Exp Appl Acarol (2010) 52:427–438
DOI 10.1007/s10493-010-9373-9

A quantitative comparison of two sample methods for collecting *Amblyomma americanum* and *Dermacentor variabilis* (Acari: Ixodidae) in Missouri

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Received: 2 February 2010 / Accepted: 10 June 2010 / Published online: 29 June 2010

Abstract In studies of tick communities, sampling methodology may influence observed patterns. The objective of this study was to compare two sampling methods, dragging and dry ice baiting, in two habitats to assess abundance of off-host ticks. Tick communities were monitored from March to December in a forested and an old-field habitat in northeast Missouri. In each habitat, eight drag and eight dry ice bait samples were collected every 2 weeks on a permanent grid. The most common ticks collected were all life stages of *Amblyomma americanum* L. and adult and larval *Dermacentor variabilis* Say. Capture data was analyzed to determine if there were differences due to sampling method, habitat or an interaction for each life stage of each species across the entire monitoring period. Data indicate that there were differences in the methods. Significantly more *A. americanum* nymphs were captured by bait sampling. Dragging captured significantly more larval *A. americanum*. Significantly more larval and nymphal *A. americanum* and larval *D. variabilis* were caught in the forest, whereas significantly more adult *D. variabilis* were collected in the field. Significant interaction between site and method was found for *A. americanum* adults and *D. variabilis* larvae. These differences are likely due to differences in behavior among species and developmental age that interact with microclimate. These data indicate that community monitoring studies should use multiple sampling methodologies to avoid bias. While comparing these methods, the first documented collection of off-host *Ixodes scapularis* Say in Adair County, Missouri was made.

Keywords *Amblyomma americanum* · *Dermacentor variabilis* · Off-host sampling · Dry ice baiting · Dragging

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The collection and quantification of ticks are important for applied and basic ecological studies. As most tick species spend the majority of their lifecycles off-host while digesting, molting, and seeking another host (Oliver 1989), sampling these species off-host is essential to our understanding of population dynamics. On-host abundance is not always correlated with off-host abundance (e.g., Falco and Fish 1989). In addition, on-host sampling may introduce a bias, in that a tick species may be present in the habitat but not found on the host(s) selected by the investigator.

The two most common off-host sampling methods are dragging fabric through vegetation (called flagging or dragging) and dry ice baited traps. These methods have been specifically compared in a small number of studies with differing conclusions among species and among life stages. Dry ice bait traps were more effective for adult *Dermacentor andersoni* Stiles (Garcia 1965), larval *Ixodes dammini* (now *I. scapularis* Say; Falco and Fish 1992), adult and nymphal *Amblyomma triguttatum* Koch (Guglielmone et al. 1985) while drag sampling captured more *I. dammini* nymphs (Falco and Fish 1992). Results for sampling *I. dammini* are less clear: dry ice baits were reported to be more effective for the larval stage and drag sampling was more effective for nymphs (Falco and Fish 1992) while Solberg et al. (1992) reported that dry ice baits were effective for all life stages. Similar disparities are reported in studies of *Amblyomma americanum* L. (Solberg et al. 1992; Kinzer et al. 1990; Schulze et al. 1997).

Sampling method bias may have contributed to this array of results. Vegetation type may impact the ability of flagging to access ground dwelling life stages (Garcia 1965; Ginsberg and Ewing 1989). Although dry ice bait traps can be placed in areas difficult to sample with flagging, the response to dry ice varies among species (Holscher et al. 1980; Ginsberg and Ewing 1989), age and sex (Holscher et al. 1980), and in different environmental conditions (Wilson et al. 1972; Holscher et al. 1980; Koch and McNew 1982; Guglielmone et al. 1985; Barré et al. 1997).

The objective of this study was to compare drag and dry ice bait sampling to capture all life stages of *Amblyomma americanum* (lone star tick) and *Dermacentor variabilis* Say (American dog tick) over the entire 8 month monitoring study of the off-host communities in two different habitats. At the onset of this monitoring study, we knew that these two species are common in Adair County, Missouri but did not know their relative abundance, the seasonal pattern of abundance for each life stage, or what other tick species we might collect. Findings of previous studies comparing these sampling methods do not clearly indicate that one method will sample all life stages of *A. americanum* in different habits (Kinzer et al. 1990; Solberg et al. 1992; Schulze et al. 1997). The effectiveness of these methods is even less clear for the different life stages of *D. variabilis*, though Ginsberg and Ewing (1989) mentioned that flagging collected adult *D. variabilis*. Dry ice may not stimulate movement of larvae or nymphs of *D. variabilis* (Semtner and Hair 1975). As both species exhibit questing and hunting host-seeking behaviors (Waladde and Rice 1982), both sampling methods may be required to effectively census the population patterns in long term monitoring studies.

Materials and methods

Study area

This study used data from a 1 year long tick monitoring study conducted on two sites at the Truman State University Farm, Kirksville, Adair County, Missouri (40° 10′ 31″ N, 92° 36′

10″ W). One site is an old-field dominated by non-native grasses and bordered by secondary forest. The other site, approximately 350 m to the southeast of the field site, is in the northeast corner of an oak-dominated secondary forest fragment approximately 35 hectares in size. Bordering the forest site to the east is a regularly hayed field and to the north, a large compost pile and cattle pasture. This study was conducted in conjunction with a small mammal trapping study (not reported here). Both studies were conducted on a rectangular grid (120 × 70 m) established in a north–south orientation in each habitat. Both grids were subdivided into 100 m^2 square areas forming north–south and east–west transects.

Sampling methods

Environmental variables, such as humidity and temperature, affect tick behavior, but the effects are unlikely to affect all species and life stages in exactly the same manner. As we were not targeting a specific species or life stage, we choose to maintain a standard protocol throughout the year. Each grid was sampled simultaneously approximately every other week beginning 22 March 2007 and ending with snow and ice cover after 29 November 2007. We did not sample in the rain and adjusted the sampling day accordingly (up to +4 and −3 days). Sampling began each day between 1130 h and 1530 h (mean collection time 1338 h); the variation in start time was affected mainly by precipitation patterns on the sampling day. Each sampling date included eight regularly spaced 30 m north–south drag samples and eight regularly spaced dry ice baited traps in each grid (Fig. 1). Permanent sampling locations were selected to reduce microhabitat variation as a sampling bias and have been shown to give similar numbers of ticks as naïve sampling sites (Koch and McNew 1981).

Drag sampling procedures were modified from those described by Zimmerman et al. (1987). Flannel cloths measuring 1 × 1 m were pinned to a 1.2 m long, 2.5 cm diameter wooden dowel on one side. The dowel was then tied at each end to approximately 1.5 m of twine. To ease movement through the vegetation, the cloth was cut into 10 equal width strips 0.8 m in length and perpendicular to the wooden dowel. The dowel and fabric were dragged as close to the ground as the vegetation would allow.

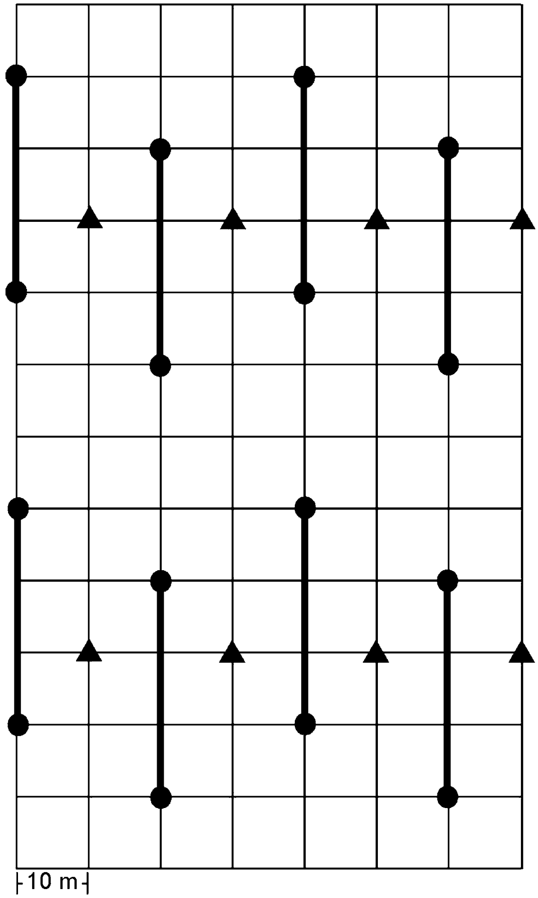
Dry ice bait sampling procedures were modified from Barré et al. (1997) and Koch and McNew (1981). Approximately 200 g of dry ice was placed in the middle of a 1 × 1 m flannel cloth laid on the ground and left to sublime for 1 h. The 1 h time interval for trapping has been used in other studies (Garcia 1962; Koch and McNew 1981).

Cloths from bait and drag samples were sealed in individual plastic bags and transported to the lab. Bags were generally placed at −60°C for a minimum of 24 h to kill the ticks before removing from cloths. Ticks were recovered from each cloth using hand lens and tweezers and preserved in 95% ethanol. Preserved specimens were identified and counted to species and life stage.

Statistical analysis

All sampling points were assumed to be independent in each trapping session and among trapping sessions. This assumption ignores potential geographic and temporal dependence. The distribution of ticks caught was not normal and did not have equal variance, mainly due to a large number of ticks captured on some dates that may be attributed to seasonal patterns of activity and possible patchy distribution within habitats. A nonparametric rank analysis (an approximation of Kruskal–Wallis test; Conover and Iman 1981) was selected

Fig. 1 Trapping grid layout with drag locations (*barbells*) and CO_2 trap locations (*triangles*). Each square is 10 × 10 m



to accommodate these violations of assumptions of the traditional analysis of variance. Two-factor analysis of variance was conducted on the ranked data. Tukey's HSD post hoc comparisons followed to further differentiate mean ranks ($\alpha = 0.05$). The SPSS 16.0 statistical package was used for all analyses (SPSS Inc. 2007).

Results

A total of 10,965 ticks were collected (Table 1), comprising all life stages of both *A. americanum* (420 adults, 1,503 nymphs, and 8,550 larvae) and *D. variabilis* (81 adults, 6 nymphs, and 405 larvae). In addition, we captured the first off-host specimens of *I. scapularis* to be documented in Adair County, Missouri. Two specimens were captured in the forest; an adult by a bait station in October 2007 and a nymph by dragging in May 2007. This species has previously been collected from a white-tailed deer (*Odocoileus virginianus* Zimmerman) taken from Adair County, Missouri (Y. Rechav, personal communication).

For the two more common species, *A. americanum* and *D. variabilis*, a discrepancy in number of captures between species and life stages is apparent, therefore the capture ability

Table 1 Summary of collection location and method of *Amblyomma americanum* and *Dermacentor variabilis*

Sample site	Method	Number of larvae		Number of nymphs		Number of adults	
		A. americanum	*D. variabilis*	*A. americanum*	*D. variabilis*	*A. americanum*	*D. variabilis*
Forest	Bait	3,923	29	910	1	308	10
	Drag	4,037	326	356	3	43	4
Field	Bait	193	44	129	1	52	40
	Drag	397	6	108	1	17	27
	Total	8,550	405	1,503	6	420	81

of the two sampling methods will be considered separately for each. Differences in number of captures of a life stage of a species between sampling sites and methods across the year show a generally consistent pattern, with one site or method or a combination of these yielding more ticks throughout the whole year (these patterns are displayed for *A. americanum* in Figs. 2a–f). This is important given the scope of this monitoring study (testing for differences across 1 year, rather than at individual sampling dates) and allows statistical differences between sites and methods to be interpreted to be consistent throughout the study period rather than artifacts from one unusual sampling date.

Capture numbers for each rank analysis test were ranked across the entire year to account for high peaks in capture numbers. The sample size for each test was $n = 608$, the total number of bait and drag samples collected in both the forest and field across the entire sampling period (8 cloths $\times$ 2 methods $\times$ 2 sites $\times$ 19 sampling dates). Summary results of all rank analysis tests are displayed in Tables 2a, b.

Adult *A. americanum* exhibited an interaction ($F = 6.907$; $df = 1, 602$; $P = 0.009$) between the site (forest or field) and the sampling method (bait or drag; Fig. 2g). Because of this, examining differences between sites or sampling methods individually is not valid, as the two variables are not independently affecting the number of ticks captured. For analysis of interacting variables, the four possible variable combinations (Forest/Bait, Forest/Drag, Field/Bait, and Field/Drag) are compared. Significantly more adult *A. americanum* adults were collected by CO_2 baiting in the forest than by any other combination (Tukey's HSD Forest/Drag, Field/Bait, and Field/Drag $P < 0.001$). Comparison of other combinations of trap method and grid yielded no significant differences (Tukey's HSD $P = 0.286$). Nymphal *A. americanum* did not have an interaction between the site and method variables ($F = 1.650$; $df = 1, 602$; $P = 0.199$); nymphs were significantly more likely to be caught in the forest site ($F = 22.434$; $df = 1, 602$; $P < 0.001$) regardless of method and were captured more often by bait cloths ($F = 9.284$; $df = 1, 602$; $P = 0.002$) regardless of which site was used. Larval *A. americanum* exhibited no interaction ($F = 2.522$; $df = 1, 602$; $P = 0.113$) and, like nymphs, were captured significantly more often in the forest ($F = 23.935$; $df = 1, 602$; $P < 0.001$). However, larvae were found more often on drag cloths than bait cloths ($F = 10.079$; $df = 1, 602$; $P = 0.002$).

No interaction between site and sampling method variables was observed in *D. variabilis* adults ($F = 0.027$; $df = 1, 602$; $P = 0.869$). There was a significant difference in captures between sites ($F = 18.175$; $df = 1, 602$; $P < 0.001$), though no significant difference was observed between sampling methods ($F = 1.807$; $df = 1, 602$; $P = 0.179$). No statistical analysis was conducted on *D. variabilis* nymphs due to the small number captured (six individuals). Larval *D. variabilis* exhibited an interaction between site and sampling method ($F = 8.947$; $df = 1, 602$; $P = 0.003$). When the four variable combinations were compared, drag cloths from the forest were significantly different from all other variable combinations (Tukey's HSD Forest/Bait $P = 0.023$, Field/Bait $P = 0.004$, Field/Drag $P < 0.001$). Other comparisons between variable combinations for *D. variabilis* larvae yielded no significant differences (Tukey's HSD $P = 0.215$).

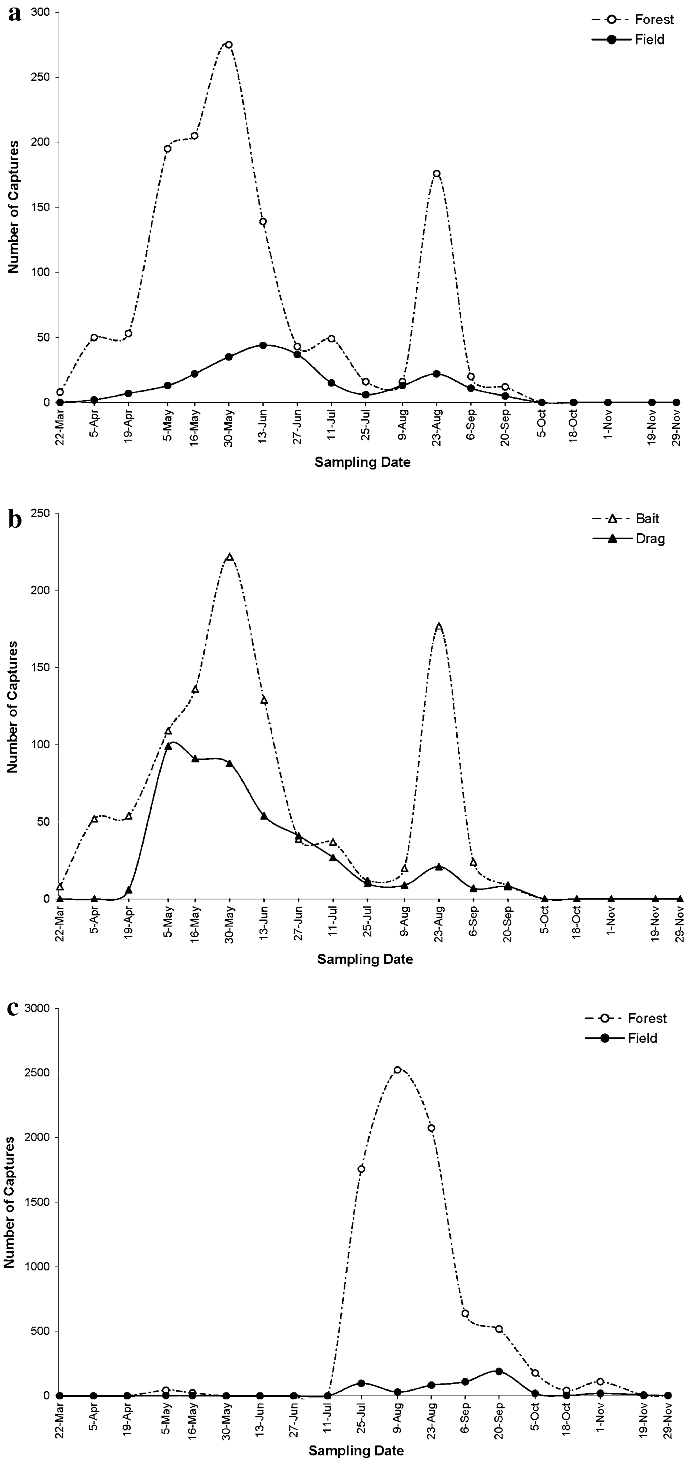
Seasonal activity patterns were strikingly similar to those reported from Mississippi by Jackson et al. (1996). Although individual sampling session data were not statistically analyzed, a spring and summer peak in abundance were observed for *A. americanum* nymphs (Fig. 2a) and adults (Fig. 2g) were observed and only a summer peak for larvae (Fig. 2c). The timing of the peaks in number of captures was similar in the forest and field for all life stages. However, drag sampling captured larvae earlier in the season and in greater numbers in more trapping sessions throughout the study (Fig. 2d). The percentage of cloths with larvae ranged from 0 to 100% (Figs. 2e and 2f) and was generally greater throughout the monitoring study with drag sampling (Fig. 2f). The percent of cloths with larvae was greater in most trapping sessions in the forest (Fig. 2e). As the monitoring progressed into the summer abundance peak there was increase in the percent of cloths with larvae. This increase began earlier in the forest than in the field.

Discussion

This study indicates that drag and dry ice bait sampling are not equivalent sampling methods for monitoring tick population and community dynamics. Sampling method was a factor in the capture number for larval and nymphal *A. americanum*; more larvae were captured with dragging and more nymphs were captured with dry ice bait sampling. Site was a factor in the capture number for larval and nymphal *A. americanum* (collected more in the forested site) and adults of *D. variabilis* (collected more in the field site). For adults of *A. americanum* and larval *D. variabilis* there was an interaction between site and forest. These findings are consistent with the predictions of previous studies that compared these methods for target species (Garcia 1965; Guglielmone et al. 1985; Falco and Fish 1992; Schulze et al. 1997). Our results for *A. americanum* are similar to those of Schulze et al. (1997) but differ from Solberg et al. (1992). Variation observed in these methods is likely due to tick behavior and habitat and the interaction of these factors.

Variation in tick behavior is one sampling bias. Host seeking behavior is different among species. All life stages of *A. americanum* are known to hunt hosts by following CO_2 emission gradients (Wilson et al. 1972; Schulze et al. 1997) while *D. variabilis* is an ambush specialist (Sonenshine 1993). These different host-seeking strategies are likely to affect sampling. Studies of response to CO_2 emissions have found differences in mobility among species (Ginsberg and Ewing 1989) and are likely different among life stages within a species as suggested by Koch and McNew (1982). In addition, the response time within a species can vary between sexes and developmental age (Holscher et al. 1980). Our data suggest that dry ice sampling is a more effective sampling tool for *A. americanum* than for *D. variabilis*. Dragging may be more effective for larval stages of both species due

Fig. 2 Seasonal capture graphs for each stage of *Amblyomma americanum*. Nymphal captures are ▶ expressed as number of captures versus sampling date by site (**a**) and by sampling method (**b**). Larval captures are expressed as number of captures versus sampling date by site (**c**) and by sampling method (**d**). Additionally, the percentage of cloths that captured larvae by site (**e**) and sampling method (**f**) are represented. Adult captures are expressed for bait samples in the forest and the mean between the other three method-site combinations (**g**)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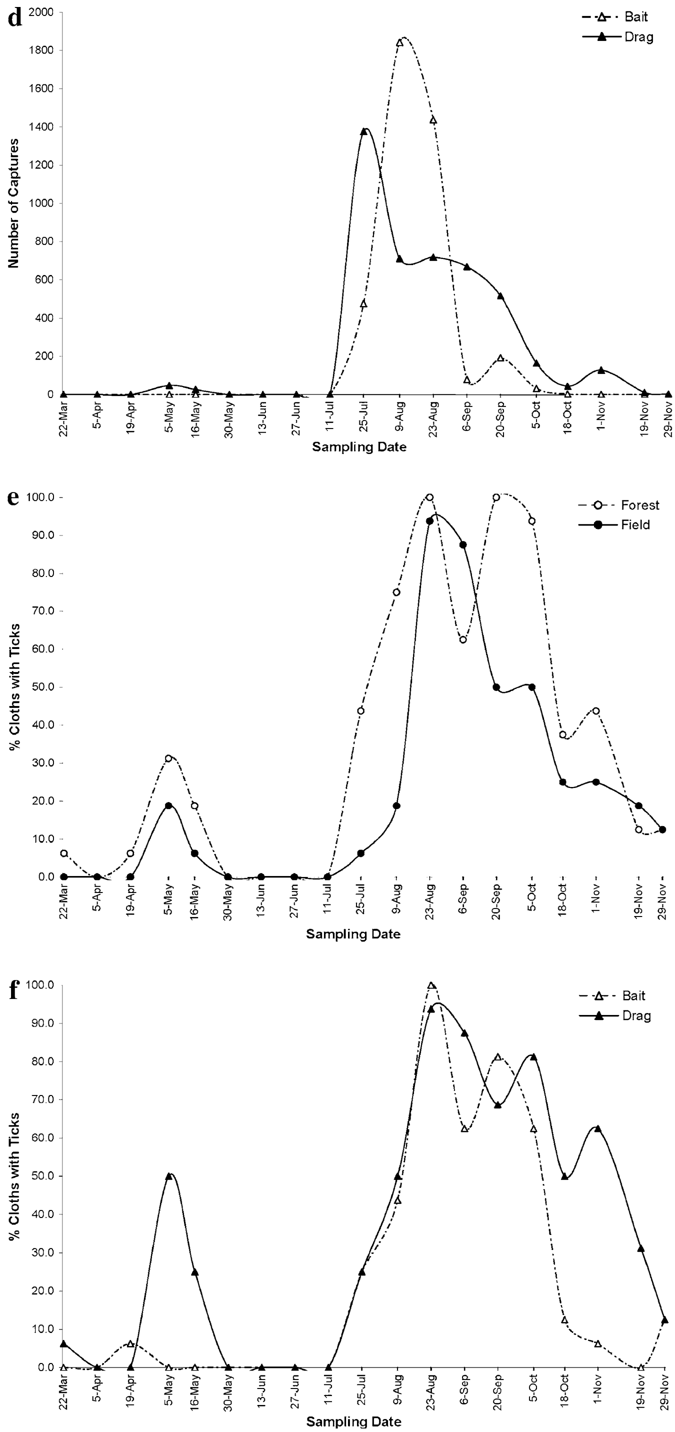

Fig. 2 continued

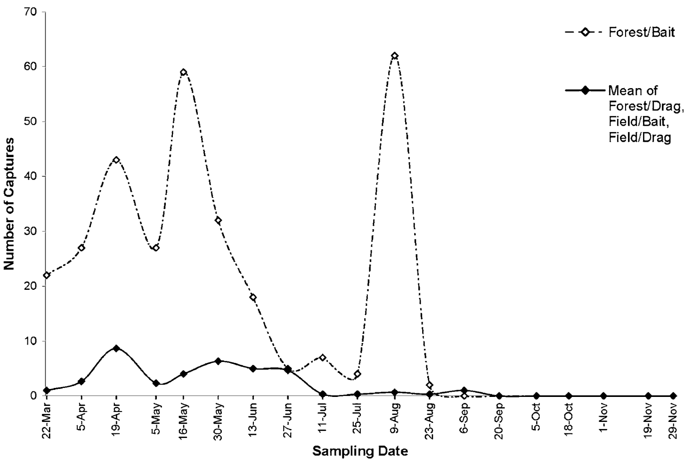

Fig. 2 continued

Table 2 (A) Most likely site and method to capture ticks, by life stage as determined by rank analysis. (B) Homogenous subjects (Tukey's HSD) of variable combinations in ascending order by number of individuals captured. Unbroken line denotes homogenous subject (no significant difference, NSD, between variable combinations)

	Amblyomma americanum			*Dermacentor variabilis*		
	Adults	Nymphs	Larvae	Adults	Nymphs	Larvae
(A)						
Interaction of variables	Yes ($P = 0.009$)	No ($P = 0.199$)	No ($P = 0.113$)	No ($P = 0.869$)	No statistical tests performed (see text)	Yes ($P = 0.003$)
Most captures						
Site	Interaction, see Table 2b	Forest ($P < 0.001$)	Forest ($P < 0.001$)	Field ($P < 0.001$)		Interaction, see Table 2b
Method		Bait ($P = 0.002$)	Drag ($P = 0.002$)	NSD ($P = 0.179$)		
(B)						
Amblyomma americanum	Adults	Field/drag	Field/bait	Forest/drag	Forest/bait	
			NSD $P = 0.286$			
Dermacentor variabilis	Larvae	Field/drag	Field/bait	Forest/bait	Forest/drag	
			NSD $P = 0.215$			

to slow response time, reduced mobility, and patchy spatial distribution that arises from aggregation around the egg mass. The earlier peak in the number of captures observed in drag sampling in *A. americanum* larvae may be due to developmental age, microclimate differences, or limited dispersal away from egg mass.

Tick behavior is likely to vary in response to daily climatic conditions. Environmental conditions at the time of sampling influence tick behavior. Meteorological variables such as temperature, vapor pressure deficit and solar radiation effect tick diel activity (Harlan and Foster 1990; Lane et al. 1995; Randolph and Storey 1999; Alekseev and Dubinina 2000; Schulze and Jordan 2003; Schulze et al. 2001), and may be controlled partly by surrounding vegetation type (Semtner and Hair 1973). In studies examining the effect of sampling methodology, temperature (Wilson et al. 1972; Guglielmone et al. 1985), humidity (Holscher et al. 1980), time of year (Barré et al. 1997), and wind direction (Guglielmone et al. 1985; Barré et al. 1997) have been reported as variables influencing sample size. The differences observed in peaks in percent of cloths with ticks observed in the field and the forest may be due to environmental differences in the two sites. Environmental differences not only influence the activity of the ticks but also influence sublimation rates of the dry ice (Koch and McNew 1982). In simultaneous sampling in two different habitats, microclimatic conditions such as temperature, humidity and wind speed, may be different. These environmental differences, as well as differences in habitat use by host species, could contribute to differences in the number of ticks sampled in the field and the forest.

Habitat vegetation may also represent a sampling bias. Some vegetation types may be difficult to drag sample. Ginsberg and Ewing (1989) argued that ground dwellers were not equally sampled in all habitats by dragging due to differences in vegetative cover. The effect of this bias may vary among species and life stage as questing height can vary. For example, larval *D. variabilis* quests lower than nymphs and adults, as their preferred hosts are smaller (Sonenshine 1993). In our study, drag cloths did not have continuous contact with the ground in both habitats and contact with the ground throughout the year was probably greater in the forest than the field due to the standing tall grass cover. In addition to sampling issues, vegetation can alter local microclimate and could be a factor in spatial variation in host occupancy and tick behavior.

Sampling biases are an important issue in study design as method choice impacts the data (Solberg et al. 1992; Schulze et al. 1997). Although the response to various sampling methods has been studied for a few species and used as a population density estimator is available for *I. scapularis* (Daniels et al. 2000), an understanding of how methodology affects abundance estimates is unknown for most species. Laboratory studies of adult *D. variabilis* indicate that the response time to CO_2 varies with age and sex (Holscher et al. 1980). Studies with other *Dermacentor* species indicate adults and/or nymphs can be attracted by dry ice baits (Garcia 1962; Garcia 1965; Semtner and Hair 1975). Further study of the response of larvae and nymphs of *D. variabilis* to dry ice are needed.

Different sampling methods provide species and life-stage specific biases that need to be accounted for in order to accurately represent tick community composition and dynamics. Given the variation in capture success in this and similar studies, a single "standard" sampling method in monitoring studies may not be adequate given the numerous uncontrolled variation present in natural tick populations. In addition to these off-host tick sampling methods, less conventional means such as on-host sampling might be important for understanding tick demography and community dynamics.

Acknowledgments We would like to acknowledge the extensive collection and identification efforts made by Brian Hilliard, Jamie Spencer, Kurt Munzer, and Cara Willoughby. Additionally, we are grateful for the contributions made by those assisting with tick collection, identification, and data management: Enato Esangbedo, Neal Haley, Emily Twining-Gerdes, Rauleen Caballas, Laura Naegele, Ben Hale, and Brian Ruiz. Yigal Rechav and Glen Needham provided manuscript assistance. This research was supported by Truman State University, the Mathematical Biology Program, the Science, Technology, Engineering &

Mathematics Talent Expansion Program (STEP), and by the National Science Foundation under grants DUE-0431664 and DUE-0436348.

References

Alekseev AN, Dubinina HV (2000) Abiotic parameters and diel and seasonal activity of *Borrelia*-infected and uninfected *Ixodes persulcatus* (Acarina: Ixodidae). J Med Entomol 37:9–15

Barré N, Garris GI, Lovrvelec O (1997) Field sampling of the tick *Amblyomma variegatum* (Acari: Ixodidae) on pastures in Guadeloupe; attraction of CO_2 and/or tick pheromones and conditions of use. Exp & Appl Acarol 21:95–108

Conover WJ, Iman RL (1981) Rank transformations as a bridge between parametric and nonparametric statistics. Am Statistician 35:124–133

Daniels TJ, Falco RC, Fish D (2000) Estimating population size and drag sampling efficiency for the blacklegged tick (Acari: Ixodidae). J Med Entomol 37:357–363

Falco RC, Fish D (1989) The use of carbon dioxide-baited tick traps for sampling *Ixodes dammini* (Acari: Ixodidae). Acarologia 30:29–33

Falco RC, Fish D (1992) A comparison of methods for sampling the deer tick, *Ixodes dammini,* in a Lyme disease endemic area. Exp Appl Acarol 14:165–173

Garcia R (1962) Carbon dioxide as an attractant for certain ticks (Acarina: Argasidae and Ixodidae). Ann Entomol Soc Am 55:605–606

Garcia R (1965) Collection of *Dermacentor andersoni* (Stiles) with carbon dioxide and its application in studies of Colorado tick fever virus. Am J Trop Med Hyg 14:1090–1093

Ginsberg HS, Ewing CP (1989) Comparison of flagging, walking, trapping, and collecting from hosts as sampling methods for northern deer ticks, *Ixodes dammini*, and lone-star ticks, *Amblyomma americanum* (Acari: Ixodidae). Exp Appl Acarol 7:313–322

Guglielmone AA, Moorhouse DE, Wolf G (1985) Attraction to carbon dioxide of unfed stages of *Amblyomma triguttatum triguttatum* Koch, under field conditions. Acarologia 26:123–129

Harlan HJ, Foster WA (1990) Micrometeorologic factors affecting field host-seeking activity of adult *Dermacentor variabilis* (Acari: Ixodidae). J Med Entomol 27:471–479

Holscher KH, Gearhart HL, Barker RW (1980) Electrophysiological responses of three tick species to carbon dioxide in the laboratory and field. Ann Entomol Soc Am 73:288–292

SPSS Inc (2007) SPSS 16.0 base user's guide. Prentice Hall, Upper Saddle River

Jackson LK, Gaydon DM, Goddard J (1996) Seasonal activity and relative abundance of *Amblyomma americanum* in Mississippi. J Med Entomol 33:128–131

Kinzer DR, Presley SM, Hair JA (1990) Comparative efficiency of flagging and carbon dioxide-baited sticky traps for collecting the lone star tick, *Amblyomma americanum* (Acarina: Ixodidae). J Med Entomol 27:750–755

Koch HG, McNew RW (1981) Comparative catches of field populations of lone star ticks by CO_2-emitting dry-ice, dry-chemical, and animal-baited devices. Ann Entomol Soc Am 74:498–500

Koch HG, McNew RW (1982) Sampling of lone star ticks (Acari: Ixodidae): dry ice quantity and capture success. Ann Entomol Soc Am 75:579–582

Lane RS, Kleinjan JE, Schoeler GB (1995) Diel activity of nymphal *Dermacentor occidentalis* and *Ixodes pacificus* (Acari: Ixodidae) in relation to meteorological factors and host activity periods. J Med Entomol 32:290–299

Oliver JH (1989) The biology and systematics of ticks (Acari: Ixodida). Ann Rev Ecol Syst 20:397–430

Randolph SE, Storey K (1999) Impact of microclimate on immature tick-rodent host interactions (Acari: Ixodidae): implications for parasite transmission. J Med Entomol 36:741–748

Schulze TL, Jordan RA (2003) Meteorologically mediated diurnal questing of *Ixodes scapularis* and *Amblyomma americanum* (Acari: Ixodidae) nymphs. J Med Entomol 40:395–402

Schulze TL, Jordan RA, Hung RW (1997) Biases associated with several sampling methods used to estimate abundance of *Ixodes scapularis* and *Amblyomma americanum* (Acari: Ixodidae). J Med Entomol 34:615–623

Schulze TL, Jordan RA, Hung RW (2001) Effects of selected meteorological factors on diurnal questing of *Ixodes scapularis* and *Amblyomma americanum* (Acari: Ixodidae). J Med Entomol 38:318–324

Semtner PJ, Hair JA (1973) The ecology and behavior of the lone star tick (Acarina: Ixodidae): IV. The daily and seasonal activity patterns of adults in different habitat types. J Med Entomol 10:337–344

Semtner PJ, Hair JA (1975) Evaluation of CO_2-baited traps for survey of *Amblyomma maculatum* Koch and *Dermacentor variabilis* Say (Acarina: Ixodidae). J Med Entomol 12:137–138

Solberg VB, Neidhardt K, Sardelis MR, Hildebrandt C, Hoffmann FJ, Boobar LR (1992) Quantitative evaluation of sampling methods for *Ixodes dammini* and *Amblyomma americanum* (Acari: Ixodidae). J Med Entomol 29:451–456

Sonenshine DE (1993) Biology of ticks, vol 1. Oxford University Press, Oxford

Waladde SM, Rice MJ (1982) The sensory basis of tick feeding behavior. In: Obenchain FD, Galun G (eds) Physiology of ticks. Pergamon, New York, pp 71–118

Wilson JG, Kinzer DR, Sauer JR, Hair JA (1972) Chemo-attraction in the lone star tick (Acarina: Ixodidae): 1. Response of different developmental stages to carbon dioxide administered via traps. J Med Entomol 9:245–252

Zimmerman RH, McWherter GR, Bloemer SR (1987) Role of small mammals in population dynamics and dissemination of *Amblyomma americanum* and *Dermacentor variabilis* (Acari: Ixodidae) at land between the lakes, Tennessee. J Med Entomol 24:370–375