprises grassy areas that are anthropogenically maintained through annual mowing as well as preserved dune and maritime forest communities.

At each site where *A. maculatum* was collected, other common species of ticks were also found, including *Dermacentor variabilis*, *Amblyomma americanum*, *Ixodes affinis*, and *Ixodes scapularis* (Table 3). At almost every site, *A. americanum* was by far the most abundant tick species, with the exception of *D. variabilis* being most abundant at two sites, PT1 and CH2. *Amblyomma maculatum* was the second most abundant tick species at only one site, VB1.

Of 370 individual large animal hosts, from 15 species sampled, and 3,293 ticks removed, only seven were adult *A. maculatum*. These seven ticks were collected from six individual animals, including a cat (*Felis catus*), a dog (*Canis lupus familiaris*), three white-tailed deer (*Odocoileus virginianus*), and a feral hog (*Sus scrofa*) between 2010 and 2014 (Table 4). Most *A. maculatum* were sharing hosts with other common ticks at the time of collection, including *Dermacentor albipictus*, *D. variabilis*, *A. americanum*, and *I. scapularis* (Table 4).

Immature *A. maculatum* were more difficult to sample than adults. Of 643 small mammals captured and 1,087 individual ticks collected from these small mammals, only seven engorged immature *A. maculatum* from five rodents could be conclusively identified using molecular techniques (Table 4). Of 944 ticks collected and identified using molecular techniques from 1,888 birds sampled year-round from 2012–2014, not a single *A. maculatum* immature was collected (Heller et al., 2016; Walters laboratory, unpublished data). Similarly, 11 larval ticks collected from 81 native reptiles were determined, via sequencing, to be *I. scapularis*. Of 544 ticks found crawling on or attached to humans that were submitted to the Old Dominion University tick laboratory between 2011 and 2014, four adult *A. maculatum* were identified (<1%).

DISCUSSION

Phenology

The seasonal phenology of *A. maculatum* shifts depending on geographical distribution (Teel et al., 2010). The three life stages minimally overlap in peaks of activity; however, *A. maculatum* from inland populations in Oklahoma and Kansas become active five months earlier than ticks from historic populations in Texas (Williams and Hair, 1976; Johnson, 1990; Teel et al., 1998; Teel et al., 2010). In Texas, adults feed in September while in Kansas and Oklahoma, adults feed from April through early June (Teel et al., 2010). The phenology of *A. maculatum* adults in Virginia falls between those described for Texas and Oklahoma (Teel et al., 2010), with peak adult collections in the month of June. It is most similar to populations described from Mississippi, where adults were collected from March through November with peaks in July and August (Goddard and Paddock, 2005). Survival and duration in each life stage is dependent on environmental variables, including habitat, temperature, and humidity (Teel et al., 2010). A period of fall and winter quiescence of adults is standard in all areas in the U.S. where this tick species has been collected.

Virginia *A. maculatum* nymphs were collected from March through September and a few larvae were collected on flags in April, but these small numbers were insufficient to establish immature phenology. In Texas, peak larval and nymphal feeding seasons are in January and February, respectively, while in Kansas and Oklahoma, larvae peak in June and nymphs in July (Teel et al., 2010). Mississippi *A. maculatum* nymphs have been collected from February through August, and larvae have been collected from June though November (Paddock and Goddard, 2005; Portugal and Goddard, 2015). If the trends from these populations hold true for Virginia *A. maculatum*, peak larval abundance would be expected several months after the adult peak, followed closely by nymphs, probably in late summer and early fall. Immature *A. maculatum* are notoriously difficult to collect (Goddard, 2007), and additional work with novel collection methods such as swabbing rodent burrows should increase our understanding of immature phenology in this tick species (Portugal and Goddard, 2015).

Predictors of *A. maculatum* presence and absence

Established populations of *A. maculatum* were discovered at only four of twelve sites sampled continuously over multiple years, indicating that high sampling frequency does not guarantee discovery of this tick. Unlike *A. americanum*, this tick is not universally distributed throughout the landscape of southeastern Virginia. A specific set of abiotic and biotic factors may be necessary to support a population; if these factors are in place, large numbers of *A. maculatum* may emerge in just a few years. The life cycle of *A. maculatum* is generally completed in 1–2 years (Teel et al., 2010). Engorged females lay an average of 8,000 and up to 15,000 eggs (Drummond and Whetstone, 1970; Wright, 1971), demonstrating the ability of this tick species to undergo rapid population expansion after arrival in a suitable new habitat.

In southeastern Virginia and throughout its range, *A. maculatum* has been found sharing habitats and hosts with other ticks. One observed trend of where *A. maculatum* would be found was the presence of *D. variabilis*, as the habitat and host preferences of these ticks seem to strongly overlap (Table 3). Because of this overlap, as well as superficial morphological similarities between immature stages and females of these two tick species (Paddock and Goddard, 2015), recognizing when *A. maculatum* has invaded may require careful surveillance by experienced acarologists.

In addition to populations of *D. variabilis* at sites where many *A. maculatum* were found, these sites had other commonalities, most notably particular habitat characteristics. No *A. maculatum* were found in forested habitats including bald cypress-tupelo swamps, pine savannahs, and mixed hardwood forests. All *A. maculatum* sites comprised open successional old field habitat with little shade, dominated by grasses and shrubs (Table 1). These xeric habitats are similar to other areas where *A. maculatum* have been found in other regions; along the Gulf Coast and in the inland Midwestern U.S., *A. maculatum* is common in grass-dominated habitats such as prairies, scrublands, oak savannahs, and mesquite (Scifres et al., 1988; Teel et al., 2010). Other newly identified populations of *A. maculatum* in the Mid-Atlantic have been found in disturbed grassy habitats, including a large population at a landfill in northern Virginia (Fornadel et al., 2011) and small numbers in a disturbed secondary growth habitat (Florin et al., 2014). In general, *A. maculatum* habitat has been described as southern coastal habitat with high rainfall, temperature and humidity, with open, non-shaded habitats where *A. maculatum* can quest for hosts in the heat of the day (Paddock and Goddard, 2015).

Most open habitats in Virginia are anthropogenically influenced through prescribed burning, tree clearing, or mowing to create fields or other open spaces for human use. All observed successional-related events at field sites are noted in Table 1. Once these open habitats are created, ecological succession is inevitable unless they are anthropogenically maintained, because of the continual fire suppression along the east coast (for a review of fire and is effects on *A. maculatum*, see Paddock and Goddard, 2015). *Amblyomma maculatum* populations appear in secondary successional habitats in Virginia, when there is tall grass with shrubs, but populations seem to disappear as the canopy closes and field becomes forest, as observed at our CHS site (Table 1). The landscape of the U.S. east coast is extremely developed, so patches of open habitat occur mainly by human design, such as when an agricultural field is left fallow, or an area is cleared for construction. These sites are often near areas with large human populations, including patches in urban or suburban developments. By creating and maintaining these open habitats, especially in areas with significant human habitation, humans are inviting *A. maculatum* to establish and generating new human health risks.

Regulation of *A. maculatum* populations

If open areas are not maintained by natural fire or anthropogenic influence, *A. maculatum* populations seem to be unable to last more than a few years in southeastern Virginia habitats. This ephemeral nature may be unique to *A. maculatum* populations in the southeast, as open habitats and rangelands persist along the Gulf Coast and in the central U.S. where *A. maculatum* are well established. As *A. maculatum* ticks move northward into the Mid-Atlantic, more ephemeral populations can be expected, with short-lived open habitats used as stepping stones to continue the process of expansion into otherwise unsuitable habitat. Anthropogenically disturbed habitat islands seem to be the habitat best able to facilitate the establishment and spread of *A. maculatum* populations in the Mid-Atlantic region. Inland populations of *A. maculatum* have also been described as “ephemeral” because of periodic expansions and contractions associated with patterns of drought and rainfall (Teel et al., 2010). It is possible that precipitation patterns in the central U.S. may regulate those populations as anthropogenic activity regulates coastal populations, which receive more regular precipitation. Alternatively, peripheral populations at expansion fronts may be inherently more fragile and prone to periodic extirpation than more established populations in the historic range of *A. maculatum*.

Pathways for dispersal and spread

Because Mid-Atlantic populations of *A. maculatum* generally exist in habitat islands, they are unlikely to be founded by contiguous populations of ticks (Fig. 4). In order for a population to arise, ticks must be translocated from an existing population to a suitable habitat with an appropriate population of hosts. *Amblyomma maculatum* has been collected from over 71 species of birds and mammals, including humans, in the United States alone (Teel et al., 2010). Rodents and birds are most often hosts of larvae and nymphs, while adult ticks generally parasitize larger mammals. There are no reports of *A. maculatum* collected from reptile hosts. The wide host range utilized by this tick, combined with its ability to withstand xeric habitats, has likely contributed to the successful spread of *A. maculatum* over the last few decades (Paddock and Goddard, 2015).

Because *A. maculatum* feeds on a large variety of avian and mammalian hosts with varying dispersal capabilities, there are many possible pathways for arrival at a new site. *Amblyomma maculatum* was not documented parasitizing any novel hosts in Virginia (Table 4), but it is possible to reconstruct potential pathways to colonization in the Mid-Atlantic using previously reported hosts of *A. maculatum*. Cattle have been implicated in invasions of *A. maculatum* in the central US, and previous studies have suggested that migratory birds might be transporting immature *A. maculatum*, as incidental collections of this tick have historically been along flyways (Teel et al., 2010). The expansion of feral swine across the southeastern and central U. S., and the growing population of white-tailed deer have also been suggested as facilitators of the *A. maculatum* expansion (Paddock and Goddard, 2015). There is no significant cattle industry in southeastern Virginia, so discussion of possible invasion routes will focus on wild hosts that are present in the Mid-Atlantic. To closely examine these possibilities and determine which hosts could be most important in range expansion and new population establishment, a table of relevant ecological and life history characteristics of each of the hosts of *A. maculatum* in the U. S. was compiled (Table S1). Tick dispersal ability depends on the behaviors of these hosts during the months when their life stages are questing.

Small bodied, non-migratory hosts with small home ranges have limited dispersal ability for immature *A. maculatum* ticks. This includes rodents and small non-migratory birds with home ranges generally <1 ha, that generally disperse <2 km from their natal area (Table S1). Rodent hosts can become extremely abundant in suitable habitat, with some species reaching over 100 animals per ha in prime ecological conditions (Table S1). Although these hosts probably do not play much of a role in tick movement, it is likely that high rodent densities are important at sites where *A. maculatum* arrive on more wide-ranging hosts. Large rodent populations may be necessary for a population of *A. maculatum* to establish in a new area, because rodents provide a critical food source for immature ticks. If the phenology curves are as expected (Paddock and Goddard, 2005; Portugal and Goddard, 2015; Teel et al. 2010), immature *A. maculatum* in Virginia should quest in the late summer and early fall, just as rodent populations reach seasonal peaks after reproducing during the spring and summer. Timing the arrival of *A. maculatum* to years in the successional process when field rodents have had time to establish robust populations but before the canopy closes may be critical to enable population establishment.

Small-bodied animals with home ranges <50 ha that disperse up to 200 km, including lagomorphs, sciurids, and birds that are partial migrants in Virginia have moderate dispersal potential for immature *A. maculatum* (Table S1). Partial migrants do not breed in Canada or winter in the neotropics, but will sometimes move up to a few hundred kilometers seasonally. While members of this group have the ability to disperse over long distances, they often do not move more than a few km from their natal area. Populations of these hosts are generally lower than those of small-bodied hosts with small home ranges, but the capacity of these longer-ranging hosts to transport immatures over distances is greater. Most movement of animals in this group occurs during the late summer and fall, when immature *A. maculatum* may be questing.

Medium and large mammals with home ranges over 50 ha that disperse up to and beyond 200 km are likely to be the most important long distance dispersers of adult ticks (Table S1). Adult *A. maculatum* quest in the summer months, which corresponds to the timing when first year offspring of these large mammals are dispersing from their place of birth. The natal dispersal timing of juvenile striped skunks (*Mephitis mephitis*), white-tailed deer, black bears (*Ursus americanus*), and bobcats (*Lynx rufus*) aligns particularly well with *A. maculatum* phenology. Adult *A. maculatum* were collected into August and September, so it is possible that dispersing juvenile coyotes (*Canis latrans*), grey foxes (*Urocyon cinereoargenteus*), and raccoons (*Procyon lotor*) which generally move in fall would also have an opportunity to facilitate movement of these ticks from habitat patch to habitat patch. Male *A. maculatum* attach to hosts and then release a pheromone that aggregates females to mate, increasing the tick load on these large-bodied hosts and the likelihood that hosts will distribute multiple ticks across a landscape (Gladney, 1971; Gladney et al., 1974). Because *A. maculatum* mate on-host, engorged females can lay eggs directly after detaching in a suitable habitat. Because these mammals can host many adult ticks and move them over long distances in short amounts of time, larger mammals translocate the ticks that are most able to found new populations. If engorged females drop off in areas of suitable habitat with high densities of small mammal and bird hosts, their larvae stand a good chance of survival.

Adult ticks are not the only life stage that can be moved long distances. Migratory birds are known hosts for immature *A. maculatum*, and have been documented moving engorged larval and nymphal ticks thousands of kilometers during spring and fall migrations from the ancestral range of *A. maculatum* in the neotropics north to Canada (Ogden et al., 2008; Teel et al., 2010; Scott et al., 2012; Florin et al., 2014). These birds may transport *A. maculatum* immatures southward during the fall, and northward during the spring. Immature *A. maculatum* were collected during the spring, summer, and fall in Virginia. These ticks may move northward during the spring, continuing the invasion into the Mid-Atlantic, or southward in the fall back to sites in areas where *A. maculatum* is already established. Once engorged immatures drop off birds in an appropriate habitat, they must survive to molt, mate, and reproduce in order to seed a new population. Because of challenges associated with survival in the environment, including predation and desiccation (Needham and Teel, 1991), models of tick dispersal have shown faster population establishment with mammalian dispersers (Leighton et al., 2012).

Genetic evidence indicates that long distance dispersal must be taking place in order to facilitate gene flow between remote populations, and that geographically proximate populations of *A. maculatum* do not have higher levels of gene flow than distant ones (Nadolny et al., 2015). This recent study suggests that a combination of mammalian and avian hosts are likely responsible for dispersal, but that dispersal of immatures by migratory birds is necessary to facilitate the observed gene flow between far-flung populations. Combining genetic evidence of gene flow between populations with our understanding of preferred hosts that are abundant in Virginia (Table S1), the most likely pathway for a new population of these ticks to arise in the Mid-Atlantic seems to be through the introduction of multiple genotypes to an anthropogenically disturbed isolated habitat patch by migratory birds and long-distance dispersing mammals. The habitat patch must be at an appropriate stage in ecological succession to be dominated by large populations of rodent hosts in order to provide sufficient blood meals for immature ticks. Using abundant local hosts, a population can grow to large numbers in a short period of time. Once established, the *A. maculatum* population may be more likely to persist only until the canopy closes and the community of small, high-density hosts such as field rodents declines (Langley and Shure, 1980). Ticks may then disperse to other patches, either geographically proximate or distant.

Adult *A. maculatum* were found feeding on domestic dogs and cats in Virginia, and anthropogenic movement of these ticks may be an important factor in this tick's range expansion. *Amblyomma maculatum* adults have been removed from dogs and cats with no travel history in Ontario, Canada, where these ticks are not established (Scott et al., 2001). Willingness to feed on domesticated animals may enable *A. maculatum* to invade human-dominated areas faster than otherwise predicted.

In conclusion, tick ranges are not fixed in time or space and may change rapidly; the geographic range of *A. maculatum* is much more extensive today than it was 70 years ago (Teel et al., 2010; Paddock and Goddard, 2015). This tick species is one of the top four tick species parasitizing humans in the southeastern US, and human infections with *R. parkeri* seem to arise concurrently with the discovery of newly established *A. maculatum* populations (Paddock and Goddard, 2015). Because of the morphological similarities between *A. maculatum* and *D. varabilis* at all but one life stage, it may be difficult to tell when *A. maculatum* have arrived, so vigilance is required. Enhanced surveillance is recommended in anthropogenically disturbed open habitats during the summer months in Mid-Atlantic states to detect new populations of this invader. Once detected, medical and veterinary personnel should be alerted to the increased threat of pathogens vectored by this tick species.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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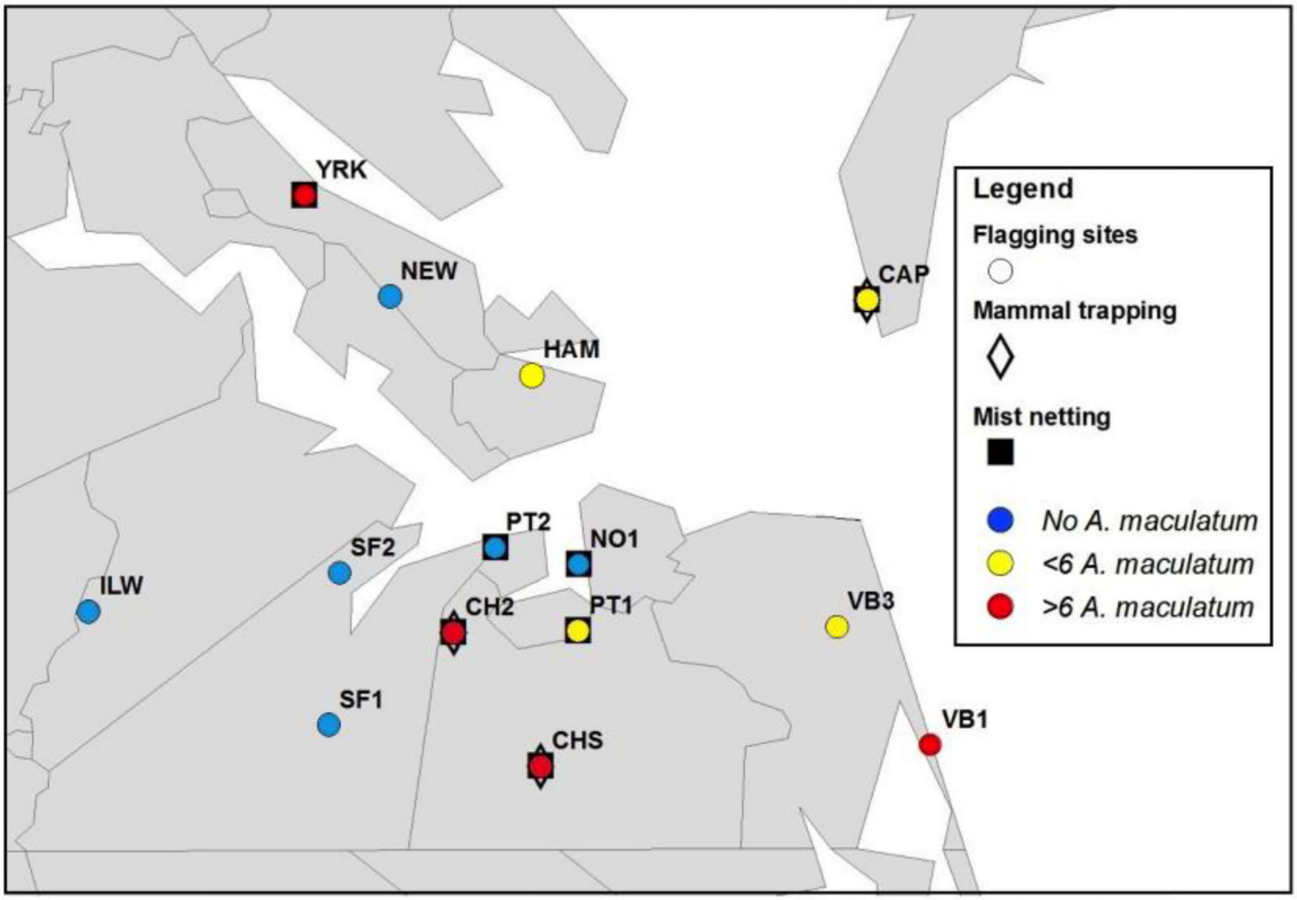

Figure 1.

Map of *Amblyomma maculatum* collection sites, 2010–2014. Map shows southeastern Virginia, U.S. counties and independent cities, with circles marking sites that were flagged weekly or bi-weekly from 2010 to 2014. For years of sampling and brief habitat descriptions of these sites, see Table 1. Sites where mist netting also took place are surrounded by a square, and sites where small mammal trapping also took place are marked with a diamond. Fifteen sampling sites in southeastern Virginia were sampled, eight of which yielded at least one *A. maculatum* in five years of sampling from 2010–2014. Blue sites yielded no *A. maculatum*, yellow sites indicate where fewer than six *A. maculatum* were collected, and red sites indicate established populations of more than six *A. maculatum* collected over five years.

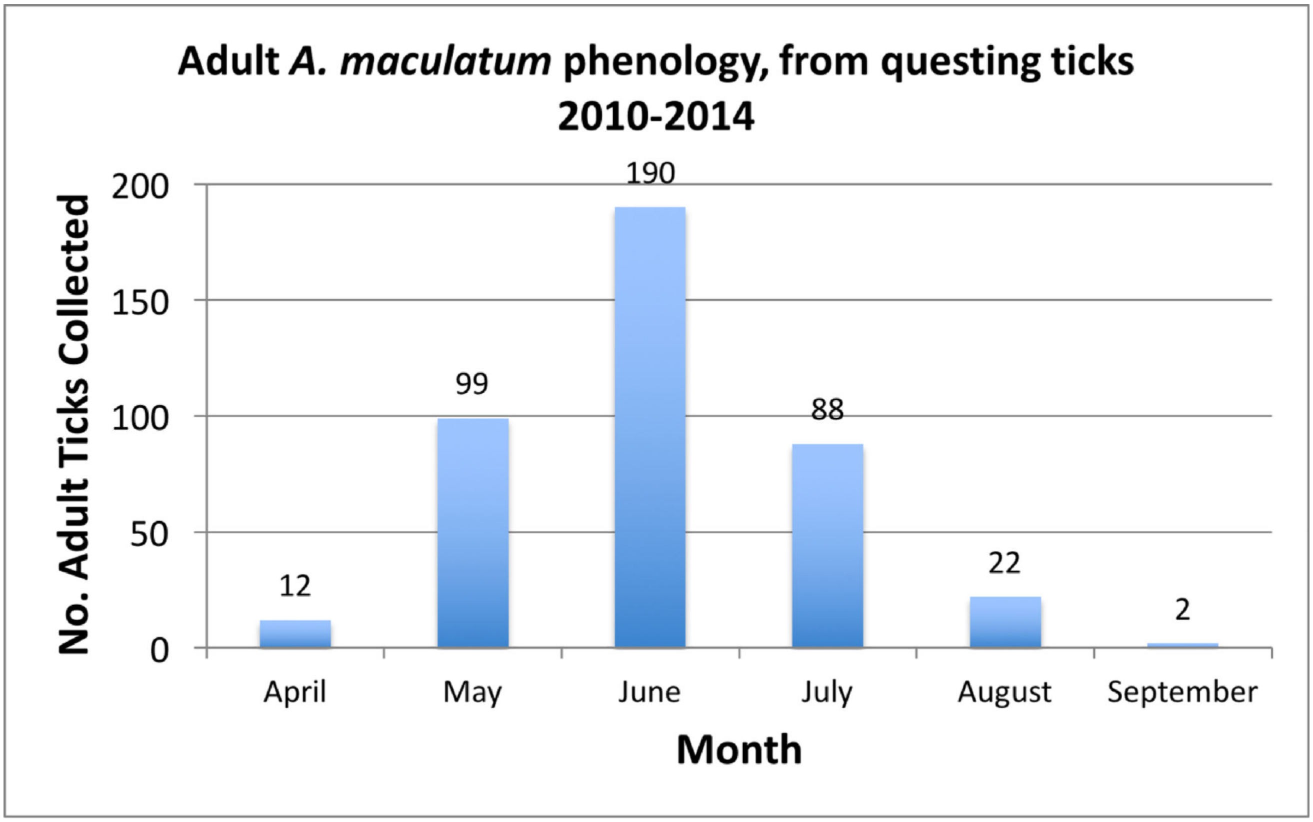

Figure 2.

Phenology of adult *Amblyomma maculatum* collected in Virginia, U.S. over five years. Numbers shown are total adult *A. maculatum* collected at all sites and in all years through equal weekly flagging effort.

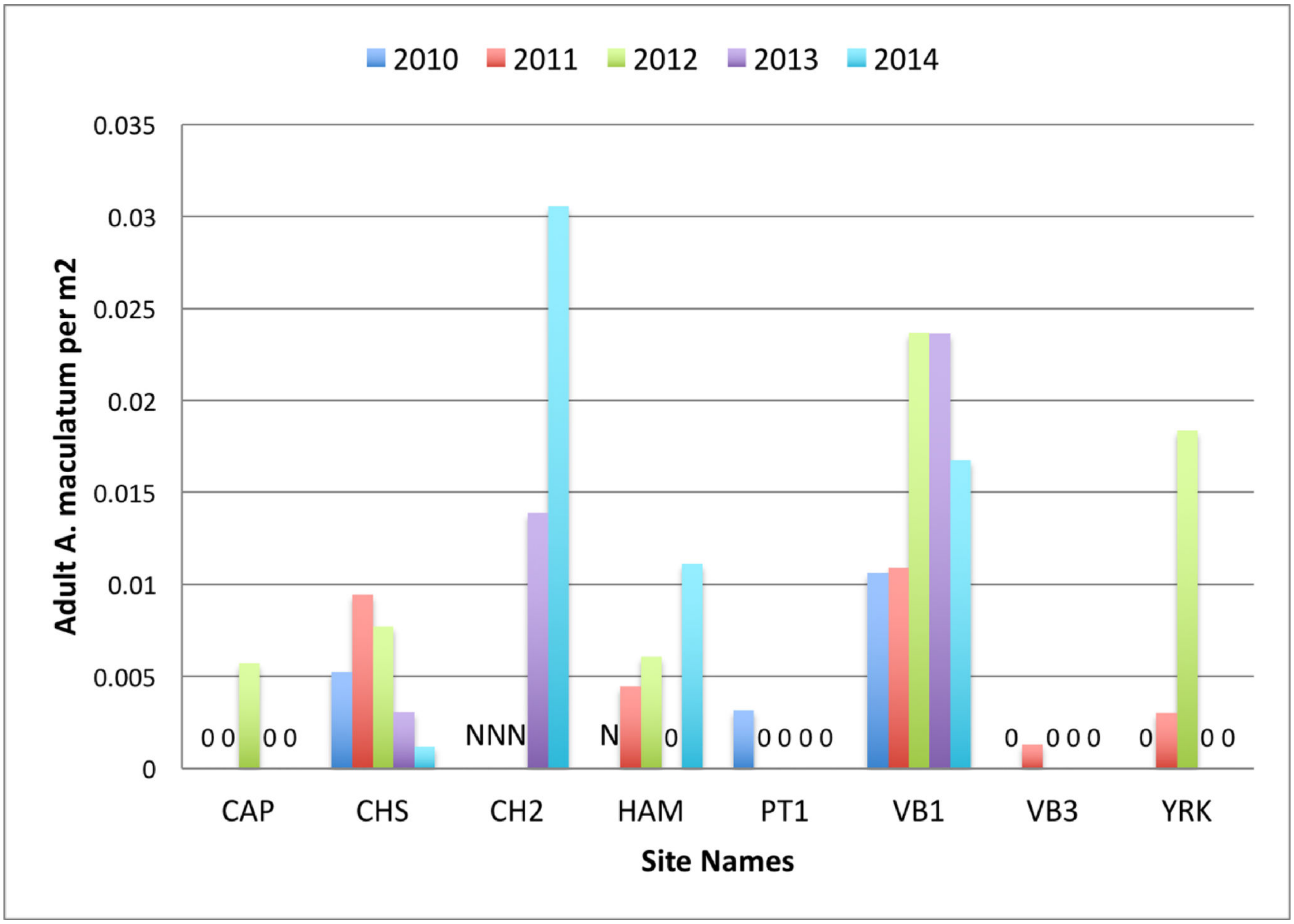

Figure 3.

Amblyomma maculatum adults collected per m^2 at each site, 2010–2014, Virginia, U.S. The numbers of ticks collected per m^2 sampled are low because all sampling events, including during times when *A. maculatum* were not active, are included in the denominator.

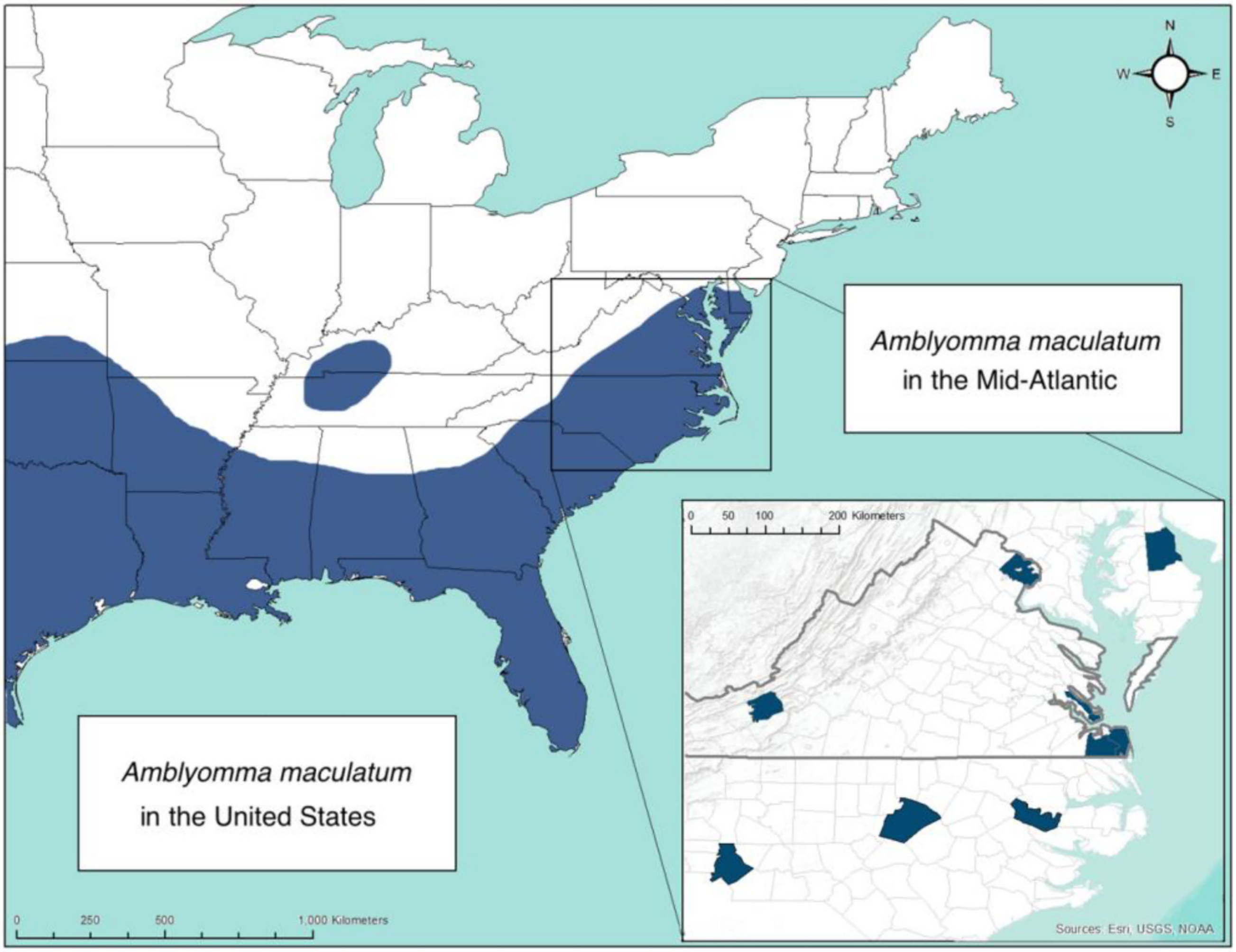

Figure 4.

Range map of *Amblyomma maculatum* in the United States. Dark blue indicates the known range of *A. maculatum* in the eastern U.S. Virginia is demarcated in bold grey. Inset map shows counties with reported populations of >6 adult or multiple life stages of *A. maculatum* collected in North Carolina, Virginia, and Delaware. The data included in the main map are from Paddock and Goddard 2015, data for the inset map are from David Gaines, personal communication (western Virginia population), Florin et al. 2014 (Delaware), Nadolny et al. 2014, Wright et al. 2011, this study (Virginia), and Varela-Stokes et al. 2011 (North Carolina).

Table 1

Amblyomma maculatum (AM) adults collected by flagging, 2010–2014. All sites were in southeastern Virginia. Site codes correspond to those mapped in Figure 1, and habitat types and *A. maculatum* density are included for each site. NS indicates that that site was not sampled in those years. General habitat types were determined by observing vegetation communities along transects. Observed successional events are qualitative changes to each site from natural or anthropogenic factors observed during the study period.

County	Site	AM 2010	AM 2011	AM 2012	AM 2013	AM 2014	Total AM	AM/ 100 m^2	Habitat Type	Observed Successional Events
Chesapeake	CHS	54	104	88	17	7	270	2.66	Lowland mid-successional old field with drainage ditches	Grass/perennials to shrubs/young trees
Chesapeake	CH2	NS	NS	NS	6	18	24	4.44	Early and mid-successional old field, bordering pine-mixed hardwood forests	Grass/perennials to shrubs
Hampton	HAM	NS	2	2	0	5	9	2.16	Old field and mixed hardwood forest edge; Early successional old field	Annual mowing to maintain grass/perennials at old field
Isle of Wight	ILW	0	0	0	0	0	0	0	Loblolly-longleaf pine savannah; Edge of bald-cypress-tupelo swamp bordering loblolly pine-oak forest	Longleaf pine savannah maintained through prescribed burns
Newport News	NEW	NS	NS	NS	NS	0	0	0	Pine-mixed hardwood forest edge	None
Norfolk	NO1	NS	0	0	0	0	0	0	Pine-mixed hardwood forest	None
Northampton	CAP	0	0	1	0	0	1	0.57	Pine-mixed hardwood forest; Rear dune shrub community bordering parking lot; Early successional old field	Frequent mowing to maintain grass in old field
Portsmouth	PT1	3	0	0	0	0	3	0.31	Pine-mixed hardwood forest, some bordering a salt marsh	Clear cut portion of forest to rebuild wetlands
Portsmouth	PT2	0	0	0	0	0	0	0	Pine-mixed hardwood forest, some bordering a salt marsh	None
Suffolk	SF1	NS	NS	0	0	NS	0	0	Early successional old field bordering pine-mixed hardwood forest	Closed landfill, fields maintained through frequent mowing
Suffolk	SF2	NS	NS	NS	NS	0	0	0	Pine-mixed hardwood forest	None
Virginia Beach	VB1	9	6	27	31	18	91	8.55	Maritime live oak forest edge; Early successional old field	Biennial mowing to maintain grass/ perennials at old field
Virginia Beach	VB3	0	1	0	0	0	1	0.13	Pine-mixed hardwood forest; Loblolly pine-oak forest; Maritime dune grassland	None
York	YRK	0	1	13	0	0	14	2.14	Pine-mixed hardwood forest bordering river and bald cypress-tupelo swamp; Early successional old field; Mature loblolly pine-oak forest bordering managed pine forest	Biennial mowing to maintain grass/ perennials at old field

Table 2

Amblyomma maculatum immatures collected by flagging, 2010–2014. All *A. maculatum* (AM) nymphs and larvae were collected in southeastern Virginia. Site codes correspond to those mapped in Figure 1.

Month	AM nymphs	AM larvae	Site
March	9		VB1
April	1	5	CH2 (n), YRK (l)
May	1		VB1
August	6		VB1
September	2		VB1

Table 3

Adult tick species composition of sites where *A. maculatum* was collected, 2010–2014. Site codes correspond to those mapped in Figure 1. Combined 2010–2014 collections of questing adult *Amblyomma maculatum* (AM), *Dermacentor variabilis* (DV), *Amblyomma americanum* (AA), *Ixodes affinis* (IA), and *Ixodes scapularis* (IS) are included for each site.

County	Site	DV	AA	IS	AM	IA	Total adults	% AM
Chesapeake	CHS	879	1360	50	270	130	2689	10.04%
Chesapeake	CH2	234	202	1	24	25	486	4.94%
Hampton	HAM	112	586	41	9	17	765	1.18%
Northampton	CAP	65	448	17	1	42	573	0.17%
Portsmouth	PT1	135	25	2	3	0	165	1.82%
Virginia Beach	VB1	83	298	9	91	3	484	18.80%
Virginia Beach	VB3	25	857	77	1	321	1281	0.08%
York	YRK	27	1423	54	14	57	1575	0.89%
Total		1560	5199	251	413	595	8018	5.15%

Table 4

Hosts infested with *Amblyomma maculatum* in southeastern Virginia. Hosts were infested with one or more *A. maculatum* (AM) adult (A), nymph (N), or larva (L).

Host	Site	Month	AM (L)	AM (N)	AM (A)	DV (A)	AA (L)	AA (N)	AA (A)	IS (A)	DA (N)	Total ticks	Monthly host IR	Annual host IR
Felis catus (Domesticated Cat)**														
	HAM	Jul			1							1	33.33%	4.35%
Odocoileus virginianus (White-tailed Deer)														
	VB1	Oct			2			1	1	2	2	8	1.85%	2.50%
	CHS	Dec			1					8		9	10.00%	2.50%
Tappahannock		Jun			1			6	7			14	12.50%	2.50%
Canis lupus familiaris (Domesticated Dog)														
	NEW	May			1							1	1.72%	0.81%
Sus scrofa (Feral Swine)														
	VB1	Jul			1	15		2	11			29	100.00%	5.26%
Microtus pennsylvanicus (Meadow Vole)														
	CHS	Feb		1*								1	NA	NA
	CHS	Apr		1								1	NA	NA
Sigmodon hispidus (Hispid cotton rat)														
	CHS	Aug	2									2	NA	NA
Oryzomys palustris (Marsh Rice Rat)														
	CHS	July	2									2	NA	NA
	CHS	Dec	1									1	NA	NA

Immatures were identified using a RFLP assay, with * indicating sequence confirmation. Site and month where the host was collected are included for each host. For mammals hosting adults, co-feeding ticks collected from the same host are reported, including *Dermacentor variabilis* (DV), *Amblyomma americanum* (AA), *Ixodes scapularis* (IS), and *Dermacentor albipictus* (DA). The monthly and annual infestation rate (IR), or percentage of hosts checked infested with AM, are included for each host species hosting adults. Co-feeding ticks and IR are not reported for rodent hosts, because of challenges associated with identifying immature engorged ticks.

** The actual number of ticks from this cat is unknown; this *A. maculatum* tick may have been co-feeding with *A. americanum* larvae or *I. scapularis* adult ticks that were received by the ODU Tick Research Team from one veterinary clinic on the same day