Density of *Ixodes scapularis* ticks on Monhegan Island after complete deer removal: A question of avian importation?

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ABSTRACT: Questing adult blacklegged tick (*Ixodes scapularis* Say) abundance declined markedly three years after the 1999 removal of white-tailed deer (*Odocoileus virginianus* Zimmermann) from Monhegan Island, ME. Since 2000, subadult ticks have not been found on Norway rats (*Rattus norvegicus* Berkenhout); questing nymphs have not been found since 2002. This suggested *I. scapularis* was reintroduced annually via bird importation of subadult ticks, but unable to complete its two-year life cycle on the island due to lack of deer. To investigate this, we used uncertainty analysis to estimate 1) questing adult ticks/ha that would result from avian importation of nymphs, and 2) questing adult ticks/ha on Monhegan Island, using bird capture and tick burden data from Appledore Island, ME, flagged tick data from Monhegan Island, and ten uncertain parameters. During the deer-fed period (1990-2001), estimated tick density on Monhegan Island was 18 times greater than that of imported ticks. During the post-deer-fed period (2002-2008), Monhegan Island tick density was equivalent to imported tick density. This supported the premise that all *I. scapularis* ticks on Monhegan Island have been bird-derived since 2002. ***Journal of Vector Ecology* 36 (1): 11-23. 2011.**

Keyword Index: Avian importation, *Ixodes scapularis,* blacklegged tick, tick density, white-tailed deer.

INTRODUCTION

Birds influence public health because they disperse arthropod vectors of parasites and carry zoonotic pathogens, contributing to establishment and re-establishment of endemic foci of disease over great distances (e.g., Hoogstraal and Kaiser 1961, Humair 2002, Reed et al. 2003, Hubálek 2004, Comstedt et al. 2006, Brinkerhoff et al. 2009). Anderson et al. (1986) first described the role of birds in the epidemiology of Lyme disease. Smith et al. (1996) confirmed the ability of passerine species to introduce blacklegged ticks (*Ixodes scapularis* Say) infected with the Lyme agent, *Borrelia burgdoferi* Johnson et al., to a nonendemic island off the Maine coast. Many studies document tick dispersal during bird migration (e.g., Klich et al. 1996, Smith et al. 1996, Rand et al. 1998, Rand et al. 2007, Ogden et al. 2008).

While there seems to be little controversy over the concept that birds can disperse populations of *I. scapularis*, there have been few attempts to quantify avian importation of ticks. Madav et al. (2004) simulated the establishment of a tick population across a landscape using deterministic models and estimated that 200 American robins (*Turdus migratorius* Linnaeus) per hectare per year could import 300 subadult ticks per hectare per year, which would establish a tick population for at least 18 years on a hypothetical study grid, assuming a suitable host community for subadult and adult ticks. The authors recommended future studies use a broader range of species and more accurate values for parameters in models of avian tick dispersal. Therefore, we paired two long-term datasets:, one of migrant bird *I. scapularis* tick burdens, the other of questing adult *I. scapularis*, to quantify avian tick dispersal.

Appledore Island, ME, lies within the Atlantic flyway and is a regular stopover site for migrant birds (Gellin and Morris 2001, Morris et al. 2005, Morris et al. 2006, Morris et al. 2007). Mist-netting during spring and fall migrations on Appledore Island, 1990-2008, has produced a long-term time series of avian migrant capture and tick burden data and presented the opportunity to model the number of adult ticks per hectare that would result from avian importation of nymphal ticks along the coast of Maine.

Fall flagging on Monhegan Island, ME, 1990-2008 has produced a long-term time series on questing adult *I. scapularis.* Following complete removal of white-tailed deer (*Odocoileus virginianus* Zimmermann) from Monhegan Island by the end of 1999, Rand et al. (2004) reported a marked drop in *I. scapularis* abundance. Before deer removal, highly reservoir-competent Norway rats (*Rattus norvegicus* Berkenhout) were the primary subadult *I. scapularis* hosts. Since 2000, there have been no ticks on trapped rats and no *B. burgdorferi* detected in rat tissue (Rand, unpublished data). No questing nymphs have been flagged on Monhegan Island since 2002 (Rand et al. 2004, Rand, unpublished data). Taken together, this suggested that *I. scapularis* was reintroduced annually via bird importation, but unable to complete its two-year life cycle. If so, the density of questing adult ticks resulting from migrant bird importation of *I. scapularis* nymphs would coincide with the density of questing adult *I. scapularis* on Monhegan Island since die-out of the last deer-fed tick cohort.

Accordingly, we attempted to estimate of the number of ticks incoming per hectare using data obtained from Appledore Island, and to compare this with estimates of questing ticks on Monhegan Island. Monhegan Island is a well-known "migrant trap" with intense bird activity during migration season (Smith et al. 1993), but no long-term field data documenting avian tick burdens. However as they are similar off-shore migrant stopover sites ~150 km apart along the Atlantic flyway, we postulated that the number of incoming ticks per hectare on Appledore and Monhegan Islands would be comparable.

Our premise was that all *I. scapularis* ticks on Monhegan Island have been bird-derived since 2002. For the 1990-2001 deer-fed period, our hypothesis was that there were more questing adult *I. scapularis*/ha on Monhegan Island than imported ticks. For the 2002-2006 post deer-fed period, our hypothesis was that *I. scapularis*/ha would be equivalent, since adult ticks would originate from avian importation of nymphs, and without deer, be unable to complete the two-year life cycle. Our objectives were to 1) obtain ranges from the literature and expert opinion for the following parameters: mist-net effort, bird capture probability, nymphal find probability, nymphal survival to engorgement, nymphal attachment duration, proportion and stopover duration of long- and short-stopover birds, nymphal development duration and probability of survival to adulthood, and questing adult tick flagging efficiency, 2) obtain annual estimates of questing adult *I. scapularis*/ha that would result from importation of nymphs by spring migrants based on Appledore Island data and nine uncertain parameters, 3) obtain annual estimates of questing adult *I. scapularis*/ha, based on Monhegan Island data and one uncertain parameter (flagging efficiency), 4) compare estimated means of imported versus Monhegan Island questing adult ticks/ha by period (during and post deer-fed), and 5) use sensitivity analysis to assess which input parameters contributed most prediction variability in the models.

We used uncertainty analysis to estimate density of adult *I. scapularis* using four parameters from the Appledore and Monhegan Island time series data in conjunction with 10 other life-history parameters extracted from the literature and expert opinion. Uncertainty analysis has been used to model processes in a range of disciplines (e.g., Blower and Dowlatabadi 1994, Cuthbert et al. 2001, Tenhumberg et al. 2008).

MATERIALS AND METHODS

Study areas and field sampling

Mist-netting was conducted on 38.5-ha Appledore Island, ME (42.97N, 70.62W), the largest of the Isles of Shoals ~10 km southeast of Kittery, ME (Figure 1). Shrub/scrub is the dominant habitat, with marshes, low trees, and open fields. Smith et al. (1996) found no ticks on Appledore's two mammal species (Norway rats and muskrats (*Ondatra zibethicus* Linnaeus), no questing nymphs on vegetation in June, and few questing adults in October, suggesting ticks are not indigenous to the island and ticks on birds are derived from other sites. Migrating birds were captured using nine to ten mist nets (12 m, 30 mm mesh) from 1990 through 2008 in an approximately 1-ha area of the island. In years when migrants were abundant, several nets were closed so catch rate would not exceed ability to safely process birds. Spring banding ran from early May to mid-June and autumn banding from mid-August until late September or early October. Mist-nets were opened daily from sunrise to sunset except during inclement weather, and checked at least every 30 min. To reduce likelihood of injury, nets were set 0.5 m above the ground, thus potentially missing some ground-foraging birds. All birds were taken to a central location for banding and examined for ticks, especially around the head, throat, and neck (Scharf 2004, Stafford et al. 1995). All ticks found were removed and shipped to the Vector-borne Disease Laboratory for identification.

Fall flagging for questing adult ticks was conducted on 237-ha Monhegan Island (43.46N, 69.19W), located 16.4 km off Maine's mid-coast (Figure 1). The island is dominated by mature spruce and stands of mixed deciduous species with dense understory. The island is home to ~75 year-round and ~250 seasonal residents. Deer density was 45/km^2 (105-108 deer island-wide) in 1996 and 0 by the end of the removal program in 1999. In 2002-03 there were 13 dogs and 34 cats on the island, with similar numbers through the 1990's (Rand et al. 2000). Norway rats were ubiquitous in

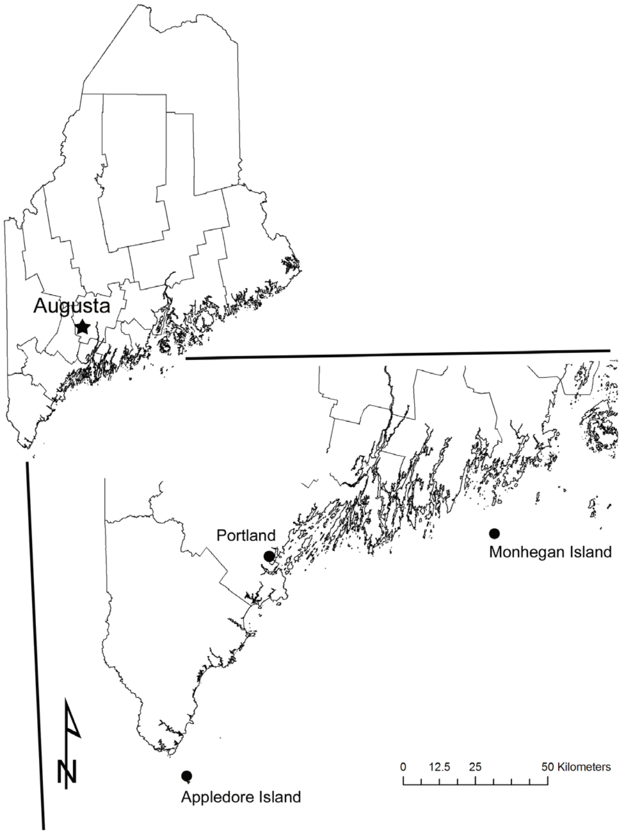

Figure 1. Location of Appledore and Monhegan Islands, ME.

every habitat island-wide including peridomestic settings (Rand et al. 2004). Before deer removal, Norway rats were the primary subadult *I. scapularis* hosts; through 2001, larval and nymphal *I. scapularis* burdens ranged from 2-18 and 1-4/ rat, respectively (Smith et al. 1993). Mice, voles, squirrels, and other small mammals are absent (Smith et al. 1993), as are mustelids and rabbits (Rand, unpublished data). Muskrats (*Ondatra zibethicus* Linnaeus) appeared in low density and harbored few *I. scapularis* (Smith et al. 1993). From 1990 through 2008, annual flagging was conducted along 1 m survey transects on either side of island trails. Ticks were collected from vegetation using 1 m^2 flags consisting of light-colored corduroy attached to a 150 cm pole, dragged over leaf litter and brush in the adult season (October- early November) when temperatures exceeded 10° C and vegetation was dry. Flags were inspected at approximately 5 min intervals, and ticks placed in plastic vials for transportation to the laboratory for identification. Each observer recorded transect start and end points and times on geo-referenced Monhegan Island trail maps (http://www.monheganassociates.org/trails/map.htm). We superimposed each year's map over a Google Earth® satellite image of Monhegan Island (http://earth.google.com). Using the Google Earth® path tool we measured the length of flagged transects in meters and computed total area flagged by year (length × 2 m).

Analysis

With the Appledore Island data, we summarized overall number of individual birds captured for spring and fall. For each tick species, we summarized number and percent of all bird hosts, number of bird species hosting ticks, percent of birds infested (number of bird hosts per season/total number of individual birds captured x 100) and larval and nymphal burdens (number of ticks/number of individual birds captured), for spring and fall. For *I. scapularis* ticks only, we summarized annual number of individual birds captured and tick infestation rates and burdens, for spring and fall. For the spring and fall bird infestation time series, we tested for trend. We summarized annual number of ticks flagged per hour and area flagged in hectares on Monhegan Island. Subsequently, we used the Monhegan and Appledore Island time series for the uncertainty analysis.

We ran two uncertainty models: one based on the Appledore Island bird data to estimate the number of questing adult ticks per hectare that could result from avian importation of nymphs, and one based on the Monhegan Island flagging data to estimate the number of questing adult ticks per hectare on the island. Uncertainty in the models was introduced from measurement error in four study-based parameters and uncertainty in 10 parameters based on the literature and expert opinion (Table 1). How each of the parameters and ranges were derived will be discussed in detail after defining the models and modeling strategy.

For the importation model, there were two groups of birds: long- and short-stopover birds. For the long-stopover birds:

number of engorged nymphs dropped$_{\text{long-stopover birds}}$ =
(bird captures per hectare/bird capture probability)
× (nymph burden/nymph find probability)
× probability of tick survival to drop-off
× proportion of long-stopover birds
× (stopover duration of long-stopover birds/nymphal attachment duration).

The proportion of short-stopover birds was 100%–long-stopover %, and number of engorged nymphs dropped$_{\text{short-stopover birds}}$ was computed as above. The importation model thus was:

questing adult ticks per hectare =
(number of engorged nymphs dropped$_{\text{long-stopover birds}}$
+ number of engorged nymphs dropped$_{\text{short-stopover birds}}$)
× weekly probability of nymph survival to questing adult$^{\text{duration of molt in weeks}}$

The questing adult tick/hectare model was:

$$\text{questing adult ticks per hectare} = \frac{\text{(questing adult ticks flagged/flagging efficiency)}}{\text{area flagged in hectares}}$$

Computing questing adult ticks per hectare based on deterministic models would not account for uncertainty, so to accomplish this we used Latin Hypercube Sampling (LHS) (Blower and Dowlatabati 1994), a type of stratified Monte Carlo sampling (McKay et al. 1979). The technique involves 1) the definition of probability distribution functions for each of the K input parameters; 2) the division of the range of each parameter into N equi-probable intervals; and 3) the generation of the LHS K-sets of parameters by randomly sampling values without replacement from each probability distribution function. With the exception of flagging efficiency (parameter 14), we had no information on the true distributions of parameters, so we used uniform probability distribution functions (Hilborn and Mangel 1997).

Blower and Dowlatabadi (1994) stated that a formula for the number of simulations, N, does not exist in the literature, but 1) the lower limit to N should be at least K (number of parameters) + 1, and 2) that McKay et al. (1979) empirically established that N should be >4/3K. Blower and Dowlatabadi (1994) also suggested N be determined by the desired significance level for the partial rank correlation coefficients of a subsequent sensitivity analysis; they set their N to 100 (K=20). Latin hypercube sampling produces larger average standard deviations than simple random sampling with the same number of simulations, and captures more variability in the sample space especially when the number of simulations is small (Chonggang et al. 2005). There were 14 parameters and 4/3 × 14 = 18.6, so we ran 19 iterations per year. We chose the lower limit for N because 1) we wanted to capture maximum variability in the sampling space, and 2) in the sensitivity analysis we ranked parameter importance on strength of correlations (Cohen 1988, see below) independent of P-values. For each iteration of the

Table 1. Parameters and their ranges used to estimate the number of questing fall adult *Ixodes scapularis*/hectare that would result from avian importation of nymphs, based on data from Appledore Island, ME, 1990-2008, and the number of questing fall adult *I. scapularis*/hectare on Monhegan Island, ME, based on data from that island, 1990-2008. Base values, in bold face, were derived from study data; otherwise from the literature and/or expert opinion. Ranges were derived from the literature and/or expert opinion.

Dataset	Parameter	Parameter Ranges Lower Bound	Parameter Ranges Upper Bound	Source
Appledore Island spring migration data				
	1. **Individual bird captures/ha**	-1%	+1%	Johnson et al. (2009)
	2. **Capture probability**	5%	15%	Morris et al. 2005, Morris et al. 2006
	3. Burdens (nymphs/bird)	-1%	+1%	Johnson et al. (2009)
	4. Nymph find probability	0.82%	1.00%	Richter et al. (2000), Balmforth (2002)
	5. Nymph survival to engorgement probability	0.37%	0.91%	Balmforth (2000)
	6. Nymph attachment duration (days)	2.5	5.6	Balmforth (2000)
	7. Proportion of long stopover birds (% of all birds)[a]	4.4%	4.8%	Gellin and Morris (2001), Morris et al. (2007)
	8. Stopover duration of long stopover birds (days)	0.76	11.24	Gellin and Morris (2001), Morris et al. (2007)
	9. Stopover duration of short stopover (nocturnal) birds	0.67	0.83	Gauthreaux and Belser (1998), Gellin and Morris (2001), Morris et al. (2007)
	10. Nymph survival to adult probability	0.973500	0.984024	Mount et al. (1997)
	11. Development duration (weeks)	18	26	Ogden et al. (2004), Elias (unpublished data)
Monhegan Island fall flagging data				
	12. Flagged adult ticks	-1%	+1%	Johnson et al. (2009)
	13. Area flagged (hectares)	-15%	+15%	±15% measurement error from this study
	14. Flagging efficiency	1.9%	6.4%	Daniels et al. (2000)

LHS, parameter combinations varied simultaneously. From each unique parameter combination we calculated the outcome, adult ticks/ha. The total number of observations generated per model was 361 (19 samples/year × 19 years).

We combined the generated datasets and designated tick 'source' as either 'imported' or 'Monhegan Island'. The data comprised non-integer responses with a probability density function most closely approximated by the negative binomial distribution. Therefore we used a generalized linear model (GLM) approach (Nelder and Wedderburn 1972) to obtain least squares means by year. The annual GLM took the form ticks/ha = $\beta_0 + \beta_1$source + $\beta_2$year + $\beta_3$source×year + ε. We output the 95% Wald confidence limits on annual mean ticks/ha to a dataset for plotting annual trends. We also output annual mean ticks/ha to a dataset for the by-period model. This GLM took the form ticks/ha = $\beta_0 + \beta_1$source + $\beta_2$period + $\beta_3$source×period + ε and we compared mean imported versus Monhegan Island ticks/ha for the periods 1990-2001 and 2002-2008.

To identify which parameters were most important in contributing to prediction imprecision in the imported and Monhegan Island ticks/ha models, we conducted a Partial Rank Correlation sensitivity analysis by calculating partial rank correlation coefficients (Blower and Dowlatabati 1994). We ranked importance on strength of correlations, with thresholds of ±0.3, ±0.5, and ±0.8 for weak, moderate, and strong, respectively (Cohen 1988). For all analyses we used SAS® software, Version 9 of the SAS System for Windows, Copyright © 2002-2003 by SAS Institute Inc., Cary, NC, USA.

The 14 model parameters are summarized in Table 1. Assumptions and derivations of lower and upper parameter bounds are discussed in detail below.

Importation model parameters

We used Appledore Island spring data on nymphs for the uncertainty analysis given several general assumptions. Birds carried larvae, but we assumed larval survival on Monhegan Island was negligible because 1) we had not flagged questing nymphs since 2002, suggesting absence of larvae, and 2) lack of subadult ticks on Norway rats since 2000. Given the lateness of the season, we assumed the survival of fall-imported nymphs was negligible. We assumed that no adults survived to lay eggs due to lack of white-tailed deer and insufficient numbers of alternate hosts for adult *I. scapularis*.

Parameter 1. Individual bird captures/ha. The configuration of mist nets sampled a 1-ha area assuming the array of 5 horizontal and 4 vertical nets each sampled ~80 meters, including birds on 10 meters on either side of the nets. Annual number of birds captured/ha were base values for the model. In an evaluation of fisheries data, Johnson et al. (2009) found that total measurement error (field-related and data entry) in the dataset averaged 0.79%. We set bounds as annual captures ± 1%.

Parameter 2. Capture probability. Capture probability is a function of uncertain factors such as species, weather, and energetic condition (e.g., Silkey et al. 1999, Simons et al. 2004). Also, mist-net effort in this study varied inter-annually from 1,766 to 4,550. Based on these sources of uncertainty and on open population models from Appledore Island banding studies (Morris et al. 2005, Morris et al. 2006, Morris, unpublished data), capture probability for these migrants as a group could range from 5% - 15%. We assumed net avoidance in non-breeding birds would not bias capture probability; ~4% and ~15% of spring and fall migrants, respectively, were recaptured (Morris, unpublished data), thus based on fall data, birds did not appear to be learning net locations.

Parameter 3. Burdens (nymphs/bird). As enumeration of nymphs might be subject to a small amount of measurement error (Johnson et al. 2009), we set bounds as annual burden ±1%.

Parameter 4. Nymph find probability. We did not find nymphal find rate for birds in the literature, but Balmforth (2002) found between 38.3-81.7% of larvae. We estimated nymphal find probability at 0.90-1.00 based on banding studies in southern coastal Maine (Smith et al. 1996, Rand et al. 1998). We assumed lower and upper bounds of 0.82 (upper bound of larval find probability) and 1.00.

Parameter 5. Nymph survival to engorgement probability. Balmforth (2002) reported a retrieval rate of 37% of laboratory-placed nymphs from American Robins and Song Sparrows (*Melospiza melodia* Wilson), and Richter et al. (2000) reported an 82-100% retrieval rate from American Robins. Both were laboratory studies, and since 100% survival seemed unlikely under natural conditions, we assumed lower and upper bounds of 0.37 to 0.91.

Parameter 6. Nymph attachment duration (days). The percent of engorged nymphs that would drop off avian migrants at a stopover site would depend on tick attachment duration and bird stopover duration. Balmforth (2002) found that on two passerine species, laboratory-applied *I. scapularis* nymphs remained on birds between 64 and 134 hours (2.7 to 5.6 days) before dropping off. Thus, we assumed lower and upper bounds of 2.7 and 5.6 days. Ginsberg et al. (2005) reported a tendency towards greater drop-off of *I. scapularis* from passerines during the day, while Matuschka et al. (1990) found that all subadult *Ixodes ricinus* dropped from bird hosts during daylight hours regardless of time of attachment. Detachment stimulus remains speculative (Matuschka et al. 1990) but in migrating birds could be related to geochemical cues, photophase, temperature, and a decrease in activity level from nocturnal flight to diurnal foraging or resting. Therefore we assumed tick detachment at stopover sites.

Parameter 7. Proportion of long-stopover birds (% of all birds). Based on stopover ecology studies, Morris et al. (2006) stated that regularly < 5% of birds are recaptured at least one day after capture and >95% of birds are captured only once. On Appledore Island, ~4.4% of spring migrants were recaptured (Gellin and Morris 2001). Recaptures comprised mainly birds requiring long-stopovers (>1 day) while single captures comprised mainly nocturnal migrants with short-stopovers <1 day (Morris, unpublished data). Birds captured only once are not necessarily short (nocturnal) stopover birds, however, so estimated proportion of long-stopover birds may be biased low. Proportion of long-stopover birds might vary positively by 10%, but probably not vary negatively. We assumed lower and upper bounds of 4.4 and 4.8%. Short-stopover % was (100% - long-stopover %).

Parameter 8. Stopover duration of long-stopover birds. Stopover duration of long-stopover migrants ranged from 0.76 to 11.24 days (Morris et al. 2006), so we assumed lower and upper bounds of 0.76 and 11.24 days. We note it would be difficult to separate breeding birds from migrants, but this would not bias the model adversely, because the critical piece is what happens (in terms of tick drop-off) upon a bird's arrival.

Parameter 9. Stopover duration of short-stopover (nocturnal) birds. Based on radar studies from the Louisiana and Texas (Gauthreaux and Belser 1998), nocturnal migration begins 30-40 min. after sunset and peaks in the first half of the evening. Thus, migrating songbirds likely stop between midnight and 0300-0400, then take off about an hour after sunset, i.e., stay on site ~16-20 h. We assumed lower and upper bounds of 0.67 and 0.83 days.

Parameter 10. Nymph survival to adult probability. For engorged nymphs that dropped off birds in spring, we adopted weekly survival rates of 0.9735 for edge habitat and 0.984024 for forested habitat (Mount et al. 1997) which was consistent with Monhegan Island's habitat mosaic.

Parameter 11. Development duration (weeks). The earliest arrival of the common yellowthroat (most prolific bearer of *I. scapularis* nymphs in spring) on Appledore Island was 3 May and the earliest Lincoln County (location of Monhegan Island) tick submitted to the Vector-borne Disease Lab (Rand et al. 2007) was 6 September, an interval of 18 weeks. The latest capture was 10 June and the latest tick 12 December, an interval of 6 weeks (Elias, unpublished data); therefore we assumed a nymphal development period (feeding to molt) ranging from 18 to 26 weeks. The lower bound was consistent with field observations by Odgen et al. (2004).

Questing adult ticks/hectare model parameters. General assumptions were that the population of questing adult ticks was closed (mortality, immigration, emigration, and recruitment negligible) and that sampling time was negligible. We think the former assumption was met based on work by Falco and Fish (1991), who found that adult ticks dispersed an average of only 1.8 m from their release site. We think the latter assumption was met since we flagged at the peak of adult tick season, and because our transect sampling periods were short (≤120 min). Daniels et al. (2000) judged their 60-90 min per day sampling short enough to preclude major unobserved changes in tick population size. Tick counts were not biased by sampling trails, because trails ranged through all island habitats, and flagging in the interior has produced comparable numbers of ticks/hour (Rand, unpublished data). Island trails were narrow (0.5-1.5 m) and not a barrier to the movements of rats or other wildlife.

Parameter 12. Flagged adult ticks. Enumeration of flagged ticks was subject to little measurement error. We set bounds to annual base value ±1% (Johnson et al. 2009).

Parameter 13. Area flagged (hectares). Our sampling substrate and temperature/humidity conditions were consistent. Two observers mapping trail length varied up to 15% in estimates, so we allowed annual estimates of area to vary ± 15%.

Parameter 14. Flagging efficiency. Daniels et al. (2000) reported flagging efficiencies ranging from 1.9% to 6.4% (Table 1).

RESULTS

On Appledore Island, 49,338 individual birds were captured during spring migration from 1990 through 2008 (Table 2). Overall, 2.61% of birds were infested with ticks, with 2.56% infested with *I. scapularis*. Ninety-eight percent of tick hosts hosted *I. scapularis* (Table 2). Other spring bird-borne ticks were subadult rabbit ticks (*Haemaphysalis leporispalustris* Packard), dog ticks (*Dermacentor variabilis* Say), and lone star ticks (*Amblyomma americanum* Linnaeus), adult mouse ticks (*I. muris* Bishop and Smith) and bird ticks (*I. brunneus* Koch). During fall migration, a total of 36,200 individuals were captured. Overall, 0.71% of birds were infested with ticks, with 0.50% infested with subadult *I. scapularis* and 0.19% infested with subadult *H. leporispalustris*. Seventy-one percent of tick hosts hosted *I. scapularis* and 26.6% hosted *H. leporispalustris* (Table 2).

The top three host species in terms of total numbers of nymphal *I. scapularis* in spring were common yellowthroat (*Geothlypis trichas* Linnaeus), Swainson's thrush (*Catharus ustulatus* Nuttall), and swamp sparrow (*Melospiza georgiana* Latham) with 1,713, 224, and 83 nymphs, respectively. The top three *I. scapularis* host species in fall were ovenbird (*Seiurus aurocapilla* Linnaeus), common yellowthroat, and northern waterthrush (*Seiurus noveboracensis* Gmelin) with 160, 141, and 128 larvae, respectively. All tick hosts were passerines with the exception of one northern flicker (*Colaptes auratus* Linnaeus) and one sharp-shinned hawk (*Accipiter striatus* Vieillot). No individual bird hosted more than one tick species in either spring or fall. *I. scapularis* nymphal burdens were greater in spring than fall (0.052 vs 0.002, $P < 0.05$), whereas *I. scapularis* larval burdens were greater in fall than spring (0.017 vs 0.002, $P < 0.05$), consistent with the two-year life cycle of this tick species (Table 2). There was a significant upward trend over time in percent of birds infested in spring only by nymphal *I. scapularis*, ($n = 19$ years, $R^2 = 0.23$, $P = 0.04$, Table 3).

On Monhegan Island, a total of 3,114 adult *I. scapularis* was flagged in fall from 1990 through 2008 along a total trail length of 24.5 km (Table 4). Hourly flagging rates ranged from 7.0-28.0 adult ticks/hr prior to die-out of last deer-fed tick cohort and from 0.7-2.8/hr after die-out (Table 4).

Figure 2 depicts the results of the uncertainty analysis, showing the 95% confidence intervals on estimated mean annual imported and Monhegan Island questing *I. scapularis* adults/ha. A decline in Monhegan Island tick density to what appeared to be a baseline importation level

Table 2. Tick species and burdens found on migrant birds during spring and fall migration on Appledore Island, ME, 1990-2008.

Tick species	Number of birds captured	Number of bird hosts	% of all hosts	Number of bird species hosting ticks	% birds infested[a]	Larvae		Nymphs		Adults	
						n	Burden[b]	*n*	Burden[b]	*n*	Burden[b]
Spring											
Ixodes scapularis		1,262	98.1	31	2.56	113	0.002	2,554	0.052		
Haemaphysalis leporispalustris		8	0.6	6	0.02	1	<0.001	9	<0.001		
Dermacentor variabilis		7	0.5	5	0.01	3	<0.001	5	<0.001		
Amblyomma americanum		4	0.3	4	0.01	6	<0.001				
Ixodes muris		3	0.2	3	0.01			1	<0.001	2	<0.001
Ixodes brunneus		2	0.2	2	<0.01					3	<0.001
No ticks											
Spring Totals	**49,338**	**1,286**			**2.61**						
Fall											
Ixodes scapularis		181	70.7	28	0.50	624	0.017	70	0.002		
Haemaphysalis leporispalustris		68	26.6	20	0.19	223	0.006	44	0.001		
Ixodes muris		6	2.3	5	0.02	46	0.001	11	<0.001	2	<0.001
Ixodes brunneus		1	0.4	1	<0.01					1	<0.001
No ticks				0							
Fall Totals	**36,200**	**256**			**0.71**						

Table 3. Number of captures of migrant birds during spring and fall migration, net-hours, subadult *Ixodes scapularis* infestation rate, and larval and nymphal burdens on Appledore Island, ME, 1990-2008.

	Spring								Fall							
					Larvae		Nymphs						Larvae		Nymphs	
			Infested[a]						Captures/		Infested[a]					
Year	Captures	Net-hours	*n*	(%)	*n*	Burden[b]	*n*	Burden[b]	ha	Net-hours	*n*	(%)	*n*	Burden[b]	*n*	Burden[b]
1990	1,445	1,777.0	11	0.76	2	0.001	18	0.012	1,258	2,970.4	0	0.00	0	0.000	0	0.000
1991	2,418	1,766.1	8	0.33	2	0.001	11	0.005	1,464	2,894.5	0	0.00	0	0.000	0	0.000
1992	2,482	2,428.0	59	2.38	1	0.000	150	0.060	1,432	2,652.3	0	0.00	0	0.000	0	0.000
1993	2,444	2,406.5	22	0.90	1	0.000	38	0.016	1,385	3,180.6	10	0.72	43	0.031	1	0.001
1994	3,120	3,460.5	30	0.96	4	0.001	87	0.028	2,672	5,803.9	7	0.26	13	0.005	8	0.003
1995	3,601	4,549.6	76	2.11	3	0.001	135	0.037	2,829	5,992.9	14	0.49	54	0.019	1	0.000
1996	2,230	3,512.5	22	0.99	2	0.001	38	0.017	2,017	3,696.8	1	0.05	0	0.000	3	0.001
1997	2,105	3,381.8	55	2.61	29	0.014	102	0.048	1,890	4,695.5	11	0.58	26	0.014	5	0.003
1998	3,224	3,929.2	127	3.94	3	0.001	233	0.072	2,260	5,284.2	13	0.58	34	0.015	3	0.001
1999	2,636	4,102.9	99	3.76	13	0.005	241	0.091	1,998	5,038.0	2	0.10	3	0.002	0	0.000
2000	2,562	4,092.5	72	2.81	0	0.000	126	0.049	2,585	4,871.6	24	0.93	116	0.045	8	0.003
2001	2,684	4,493.6	100	3.73	0	0.000	179	0.067	2,975	5,187.5	22	0.74	69	0.023	8	0.003
2002	2,519	3,591.4	119	4.72	12	0.005	274	0.109	2,054	4,715.7	8	0.39	47	0.023	6	0.003
2003	2,471	3,718.1	141	5.71	11	0.004	327	0.132	1,379	4,209.7	14	1.02	48	0.035	4	0.003
2004	2,433	3,345.7	49	2.01	13	0.005	90	0.037	1,775	4,658.4	12	0.68	40	0.023	5	0.003
2005	3,276	2,657.3	119	3.63	7	0.002	215	0.066	2,126	4,507.3	22	1.03	48	0.023	13	0.006
2006	2,116	2,801.8	51	2.41	7	0.003	95	0.045	1,578	4,289.9	10	0.63	48	0.030	2	0.001
2007	3,110	3,404.3	48	1.54	2	0.001	95	0.031	1,315	4,411.8	4	0.3	28	0.021	1	0.001
2008	2,462	3,404.0	54	2.19	1	0.000	100	0.041	1,208	4,399.2	7	0.58	7	0.006	2	0.002
Totals	**49,338**		**1,262**		**113**		**2,554**		**36,200**		**181**		**624**		**70**	

Table 4. Number of adult *Ixodes scapularis* flagged in fall along trails on Monhegan Island ME, 1990-2008. White-tailed deer (*Odocoileus viginianus*) were removed from the island during 1996-1999 and the last deer-fed tick cohort died out by 2002 resulting in a sharp decline in *I. scapularis* from 2002 through the present.

Period	Year	Adult Ticks Flagged	Hours Flagged	Ticks/hour	Trail Length Flagged (m)[a]
Deer-fed tick cohorts					
1990-2001	1990	89	11.1	8.0	8,063
	1991	99	14.1	7.0	4,795
	1992	163	12.5	13.0	13,949
	1993	70	11.7	6.0	7,198
	1994	156	11.1	14.0	8,754
	1995	248	17.7	14.0	6,857
	1996	374	22.0	17.0	7,440
	1997	166	23.7	7.0	10,333
	1998	356	27.4	13.0	9,230
	1999	564	20.1	28.0	10,016
	2000	459	25.6	17.9	22,000
	2001	140	18.9	7.4	9,946
After die-out of deer-fed tick cohorts					
2002-2008	2002	54	51.4	1.1	11,772
	2003	11	16.4	0.7	19,099
	2004	65	29.4	2.2	16,965
	2005	33	11.8	2.8	13,248
	2006	23	30.3	0.8	36,693
	2007	33	19.6	1.7	22,339
	2008	11	14.9	0.7	6,178
	Totals	**3,114**			**244,875**

Table 5. Estimated mean adult *I. scapularis*/hectare that would result from spring importation of nymphs by migrant birds versus estimated mean adult *I. scapularis*/hectare on Monhegan Island, ME, before and after die-out of last deer fed tick cohort on Monhegan Island, 1990-2008.

		Ticks/ha				
Period	Source	Mean[a]		SE	L95CL	U95CL
Deer-fed tick cohorts (1990-2001)	Monhegan Island	3,442	A	658.3	2,333	5,077
	Imported	185	B	35.6	125	273
After die-out of deer-fed tick cohorts (2002-2008)	Monhegan Island	298	B	74.8	179	496
	Imported	274	B	68.9	165	457

[a] Means with the same letter are not different, *P* > 0.05. General linear model, *n* = 38, DF = 33.4, Pearson X^2/DF=0.98.

was apparent by 2002 (Figure 2). When estimated mean annual ticks/ha were averaged across years by the two periods, Monhegan Island tick density was 18 times greater than imported tick density (3,442 vs 185, $P < 0.0001$) during the deer-fed period, but afterwards tick densities were not different (298 vs 274, $P = 0.82$, Table 5).

In the importation model's sensitivity analysis, nymphal burden had a strong influence on prediction imprecision; bird capture probability, nymph survival to engorgement probability, and nymph attachment duration had moderate influences (Table 6). In the Monhegan Island model sensitivity analysis, all three parameters (flagged adult ticks, area flagged, and flagging efficiency) had strong influences on prediction imprecision (Table 6). There were no correlations among parameters $\rho_{\text{Spearman}} \leq 0.10$ except for a weak correlation between bird captures/ha and nymphal burdens, $\rho_{\text{Spearman}} = 0.38$.

DISCUSSION

Uncertainty analysis supported the premise that since 2002, all questing adult blacklegged ticks on Monhegan Island, ME, have resulted from nymphs imported by migrating birds. The decline from 18 times the estimated level of imported ticks during the deer-fed period to equivalent levels for the post-deer-fed period was striking and highlights the importance of resident adult tick hosts to completion of the *I. scapularis* two-year life cycle. The weak correlation between nymph burdens and bird captures did not introduce collinearity to the model (Hosmer and Lemeshow 2000); from a biological standpoint we were confident that tick burdens did not affect condition (and therefore captures) of Appledore Island migrants (Morris et al. 2007).

Our models were a "thought" experiment (Blower and Dowlatabadi 1994) to lend preliminary credence to the concept that *I. scapularis* persistence on Monhegan Island can be accounted for by importation by birds. Still, substantial assumptions were made. For example, the 1-ha sampling area of the Appledore Island mist-nets is a conservative estimate, which might bias bird numbers upward if the sampling area were actually larger. We tested the effect of underestimating area sampled by the nets by 10% and the uncertainty and sensitivity analyses outcomes remained the same. We did not have spring flagging data for Monhegan Island and thus probably underestimated the adult tick population. In Maine, the secondary peak of overwintered adults is about 38% of the fall cohort (Rand et al. 2007). We tested the effect of underestimating the adult tick population by adjusting tick count up by 38%; the outcomes remained the same.

Comparison of means generated from observations based on uncertainty analysis should be interpreted with caution. Without known observed values for comparison, it is not possible to test the prediction precision of the models. Future efforts to quantify parameters should focus on those with strong and moderate influence on prediction precision as indicated by the sensitivity analysis. Nevertheless, the 2002-2008 estimates derived from the 11-parameter model of avian tick importation were on the same order of magnitude as the estimates of the simpler three-parameter Monhegan Island model. Furthermore, we used the Madav et al. (2004) importation estimate of 300 subadults per hectare per year, and, applying the low and high bounds

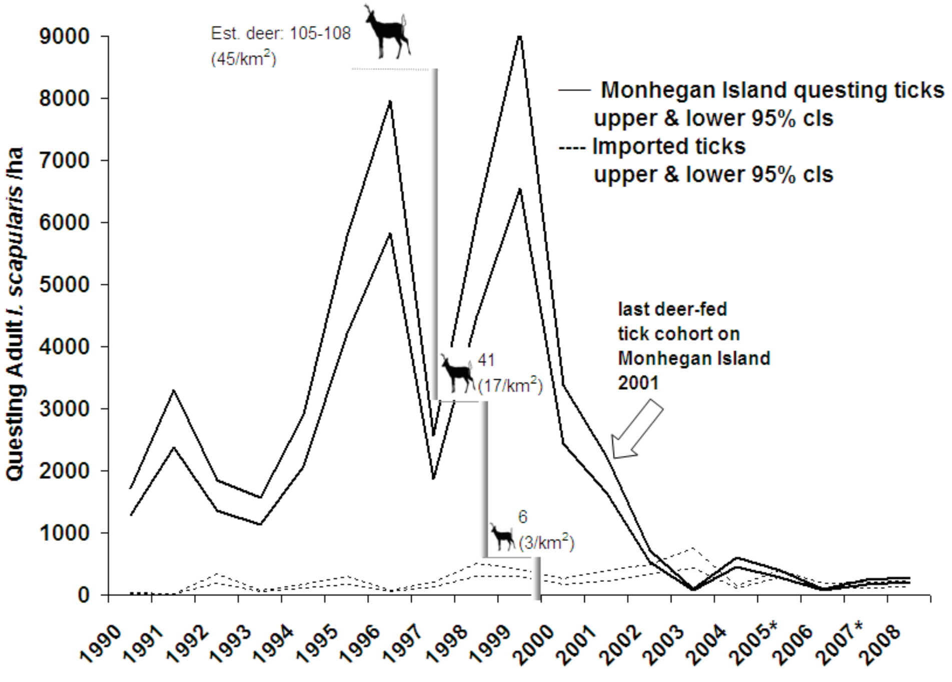

Figure 2. Estimated fall adult *Ixodes scapularis*/ha that would result from spring importation of nymphs by migrating birds (…) and estimated *I. scapularis*/hectare on Monhegan Island, ME, before and after the last deer-fed tick cohorts (—).

Table 6. Results of sensitivity analysis on parameters used to predict the number of questing *I. scapularis* adults per hectare that would result from spring importation of engorged nymphs by migrating birds, and adults per hectare on Monhegan Island, Maine, 1990-2008.

Model	Model parameter	Spearman Partial Coefficient[a]	Strength of Correlation[a]
Imported questing adult ticks/ha			
	3. Burdens (nymphs/bird)	0.82	strong
	2. Capture probability	-0.61	moderate
	5. Nymph survival to engorgement probability	0.52	moderate
	6. Nymph attachment duration (days)	0.45	moderate
	9. Stopover duration of short stopover (nocturnal) birds	0.34	weak
	1. Individual bird captures	0.29	weak
	4. Nymph find probability	-0.12	none
	10. Nymph survival to adult probability	0.11	none
	7. Proportion of long stopover birds (% of all birds)	-0.08	none
	8. Stopover duration of long stopover birds	0.07	none
	11. Development duration (weeks)	0.04	none
Monhegan Island questing adult ticks/ha			
	12. Flagged adult ticks	0.98	strong
	13. Area flagged (hectares)	0.84	strong
	14. Flagging efficiency	0.81	strong

[a]Based on Cohen (1988): thresholds for weak, moderate, and strong correlations are ±0.3, ±0.5, and ±0.8, respectively.

of weekly survival rates and development durations in our methods section, we estimated 300 subadults would result in 149-274 questing adults/ha/year. Our 95% confidence limits ranged from 165-457/ha. Despite differences in modeling approaches, tick density estimates were on the same order of magnitude, overlapped, and were corroborative.

The upward trend in percent infested in spring, and the quantity of ticks imported per hectare speak to the important ecological role birds play in establishing and re-establishing *I. scapularis* in emergent areas. At first glance, *I. scapularis* infestation rates (e.g., 2.56% in spring) and burdens (e.g. 0.052/bird in spring) may have appeared trivial, but the analysis indicated 165-457 adults/ha/year could result from importation. Ogden et al. (2008) estimated that migratory birds disperse 50 to 175 million *I. scapularis* across Canada each spring. This could lead to endemic *B. burgdorferi* where suitable host populations are present (Ogden et al. 2008).

This study focused on *I. scapularis* but also documented the roles of certain bird species as importers and dispersers of other tick species. For example, only 0.6% of infested birds hosted subabdult rabbit ticks (which can harbor the agent of tularemia, *Francisella tularensis* McCoy and Chapin) in spring, while 26.6% hosted rabbit ticks in fall. Furthermore, the common yellowthroat was the by far the dominant disperser in spring, but not fall. The ecology underlying these patterns was beyond the scope of this study but warrants further investigation.

Whether dogs and cats might sustain the *I. scapularis* life cycle peridomestically on Monhegan Island also warrants further investigation. Island dogs are mostly allowed to run free (Rand, unpublished data) and probably pick up and distribute ticks from and to the Monhegan island interior as well as trailside. Owners find ticks on their dogs and cats, although in a 2007 survey, 5 of 8 dogs (63%) and 7 of 15 (47%) cats were treated with topical acaracide (Rand, unpublished data). It is unlikely that dogs sustained the *I. scapularis* life cycle in lieu of deer because 1) acaracide would reduce the number and survival of attaching and feeding ticks; 2) the dog population has been stable and low relative to historic deer numbers (~12% of former deer population); 3) tick burdens, while not quantified for Monhegan Island dogs, might range from 0 to several dozen (Berrada and Telford 2009) vs 57-190/Monhegan deer (Rand et al. 2000); 4) peridomestic dogs (and cats) would not range island-wide; and 5) exposure would be limited to certain times of day, assuming dogs (and cats) spend time inside houses. The absence of subadult *I. scapularis* on Norway rats trapped in peridomestic as well as feral settings indicate that due to insufficient adult hosts, *I. scapularis* cannot complete its two-year life cycle on the island.

A molecular technique, such as reverse line blot (e.g., Humair et al. 2007) could be used to identify the last blood meal of questing adult ticks (i.e., the nymphal blood meal). Traces of cat, dog, or rat DNA would suggest that these hosts could be maintaining the tick's life cycle on Monhegan Island, at least peridomestically. Bird DNA only would confirm that *I. scapularis* on Monhegan Island is derived solely from avian importation.

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