

Estimating Population Size and Drag Sampling Efficiency for the Blacklegged Tick (Acari: Ixodidae)

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ABSTRACT Estimates of absolute density were determined over a 5-yr period (1990–1994) for a population of *Ixodes scapularis* Say located in Westchester County, NY, by mark-release-recapture (nymphs and adults) and removal (larvae) methods. Density estimates for larvae ranged from 5.2 to 16.5/m² and averaged 11.5/m². Values for nymphs varied as much as fourfold among successive years, ranging from 0.5 to 2.3/m² and averaging 1.2/m², whereas adult density ranged from 0.3 to 0.4/m², averaging 0.33/m². Natural mortality of nymphs and adults was measured in experimental cages during population estimation periods, and indicated that survival declined linearly over the short-term and did not significantly influence estimates. Drag sampling efficiency, the proportion of the estimated population obtained in a single sample, averaged 6.3% among all stages. Efficiency was not significantly different among stages and was independent of tick density within a given life stage. The population estimation techniques employed in this study are well suited for use with *I. scapularis* and can provide data that offer insights into mortality patterns in individual populations.

KEY WORDS *Ixodes scapularis*, population size, tick density, sampling efficiency, Lyme disease

THE GEOGRAPHIC DISTRIBUTION of *Ixodes scapularis* Say, the tick vector responsible for transmitting the agents of Lyme disease, human granulocytic ehrlichiosis (HGE), and babesiosis in the northeastern United States, has been associated with the historic resurgence of white-tailed deer, *Odocoileus virginianus* Zimmermann, populations (Spielman et al. 1985, Wilson et al. 1985) and the migratory movements of birds (Battaly et al. 1987, Weisbrod and Johnson 1989, Klich et al. 1996). Subsequently, populations of *I. scapularis* have increased, as indicated by mammal ectoparasite surveys (French et al. 1992, Daniels et al. 1993), human tick bite submissions (White et al. 1991), rising numbers of Lyme disease cases (e.g., Ciesielski et al. 1988, Cartter et al. 1989, Lastavica et al. 1989, White et al. 1991, CDC 1997), and tick sampling (Falco et al. 1995). In all but the latter case, the utility of these data for describing the magnitude of change over time at a particular site is limited because they constitute only relative measures of abundance (e.g., Southwood 1978) rather than absolute density estimates. Even where density estimates have been calculated based on drag sampling (Falco et al. 1995), seasonal changes in tick abundance, as well as the fact that all ticks in an area cannot be sampled, undermine attempts to use such estimates without accounting for these confounding variables.

Accurate density estimates are essential to understanding the dynamics of tick populations over time. For instance, interstadial mortality rates, based on population estimates of two successive stages over several generations, can be used to derive a life table (Deevey 1947) and to identify the stage most responsive to natural regulation mechanisms. In this article we describe methodology to generate absolute population estimates for each of the three active life stages of *I. scapularis*; data for 5 yr of sampling (1990–1994) at a site in Westchester County, NY. Because such estimates are labor intensive, it is also desirable to determine what proportion of the total tick population is collected in a single drag sample (i.e., estimate drag sampling efficiency). Drag sampling might then be used to generate absolute population estimates in lieu of mark-recapture or removal studies. Thus, a second goal of this study was to determine drag efficiency for each life stage and the accuracy of this method for predicting total population size.

Materials and Methods

Study Site and Permanent Grid Surveillance. Field work was conducted at the Louis Calder Center of Fordham University, located 28 km north (41° 8' N, 73° 48' W) of New York City, in the village of Armonk, Westchester County, NY. The habitat is characteristic of mixed deciduous forest and has been described elsewhere (Fish and Dowler 1989, Daniels and Fish 1990).

As part of a long-term study to monitor relative tick abundance patterns throughout the year, we conducted drag sampling, in which a 1-m² panel of white corduroy is pulled along the ground and over vege-

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tation (Falco and Fish 1992) on a "permanent" grid established in 1987. The grid, measuring 3,600 m² (60 by 60 m), was sampled 1–3 times weekly from late March through mid-December, as weather permitted. However, as the numbers of nymphs and larvae increased in the late spring and summer months, respectively, and again in the fall when adults become active, permanent grids were sampled three times per week to ensure that the week of peak abundance could be determined accurately. For each sample, 500 m² of area was dragged by randomly selecting transects through the study grid. Ticks found clinging to the cloth were removed with forceps, then stored for later identification and counting. Mean weekly densities (ticks per square meter) were calculated and plotted to determine the seasonal distribution of each tick stage (e.g., Fish 1993). Once peak abundance was attained, population estimation sampling was initiated on a second grid located ≈100 m distant. Routine drag sampling continued on the permanent grid while population estimation sampling was conducted strictly on the second grid.

Two estimation methods were used during the study. A multiple mark-release-recapture technique, the Schnabel (1938) method, was used on host-seeking nymphal and adult ticks to estimate their respective population size. Because of the large numbers of larvae collected while drag sampling, and the high probability of mortality resulting from handling, mark-release-recapture techniques were deemed inappropriate for larval estimates. Therefore, population estimates for this stage relied on removal sampling (Zippin 1958) in which counts were made of all larvae removed from each plot.

Assumptions Underlying Population Estimates.

Four assumptions underlying the estimation procedures in this study were as follows: (1) the population was closed (i.e., mortality, immigration, emigration, and recruitment were negligible, or allowances must be made for them), (2) all individuals were equally likely to be captured (i.e., marked and unmarked ticks behave the same), (3) marked individuals retained their marks throughout the study, and (4) sampling time was negligible (Southwood 1978, Seber 1982). To confirm the validity of the first assumption, we monitored mortality throughout the estimation periods. In general, mortality rates over the sampling periods had no significant impact on estimates. Likewise, immigration and emigration of host-seeking ticks is negligible. Previous studies indicated that active dispersal of *I. scapularis* was restricted to a short distance from the molting site; Falco and Fish (1991) found that adults dispersed a mean of just 1.8 m from their release site, whereas Daniels and Fish (1990) found larval movement to be even more localized. Curran et al. (1993), in a study of pesticide effectiveness in controlling nymphal *I. scapularis*, noted that repopulation of treated areas by host-seeking nymphs was insignificant after 41 d of posttreatment sampling. Studies of the American dog tick, *Dermacentor variabilis* (Say), indicate that limited horizontal movement is not restricted to *I. scapularis*. Sonenshine et al. (1966) found

that adult dog ticks moved an average of just 4.9 m (16 feet) from the point of release, concluding that there was no significant emigration.

However, because tick abundance for all stages increases to a peak and then decreases over several weeks during the season in which the particular stage is active (Wilson and Spielman 1985, Daniels et al. 1989, Fish 1993), we addressed the issue of recruitment of individual ticks into, and removal from, the active (host-seeking) tick population. First, population estimates were timed to negate any effect of recruitment on the population. Estimation studies were routinely initiated immediately after peak abundance was reached at the permanent grid site and tick numbers were stable or just beginning to decline. For those few years in which population estimation sampling was delayed for >1 wk after peak tick abundance because of weather, capture numbers were adjusted upward on the basis of drag data from the permanent grid site (percentage difference between tick abundance at peak and at the time the estimation study was begun).

Because the overall rate of host acquisition by ticks is believed to be low (e.g., <10% for *D. variabilis* larvae; Sonenshine 1975), loss of ticks from the study site in this manner was deemed negligible, particularly over the relatively short estimation period (10–20 d). Thus, we concluded that the *I. scapularis* population was effectively closed, and met the assumption number 1.

Marking was permanent over the course of the study and had no effect on survival (assumption number 3; Falco 1987, Daniels et al. 1989). Furthermore, laboratory assays comparing mortality of marked and unmarked ticks indicated that the marking did not induce mortality (Daniels et al. 1989), nor were there observable differences in behavior between the groups (i.e., marked ticks behaved the same as unmarked ticks [assumption number 2]); both could be seen questing in the glass vials in which they were held. This assumption is supported by the fact that marked ticks are routinely recaptured in the field.

Regarding assumption number 4, sampling generally required only 60–90 min/d, which was deemed short enough to preclude major unobserved changes in tick population size. Thus, sampling time was considered negligible.

Mark-Release-Recapture. The Schnabel (1938) procedure is a weighted mean technique that makes the same assumptions as the simple Lincoln–Petersen estimate (Begon 1979). Because the technique accumulates data over several days, it permits estimation of the population even if numbers of recaptures in a single day are low. Drag sampling was conducted on two plots totaling 1,400 m² site (600 and 800 m², respectively) within a 3,600-m² study area, also laid out as a 7 × 7 grid. Area dragged was increased to 2,000 m² for adult estimates conducted after 1990. The greater area was intended to increase the total number of ticks collected, including recaptures, and enhance statistical confidence given the record of routinely low adult densities.

For each 100-m² quadrat sampled, drag cloths were checked every 20 m and all *I. scapularis* removed. Captured ticks were examined visually and, aided by a portable UV light, categorized as marked (recaptured) or unmarked. Ticks were then marked for the first time, or remarked, with fluorescent powder (Radiant Color, Richmond, CA) and released at the capture site. Counts of new and recaptured ticks were recorded for each quadrat and summed for each of the two sampling areas.

To ensure that population estimates were not affected by natural mortality during the course of the study, mortality was monitored in the field. For the nymphal and adult population estimates, this was accomplished through the use of specially designed cages that permitted exposure of ticks to ambient weather conditions but prevented their loss by host removal. Cages consisted of a small metal can with the top and bottom removed to form an arena 7.5 cm high by 6.5 cm diameter. A nylon mesh bonnet (Lumite screening, BioQuip, Gardena, CA) was attached to each base with duct tape; bonnets were ≈15 cm in height and sealed at the top with a hot glue gun to prevent ticks from escaping.

Each mortality cage had either 10 nymphs or adults placed inside, depending on the stage being sampled. Although ticks were confined to the mesh bonnet, cage bottoms were pushed into the ground to a depth of 4–5 cm. Cages were placed randomly throughout the study grid. An average of three randomly selected cages was chosen for examination each week in which cages were opened in the field and all ticks that could be located either in the bonnet or in the soil or litter within each base were collected. When no additional ticks could be found, each cage bottom was excavated, making certain to keep the dirt plug within each base intact, and sealed in a plastic bag. Cages then were reexamined in the laboratory under a magnifying lamp to ensure that all live ticks were retrieved. Average mortality rates were calculated for each week and daily mortality rates were estimated by regression analysis. Subsequently, numbers of ticks recovered during each day's drag sampling efforts were adjusted to depict abundance, excluding mortality. These data permitted estimation of population size with and without adjustments for mortality.

Removal Sampling. To estimate larval density, 45 circular plots, each 3.14 m² (1-m radius) in area, were randomly selected within the 1,400-m² nymphal sampling area. Each circular plot then was drag sampled once per day a minimum of seven times over a 3-wk period. All larvae were removed with an adhesive tape lint-roller (Bemis, Minneapolis, MN); tapes were placed in plastic bags, sealed, and identified by plot number. Counts of larvae that had been removed from each plot were conducted in the laboratory. Dragging on an individual plot was halted either when further sampling yielded no additional larvae or when the 3-wk sampling period had ended.

Concurrent with removal sampling, an additional 45 plots were randomly selected twice weekly, on average. These represented control plots in which removal

sampling had not affected the number of ticks collected. Numbers of ticks on these plots were influenced both by natural larval mortality and removal by hosts; previous studies have shown that active dispersal by larvae is limited and unlikely to significantly impact estimates (Daniels and Fish 1990). Thus, the impact of removal sampling could be determined with respect to the loss of ticks by natural means, and larval estimates could be adjusted as necessary.

Because larval abundance tends to decline rapidly after reaching peak (Daniels and Fish 1990, Fish 1993), and the cumulative effect of daily tick loss requires increasingly greater adjustments in tick numbers as the estimation period continues, larval estimates were based only on the first five sample days. This length of time provided sufficient data to perform the estimation calculations without the need for excessive adjustment as a result of high cumulative tick loss. Regression analyses to determine the rate of tick loss, however, were based on the entire sampling period to provide a statistically more robust view of the process. Estimates of larval population size were calculated for each removal site with a maximum likelihood technique (Zippin 1958, Southwood 1978, Skalski and Robson 1982) that allows a measure of the standard error.

Drag Sampling Efficiency. Once absolute population estimates were calculated as described above, overall drag sampling efficiency could be determined. Efficiency was defined as the proportion of the absolute population captured in a single drag sample. To calculate efficiency for nymphs and adults, daily tick counts obtained during the estimation studies were compared with the estimated absolute population density to determine the proportion of ticks collected. For larvae, removal sampling artificially decreased the sample population, resulting in a smaller pool of potential captures and underestimating efficiency. To avoid this bias, larval drag sampling efficiency was based solely on counts from control plots.

Data Analysis. Mark-release-recapture data were analyzed using Schnabel's (1938) modification of the Lincoln-Petersen index. Population size was estimated daily on the basis of numbers of marked and unmarked ticks as follows:

$$N = \frac{\sum M_i n_i}{(\sum m_i) + 1},$$

where N = population estimate, M_i = number of marked ticks in the population to day i , n_i = number of ticks caught on day i , and m_i = number of marked ticks caught on day i .

Once estimates asymptoted, indicating little change in population size with additional sampling, dragging was halted. Standard errors of the estimates were calculated as follows (Begon 1979).

$$SE = N \sqrt{\frac{1}{(\sum m_i + 1)} + \frac{2}{(\sum m_i + 1)^2} + \frac{6}{(\sum m_i + 1)^3}}$$

Population estimates were converted to tick densities (ticks per square meter) and a single density estimate

Table 1. Larval population estimates (\pm SE) for a study site in Westchester County, NY, 1990–1994

Year	Population estimate	SE	Density (#/m ²)
1990	980	210.0	6.9
1991	728	64.2	5.2
1992	1,825	183.3	12.9
1993	2,334	30.9	16.5
1994	2,264	72.7	16.0
Mean	1,626		11.5

Sample area totaled 141.3 m².

was derived by averaging data for the final 3 d of sampling.

The larval population was estimated by the following maximum likelihood estimator.

$$N = \frac{T}{(1 - q^k)},$$

where N = population estimate, T = total number removed, $q = 1 - p$, p = probability of capture, and k = sampling periods.

Further details are provided by Zippin (1958) and Southwood (1978). Standard errors were calculated as follows:

$$SE = \sqrt{\frac{N(N - T) T}{T^2 - N(N - T)[(kp)^2 / (1 - p)]}}.$$

Drag efficiency (i.e., the percentage of total estimated tick population collected per sample) was calculated for each sampling day. Mean efficiencies were determined for each stage in each year of the study and then were arcsine-transformed (e.g., Sokal and Rohlf 1969) and plotted against log-transformed density estimates to evaluate the relationship between density and efficiency.

Results

Population estimates for larval, nymphal, and adult *I. scapularis* were calculated for the years 1990–1994. Larval sampling was conducted in late August–early September, when larval activity was at its peak in our study area (e.g., Fish 1993). Total abundance at all removal plots combined ($N = 45$) varied from as few as 728 larvae in 1991 to as many as 2,334 larvae in 1993 (Table 1). Average estimated abundance was 1,626 (± 736.8 SD) larvae per year for the 141.3 m² total area sampled. Density estimates ranged from 5.2 to 16.5 larvae per square meter in 1991 and 1993, respectively, and averaged 11.5 ticks per square meter (± 5.20) for the 5-yr study period.

Regression analyses indicated that over the course of the larval estimation studies, daily tick loss on control plots, caused by both mortality and host pick-up, fit a linear model and averaged 4.0% for the 5-yr period. Thus, average daily tick loss, independent of removal sampling, was fairly constant from year to year, ranging between 3 and 5%. Only in 1993 was there significant decline in larval numbers on control

Table 2. Nymphal population estimates (\pm SE) for a study site in Westchester County, NY, 1990–1994

Year	Population estimate	SE	Density (#/m ²)
1990	1,476	87.6	1.3
1991	701	77.7	0.5
1992	3,255	374.3	2.3
1993	615	61.9	0.5
1994	2,332	170.5	1.7
Mean	1,676		1.3

Sample area totaled 1,400 m².

plots during the removal study ($R^2 = 0.93$; $F = 0.39$; $df = 1, 3$; $P = 0.008$). Consequently, the daily number of captures on removal plots was adjusted by 5% on sample day 2, up to 35% on sample day 5, to compensate for the loss of ticks outside of removal sampling.

Nymphal sampling was conducted in late June–early July, when nymphs were at their peak, and population estimates ranged from 615 to 3,255 nymphs on the 1,400-m² site. Density estimates for the 5-yr period ranged from 0.5 (1991 and 1993) to 2.3 (1992) nymphs per square meter; mean density was 1.22 (± 0.78) ticks per square meter (Table 2).

Mortality rates were measured each year for the entire sampling period and found to have a minimal effect on nymphal estimates. In fact, only the estimate for 1991 required adjustment for mortality, given an average daily decline of 4.1%. Once data had been reexamined in this instance, estimated nymphal density rose from 0.46 to 0.5 nymphs per square meter. Overall, mortality was linear and postpeak nymphal numbers declined by an average of 2.4%/d in this study.

Studies to estimate adult population size were initiated in mid- to late November and often extended into December. However, two constraints on adult estimates were the unpredictability of the weather, which often prevented drag sampling, and the relatively low adult population size. These resulted in too few recaptures to estimate population size in 1991 and 1993. Adult density averaged 0.33 ticks per square meter for the 3 yr in which adequate numbers of ticks were collected (Table 3). As with nymphs, daily tick mortality during the sampling periods was linear and had a minimal effect on population estimates, averaging 1.6%. Timing of the adult estimation sampling pe-

Table 3. Adult *I. scapularis* population estimates (\pm SE) for a study site in Westchester County, NY, 1990–1994

Year	Population estimate	SE	Density (#/m ²)
1990	592	181.0	0.3
1991 ^a	—	—	—
1992	563	544.7	0.4
1993 ^a	—	—	—
1994	535	351.6	0.3
Mean	563		0.33

Sample area totaled 2,000 m².

^a Insufficient recaptures to calculate population size.

Table 4. Annual drag efficiency (% \pm SD) for each tick stage

Year	Larvae	Nymphs	Adults
1990	3.7	7.9	1.9
1991	18.7	4.7	—
1992	5.0	3.3	2.4
1993	13.3	9.1	—
1994	2.1	8.3	6.4
Mean	8.6 (\pm 7.1)	6.7 (\pm 2.5)	3.6 (\pm 2.5)

riods each year coincided with periods of peak abundance, and no further adjustments were necessary.

Density estimates were used to measure the efficiency of our drag sampling method. For larvae, mean drag efficiency per year ranged from 2.1% (1994) to 18.7% (1991), and averaged 8.6% (\pm 7.1%) for the 5-yr study period (Table 4). Nymphal drag efficiency varied between 3.3% (1992) and 9.1% (1993) from year to year, and averaged 6.7% (\pm 2.5%) for the same 5-yr period (Table 4). For those years in which adult population estimates were calculated ($N = 3$), efficiency ranged from 1.9% (1990) to 6.4% (1994), and averaged only 3.6% (\pm 2.5%) (Table 4). Although mean drag efficiency declined with each successive life stage, differences between stages were not significant (tests of equality using arcsine-transformed percentages, $P > 0.05$; Sokal and Rohlf 1969).

Drag efficiency also was independent of tick density within a given life stage. Regression analysis indicated no significant relationship between efficiency (arcsine transformed) and tick density for larvae ($R^2 = 0.16$; $F = 0.56$; $df = 1, 3$; $P = 0.51$), nymphs ($R^2 = 0.12$; $F = 0.42$; $df = 1, 3$; $P = 0.56$), or adults ($R^2 = 0.11$; $F = 3.04$; $df = 1, 1$; $P = 0.18$).

Discussion

Accurate assessments of tick abundance are necessary to understand how *I. scapularis* population size varies in nature. Although it is clear that *I. scapularis* exhibits seasonal patterns of activity that are highly conserved from year to year, long-term population studies of *I. scapularis*, in which the magnitude of changes in abundance is determined annually, are lacking. The current study has demonstrated the utility of multiple mark-recapture methods to estimate nymphal and adult *I. scapularis* populations. Likewise, removal sampling was found to be an effective way of estimating larval *I. scapularis* abundance, given constraints on handling individual larvae. The assumptions underlying such estimation models were met consistently by the *I. scapularis* population in this study, allowing us to quantify tick density at a specific site and begin generating long-term life history data. Ultimately, such data will help to determine how *I. scapularis* populations are regulated in nature, thereby offering insight to questions about the dynamics of tick-borne diseases (Vail and Smith 1997).

Despite the predictive seasonal pattern, data from this study illustrate how variable population size can be from one year to the next. For example, larvae showed a threefold range in population size during

this study, whereas nymphs exhibited a fourfold range in size. Of the two stages, fluctuations in the size of nymphal *I. scapularis* populations are more important epidemiologically. Nymphs are responsible for the vast majority of the Lyme disease cases in the Northeast (Fish 1993, Falco et al. 1999). Consequently, natural fluctuations in the nymphal population should directly influence human risk of infection with *B. burgdorferi*, providing that the prevalence of *B. burgdorferi* in nymphs remains constant. In fact, long-term data from Westchester County, NY, indicate that prevalence rates are much less variable than nymphal abundance from year to year (e.g., Maupin et al. 1991, Daniels et al. 1993). Recent analyses have shown that reported Lyme disease cases in the Northeast correlate well with nymphal abundance in a given year (Stafford et al. 1998, Falco et al. 1999).

Compared with the immature stages, adults did not exhibit as wide a range in annual population size for the 3 yr in which adequate numbers of *I. scapularis* were collected. These data suggest that adult abundance is not only low, but that there may be constraints on the number of nymphs successfully feeding and molting to the adult stage, which are consistent from year to year. Given the high reproductive potential of a single *I. scapularis* female (Daniels et al. 1996), population levels can apparently be maintained with few adults successfully producing offspring.

Absolute density estimates have been obtained for other North American ixodid ticks as well. Koch (1987) estimated absolute densities of adult *Amblyomma americanum* (L.) at a site in Oklahoma by using mark-release-recapture with CO₂-baited traps. Values ranged from 0.13 to 0.41 ticks per square meter over a 3-yr period, which was similar to the maximum of 0.4 adult *I. scapularis* per square meter found in this study. Reported absolute densities for adult *D. variabilis* obtained by mark-release-recapture ranged from 0.01 to 0.16/m² at a Virginia site (Sonenshine 1972). Studies conducted on populations of *D. variabilis* at two sites in Nova Scotia, Canada, found much higher density estimates of 7.8 and 20.9 ticks per square meter, respectively (Garvie et al. 1978). Although immature *D. variabilis* are not easily collected by dragging, density estimates in Virginia have been obtained by releasing ¹⁴C-labeled ticks and later collecting marked and unmarked individuals from trapped hosts (Sonenshine 1972). Larval estimates in that study ranged from 3.8 to 11.1 ticks per square meter, which is comparable to those we obtained for larval *I. scapularis*.

The use of survival cages indicated that mortality was constant and linear during the estimation periods. The mortality pattern we observed differed from that reported by Vail and Smith (1997) for *I. scapularis* at a site in New Jersey. They noted that mortality in cages was not constant, but rather was characterized by a sigmoid curve that is commonly seen in insects living on stored reserves. However, the relatively short time over which mortality was monitored in our study, as opposed to the longer period examined by Vail and Smith (1997), may explain the difference; mortality over the short term may be linear, with an increase in

the death rate arising late in the season as stored reserves are exhausted. Because our goal was to meet the assumptions of mark-recapture models that are based on a closed population, the shorter period reduced the risk of violating those assumptions (Wileyto 1994). By comparing population estimates with and without mortality adjustments, we determined that mortality during the course of each estimation period was negligible in the case of adults and nymphs, and therefore model assumptions were not violated. It should be noted that survival cages effectively excluded potential large predators of ticks. Although the significance of this is not currently known, a number of potential invertebrate predators exist in nature, including carabid beetles and spiders (T.J.D., unpublished data). Further work is needed on the role predators have in regulating tick populations naturally.

The expansion of *I. scapularis* populations in the northeastern United States (Schulze et al. 1986, Lastavica et al. 1989, White et al. 1991, Falco et al. 1995) is probably related to changes in land use practices over the last century resulting in reforestation of formerly agricultural land and the subsequent increase in white-tailed deer populations (Spielman et al. 1985, Barbour and Fish 1993). Such changes have provided ample hosts for the adult stage of *I. scapularis* to successfully reproduce (Spielman et al. 1985). However, reasons for the patterns of tick density we have documented from one year to the next at this site are unknown. Previous studies have noted that *I. scapularis* populations may be focal (Schulze et al. 1986, Daniels and Fish 1990, Daniels et al. 1993), suggesting that local environmental conditions over relatively small areas have a role in shaping the distribution of this species. For instance, McEnroe (1985) recorded an exceedingly high density of adult *D. variabilis* along roadside drag courses, indicating the impact that landscape features may play in the distribution of ticks.

Efforts to relate *I. scapularis*' abundance to abiotic (e.g., weather) and biotic (e.g., host density) factors have not been successful to date (Daniels et al. 1996, Vail and Smith 1997). A further consideration is that the disjunct nature of *I. scapularis*' distribution, and therefore abundance, suggest that the applicability of population estimates from one site to another may be limited in terms of absolute density, though not necessarily with respect to the direction of change. Our attempt to address this issue by calculating drag efficiencies for each stage indicates that site-specific estimates may be necessary wherever the goal is to determine the magnitude of population change and interstadial mortality rates. Although it is clear that drag sampling efficiency tends to be low regardless of tick species (e.g., Zimmerman and Garris 1985, Levin 1988), factors such as substrate and weather will further affect efficiency (Milne 1943). The current study reflects drag sampling efficiency in a fairly homogeneous, 60-yr-old oak-dominated eastern deciduous forest with relatively little understory (Fish and Dowler 1989). Additional determinations of absolute population density and drag sample efficiency need to

be made in other locales before the utility of drag efficiency estimates can be determined reliably.

Despite this drawback, absolute density estimates for different life stages of the same population provide the foundation for construction of a life table. Long-term data may then be used to quantify mortality patterns over time and, more important, identify those periods showing unusually high or low mortality rates. Analysis of these patterns with respect to potential sources of mortality may then clarify factors having a significant impact on *I. scapularis* populations.

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